CLADISTIC ANALYSIS OF THE PLESIOSAURIA (REPTILIA: SAUROPTERYGIA)

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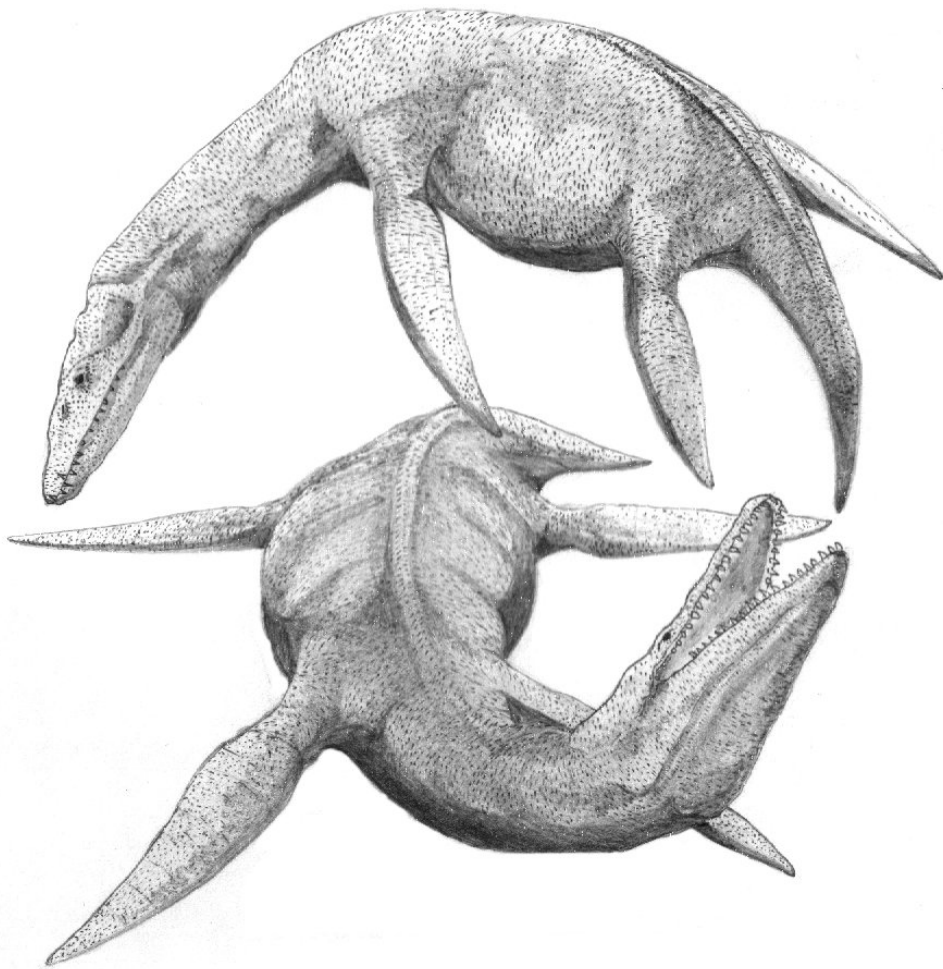
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Frontispiece. Two mutually curious pliosauroids in the early Jurassic ocean.
Original artwork by A. S. Smith.

Contents

List of Figures

List of tables

ABSTRACT. An extensive cladistic analysis comprising 41 plesiosaur taxa and 171 characters is performed and a phylogenetic hypothesis is presented. Definitions and diagnoses of all plesiosaur clades are revised and numerous controversial issues are addressed and resolved. Of significance are the identification of Plesiosauridae and Cryptoclididae as paraphyletic assemblages, the confident allocation of *'Stretosaurus' macromerus* to the genus *Liopleurodon*, and the confirmation of the systematic position of many previously controversial taxa. *Kaiwhekea* is transferred from Cryptoclididae and united with the confirmed cimoliasaurid *Aristonectes* (=*Morturneria*) within the Cimoliasauridae, the significance of which receives special attention. Elasmosauridae is recognised as a long ranging but rather plesiomorphic group, in terms of their divergence at a basal position in the plesiosauroid phylogenetic tree and in their subsequent acquisition of only a few synapomorphies. The taxon *Eretmosaurus* is recognised as problematic and prompts an assessment of the relative importance of cranial versus postcranial characters in plesiosaur systematics. Statistical, and stratophenetic approaches are employed to engage important temporal aspects, typically overlooked by cladistic methods and to investigate other possible tree topologies. A convincing fit is illustrated between plesiosaur stratigraphy and phylogeny. A unique method of combining phylogenetic hypotheses and stratigraphy is developed which overcomes the problem of losing character change information and allows the calculation of relative rates of character change among various clades.

1.1 Introduction

Plesiosaurs are a secondarily aquatic group of carnivorous reptiles belonging to the clade Sauropterygia within the diapsid clade Euryapsida (Tayor, 1989; Caldwell, 1997). Contrary to the implications of popular accounts (e.g. Lambert *et al*. 2001; Smith, 2003a), plesiosaurs were not an exclusively marine group and remains are known from abundant freshwater and lagoonal deposits (Wiffen and Moisley, 1986; Cruickshank, 1997; Sato, 2002). Ambiguous plesiosaur material occurs in Middle Triassic deposits (Benton, 1993) but the first diagnostic plesiosaurs are uppermost Triassic in age (Taylor and Cruickshank, 1993b; Storrs, 1994, 1997). The lineage reached a cosmopolitan distribution by the Early Jurassic, a maximum diversity in the Late Jurassic (Sullivan, 1987) and persisted successfully to the Uppermost Cretaceous. Plesiosaur vertebrae of putative Palaeocene age were wrongly dated (Lucas and Reynolds, 1993).

With respect to basal sauropterygians plesiosaurs are derived, in the acquisition of four hydrofoil-shaped flippers, a shortened trunk, and large plate-like limb girdles (Sues, 1987). These are all adaptations reflecting a shift from an axial to a paraxial lift-based locomotory repertoire (Robinson, 1975; Storrs, 1993). Within the lineage, pliosauromorph forms with large heads and short necks were more rapid and manoeuvrable swimmers than plesiosauromorph forms with long necks and small heads (Robinson, 1975; Massare, 1988; O'Keefe, 2001b). Despite these general morphotypes, the gross morphology of the postcrania is widely considered to have remained conservative throughout the evolution of the group (Carroll, 1988; Storrs, 1999). Famously described, including by Owen (1860 p. 230), "as a snake threaded through the trunk of a turtle", the typical plesiosauroid bauplan was spectacular enough to defy belief by contemporary scientists (Taylor, 1997; Cadbury, 2000), when Mary Anning discovered the first complete *Plesiosaurus* in 1823 (text-fig 1.1). The name *Plesiosaurus* was coined two years prior for remains "presenting many peculiarities of general structure" (De la Beche and Conybeare, 1821, p. 560).

A comprehensive phylogeny of stem-group Sauropterygia has been established during the last twenty years, through the work of Rieppel (1998, 1999a, 1999b, 2000), Storrs, (1991, 1993) and Sues (1987). However, plesiosaur relationships remain poorly resolved. As biologically unique organisms, plesiosaurs offer unique insights into evolutionary processes. It is important to understand their phylogenetic position and interrelationships because a good understanding of phylogeny is a prerequisite to interpreting biological systems (Hillis, 1995) and contributes to the ultimate goal of phylogenetics: reconstruction of the "one true tree" (Thorley and Page, 2000, p. 486) or "universal tree" (Doolittle, 1999, p. 24) of life.
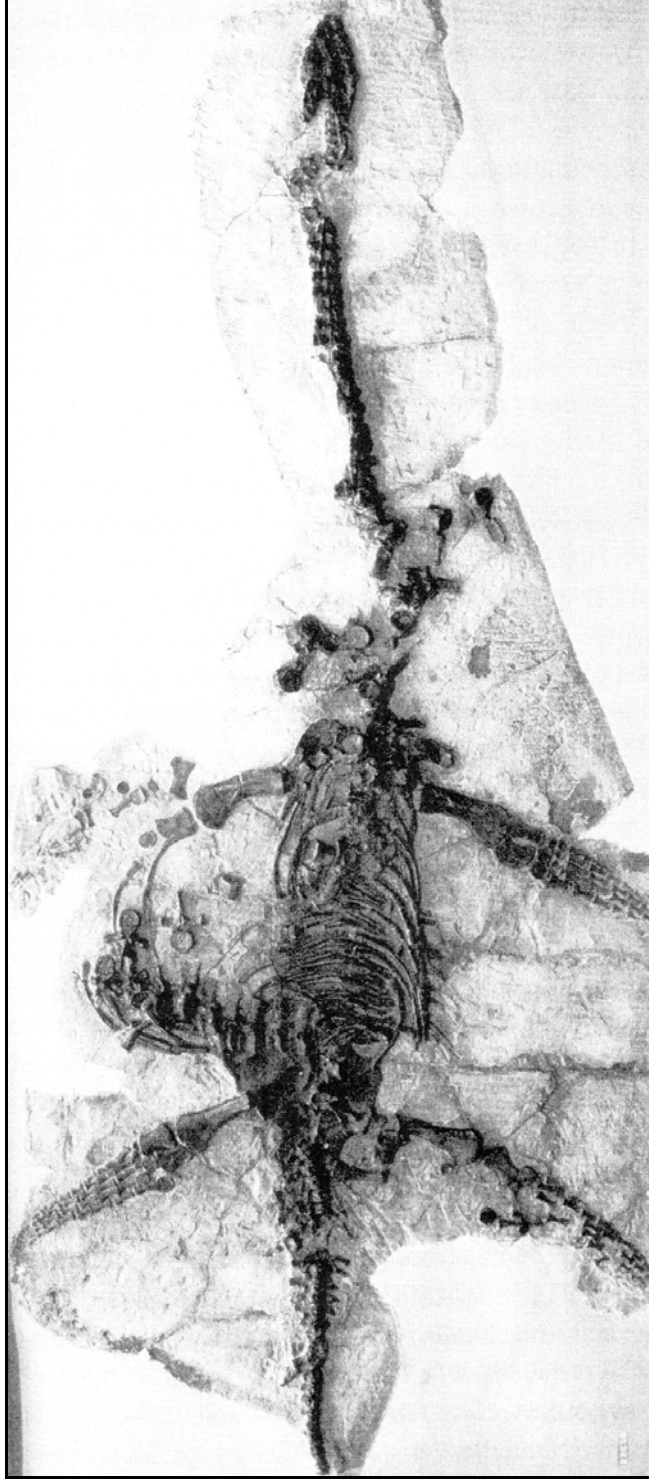
Text-fig 1.1. The holotype specimen of *Plesiosaurus dolichodeirus*, exemplifying the plesiosaur body plan. Note the flipper-like limbs, shortened trunk and tail, and iconographic long neck (from Taylor, 1997).

Institutional Abbreviations.
AMNH, American Museum of Natural History, New York, USA**; BMNH**, The Natural History Museum, London, UK; **BRSMG** Bristol Museum and Art Gallery, Bristol, UK; **CAMSM** Sedgwick Museum, Cambridge, UK; **FHSM** Sternberg Museum of Natural History, Fort Hayes, Kansas, USA; **FMNH**, Field Museum of Natural History, Chicago; **GPIT** Institut und Museum für Geolohie und Paläontologie der Universität Tubingen; **GPMUM** Geologisch-Paläontologisches Museum der Universität Münster; **HAUFF** Urwelt-Museum Hauff, Holzmaden, Germany; **KUVP**, Kansas Museum of Natural History, Lawrence, Kansas, USA; **LEICT** Leicester City Museum, Leicester, UK; **MAN UM** Manchester Museum, Manchester, UK; **MMM** Musée Municipal de Millau, Millau, France; **MNHNCu** Museo Nacional de Historia Natural de Cuba, La Habana, Cuba; **MOR** Museum of the Rockies, Bozeman, Montana, USA; **MOZ** Museo Prof. Olsacher, Zapala, Neuquén, Argentina; **MPL**, Museo de La Plata, La Plata, Argentina; **MCZ** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusettes, USA; **OU** Geology Museum, University of Otago, Dunedin, New Zealand; **OXFUM** Oxford University Museum of Natural History, Oxford, UK; **PETMG** Peterborough City Museum and Art Gallery, Priestgate, Peterborough, UK; **POKM**, Penza Regional Local History Museum, Penza region; **RSM** Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; **SM** Strecker Museum, Baylor University, Waco, Texas, USA; **SMF**, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; **SMNS** Staaliches Museum für Naturkunde, Stuttgart, Germany; **SMUSMP** Southern Methodist University Museum of Paleontology; **TTU** Museum of Texas, Tech University, Lubbock, Texas, USA; **USNM** United States National Museum (Smithsonian Institution), Washington D. C., USA; **YORYM** Yorkshire Museum, York, UK; **YPM** Yale-Peabody Museum, New Haven, Connecticut, USA;

Taxon abbreviations.
Archae, Archaeonectrus rostratus; Arist, Aristonectes parvidens; Atten, Attenborosaurus conybearii; Aug, Augustosaurus hagdorni; BMNH, Unnamed taxon BMNH R. 5488*; Brach, Brachauchenius lucasi; Branc, Brancasaurus brancai; Call, Callawayasaurus columbiensis; Cryp, Cryptoclidus eurymerus; Cym, Cymatosaurus; Dol, Dolichorhynchops osborni; Edgar, Edgarosaurus muddi; Eury, Eurycleidus arcuatus; Hauf, Hauffiosaurus zanoni; Kai, Kaiwhekea katiki; Kimm, Kimmerosaurus langhami; Kron, Kronosaurus queenslandicus; Lib, Libonectes morgani; Lio, Liopleurodon ferox; Lep, Leptocleidus capensis; Macro, Macroplata longirostris; Mare, Maresaurus coccai; Micro, Microcleidus homalaspondylus; Mur, Muraenosaurus leedsii; Occ, Occitanosaurus tournemirensis; Pachy, Pachycostasaurus dawni; P.brach, Plesiosaurus brachypterygius; P.dol, P. dolichodeirus; Pelo, Peloneustes philarchus; Pist, Pistosaurus longaevus; Plio, Pliosaurus brachydeirus; Poly, Polycotylus latipinnis; R.mega, Rhomaleosaurus megacephalus; R.vic, Rhomaleosaurus victor; R.zet, Rhomaleosaurus zetlandicus; Sim, Simolestes vorax; Stret, 'Stretosaurus' macromerus; Styx, Styxosaurus snowii; Term, Terminonatator ponteixensis; Thal, Thalassiodracon hawkinsi; Tri, Tricleidus seeleyi; Trin, Trinocromerum bentonianum; Vin, Vinialesaurus caroli.*

2. History of research

2.1. Background
The Plesiosauria has retained phylogenetic validity for well over 150 years, since the formal identification of the clade by de Blainville (1835). Unfortunately, this long history has hampered modern systematics of the group and continues to do so.

2.2. Caveats to overcome
Contributions towards our current lack of knowledge stem from many factors including the creation of numerous *nomina dubia* (Tarlo, 1960; Brown, 1981; Kear, 2002) and wastebasket genera (there are literally hundreds of species of *Plesiosaurus*) (White, 1940; Persson, 1963; Storrs, 1997), out-dated classifications based on homoplasy-prone characters such as neck length and head size (O'Keefe, 2002), and useless classifications based on plesiomorphic characters (Taylor, 1992a). Insufficient, conflicting and in some cases erroneous descriptions (examples discussed in Tarlo, (1960 p. 149) and Carpenter (1999 p. 152)) and inadequate type material (Carpenter, 1997) are further caveats to overcome when reconstructing plesiosaur phylogeny. There is also a general "lack of good skull material compared with the relative abundance of postcranial remains" (Brown, 1981, p. 335) and if this were not enough, there is also a tendency for "heads to become detached from bodies prior to fossilisation, which can make the association of cranial and post-cranial material problematic" (Forrest, 1998, p. 142). One further reason plesiosaur taxonomists struggle to create a coherent classification is made apparent here: the evolutionary history of the group is much more complicated and intricate than previously anticipated.

2.3. Current consensus
Traditionally, the dichotomy into plesiosauromorph-pliosauromorph forms (O'Keefe, 2002) has been converted directly into a systematic division comprising Plesiosauroidea and Pliosauroidea respectively. Although useful colloquially (Smith, 2003a), the definitions continue to be clouded with descriptions of so called 'pliosaur-plesiosaur intermediates' (Cruickshank, 1994a) and the last decade has seen a growing concern over the validity of their monophyly (Bakker, 1993; Carpenter, 1997; O'Keefe, 2001a).

2.4. Recent resurgence
The recent resurgence in the number of (re)descriptions (text-fig 2.1) coupled with advances in phylogenetic methodologies, preparation techniques (described in Taylor, 1992a & b; Taylor and Cruickshank, 1993a) and CAT-scan/X-ray technology (Cruickshank *et al.* 1991; Cruickshank, 1994b; Carpenter, 1997; Druckenmiller, 2002) has revived the study of plesiosaur interrelationships. Tarlo (1960) contributed significantly to our understanding of British Jurassic pliosaurs; a subject under current review (Noè, 2001). Brown (1981) reviewed the contemporary plesiosauroids recognising variation between individuals, ontogeny, and sexual dimorphism. A detailed understanding of plesiosaur bone structure ontogeny (Wiffen *et al.* 1994) and limb evolution (Caldwell, 2002) also facilitates our understanding of the relative importance of characters, and adult versus juvenile specimens (*sensu* Brown 1981). North American Cretaceous plesiosaurs have received recent attention from Carpenter (1996, 1999) and Storrs (1999). Furthermore, the interrelationships of plesiosaurs are being successfully resolved via a combination of phenetic and cladistic analyses.
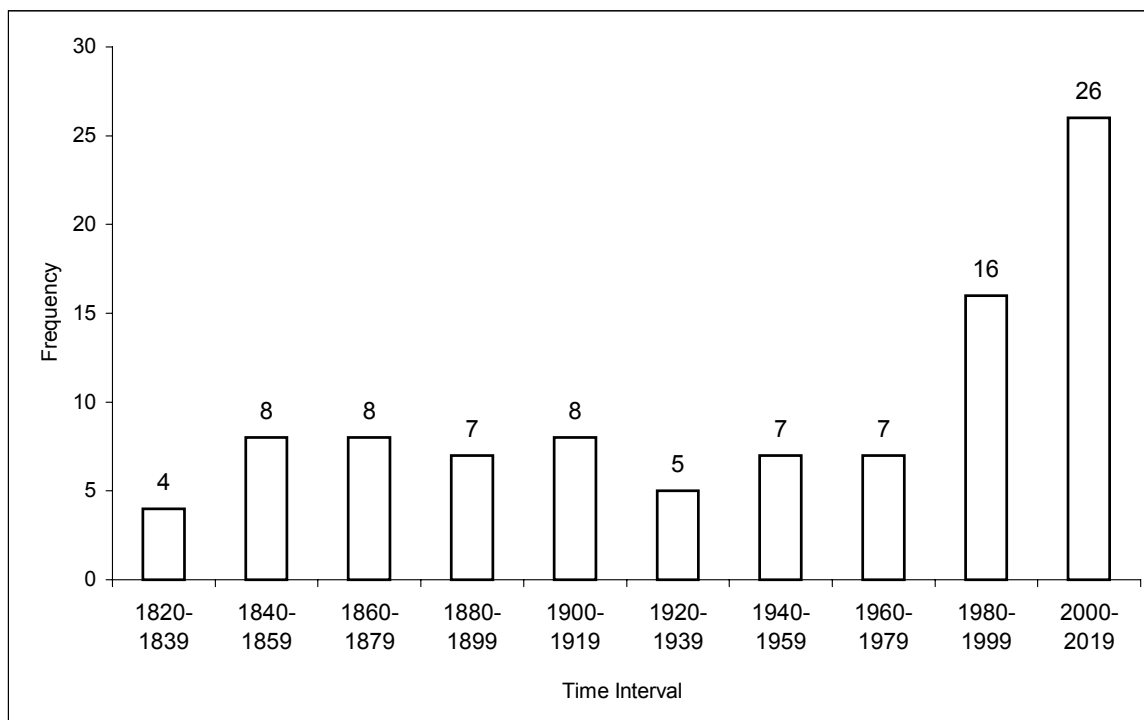
Text-fig 2.1. Graph depicting the approximate number of descriptive papers on plesiosaurs during the last 200 years and extrapolated for the next 20 years. The pattern can in part be attributed to various socio-economic events, the distinct resurgence subsequent to the nineteen-eighties is very clear and can be in part further attributed to technological advance.

TRIASSIC	JURASSIC			CRETACEOUS	
	LIAS	OXFORD	KIMMERIDGE	LOWER	UPPER
	Microcleidus	Cryptocleidus Apractocleidus	CRYPTOCLEIDIDAE	Mauisaurus	
		Muraenosaurus Tricleidus Picrocleidus	Colymbosaurus	MURAENOSAURIDAE	
	Plesiosaurus Sthenarosaurus Macroplata	PLESIOSAURIDAE	PLIOSAURIDAE		
		Pliosaurus ferox Peloneustes	Pl. grandis	Kronosaurus	Brachauchenius
	Eretmosaurus	Simolestes	ELASMOSAURIDAE		Cimoliosaurus Elasmosaurus
	Thaumatosaurus Seeleyosaurus	T. ooliticus	BRANCASAURIDAE	Brancasaurus	POLYCOTYLIDAE
		Tremamesacleis	TREMAMESACLEIDIDAE		Polycotylus Trinacromerum Polyptychodon
	Rhomaleosaurus Eurycleidus		LEPTOCLEIDIDAE	Leptocleidus	

Text-fig 2.2. Phylogeny proposed by White (1940) in which the majority of branching events occur in a hypothetical Triassic radiation followed by anagenesis throughout the Jurassic and Cretaceous. Note how the Polycotylidae offshoot from the pliosauroid family, Leptocleididae. Also interesting is the postion of *Eretmosaurus*, here considered a pliosaurid.

2.5. Phenetics
Primarily based on aspects of the pectoral girdle, White's (1940) classification of plesiosaurs is respectable; unfortunately his attempt to "express the probable relationships of the groups to each other" (p. 466), does little more than derive all families from an unknown *Plesiosaurus*-like ancestor (text-fig 2.2). Welles (1943) presents a more detailed phylogeny in a stratigraphic context, as determined from a variety of characters (text-fig 2.3) and Persson (1963) created a classification and proposed phylogenetic links (text-fig 2.4). More recently, Bakker (1993) devised a broad phylogeny based on cranial and atlas-axis morphology in a stratigraphic context (text-fig 2.5) and Brown and Cruickshank (1994) offered a phylogeny with nodes based on skull characters (text-fig 2.6), accommodating the four major plesiosaur families of Brown (1981). Carpenter (1997) constructed a similarly broad phylogeny based on a suite of cranial characters (fig 2.7).

2.6. Cladistic analyses
Bardet and Godefroit (1998) performed a preliminary cladistic analysis of the Plesiosauria, confirming the broad scale relationships deduced by phenetics. Hampe (1992) created a cladogram from a matrix of seven pliosauromorph species and 22 characters. Bardet *et al.* (1999) (text-fig 2.8a) and Gasparini *et al.* (2002, 2003a) (text-fig 2.9) performed concise cladistic analyses for the Plesiosauroidea, consisting of various characters and taxa. Smith (2003b, appendix 1) reanalysed the data in Bardet *et al.* (1999), reaching different conclusions (text-fig 2.8b). Carpenter (1999) analysed plesiosauroid, especially elasmosaurid relationships (text-fig 2.10). O'Keefe (1999; 2001a) performed the most extensive cladistic analyses of Plesiosauria, comprising 163 characters for 26 taxa, and 166 characters for 31 taxa (text-fig 2.11) respectively. Therein, the two superfamilies are retained but have very different meanings.

3.1. Aims of this study
Unfortunately many aspects of plesiosaur phylogeny remain unresolved or controversial and numerous taxa remain to be input into analyses. To quote some recent authors: Storrs (1997, p.145) points out how "the evolutionary and systematic relationships of the Plesiosauria…are almost entirely unknown"; Druckenmiller (2002, p.40) notes how they are "currently in a state of flux"; Taylor (1992a, p.51) reminds us of how "utterly confused" the taxonomy of Lower Jurassic plesiosaurs is; Carpenter (1997, p.191) observes how "the taxonomy of… Cretaceous plesiosaurs is in disarray"; and recently, when referring to the classification of Plesiosauroidea into families, Cruickshank and Fordyce (2002, p.568) remark how the "diagnoses and content are still debated". Herein, many issues are resolved; an extensive cladistic analysis of plesiosaurs is performed enabling confirmation and refutation of current consensual phylogenetic hypotheses and helping to secure a coherent systematic infrastructure for future work. A confident analysis of pliosaurs cannot be undertaken because the necessary taxonomical overhaul has yet to be performed. Unfortunately, this falls outside of the scope of the present project.
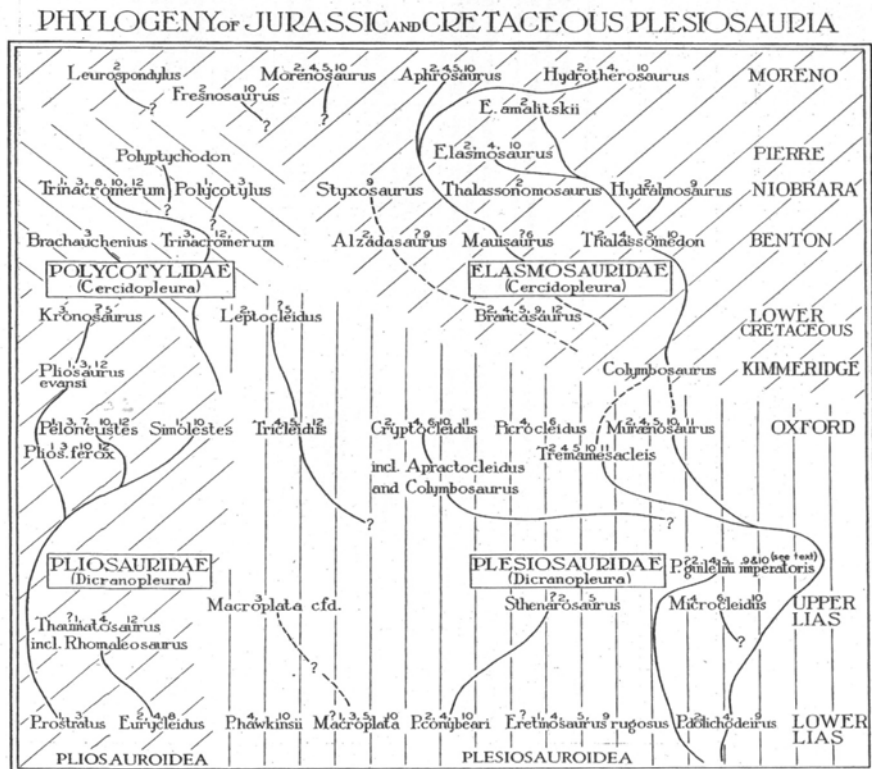
Text-fig 2.3. Phylogeny presented by Welles (1943). The classification of plesiosaurs based on number of cervical rib heads as used here (Cercidopleurus = single headed, Dicranopleurus = double headed) is problematic (Persson, 1963). Welles does not commit himself to allocating Polycotylidae to either Pliosauroidea or Plesiosauroidea.

Text-fig 2.4. The possible phylogenetic relationship between plesiosaur clades suggested by Persson (1963). 'Cryptoclidid' taxa are included in Perssons' Plesiosauridae. Note the late and unlikely (see text) divergence time postulated for Elasmosauridae.

Text-fig 2.5. Plesiosaur phylogeny modified from Bakker (1993). This commendably inventive relationship sees the Cretaceous elasmosaurids and polycotylids as derived pliosauroids (unfilled silhouettes represent this monophyletic radiation) whilst the Jurassic long necked forms (crosshatched) are victims of a terminal Jurassic extinction. Bakker's association of elasmosaurs with polycotylids is confirmed elsewhere (Carpenter, 1997) but they are more likely more closely related to plesiosauroids than pliosauroids (O'Keefe, 2001a). (See Bakker (1993) for clade node diagnoses).

Text-fig 2.6. Phylogenetic relationships between the four distinct families recognised by Brown (1981). Here Cryptoclididae is recognised as a distinguishable monophyletic family. (From Brown and Cruickshank, 1994, see therein for node diagnoses).

Text-fig 2.7. A hypothesis of relationships proposed by Carpenter (1997) to illustrate how polycotylids are derived plesiosaurids more closely related to elasmosaurids than to plio-sauroids, despite their decidedly pliosauromorph bauplan.

Text-fig 2.8. A. Unmodified original phylogeny determined using cladistic methods, redrawn from Bardet *et al.* (1999). B. Revised hypotheses of the relationships within Plesiosauroidea from Smith (2003b) using the same data matrix and giving support indi-ces. Left of node: bootstrap propor-tion, jackknife proportion and decay index (left to right respectively). Right of node: node number and char-acter class (see text therein). Above node: majority rule (50%) value %. Above taxon: maximum leaf stability.
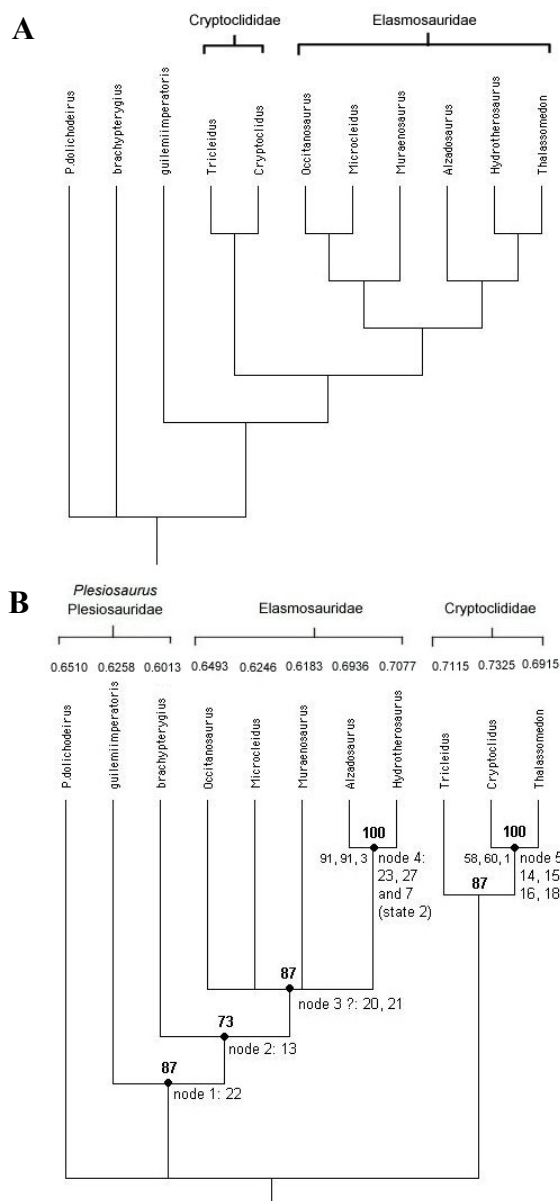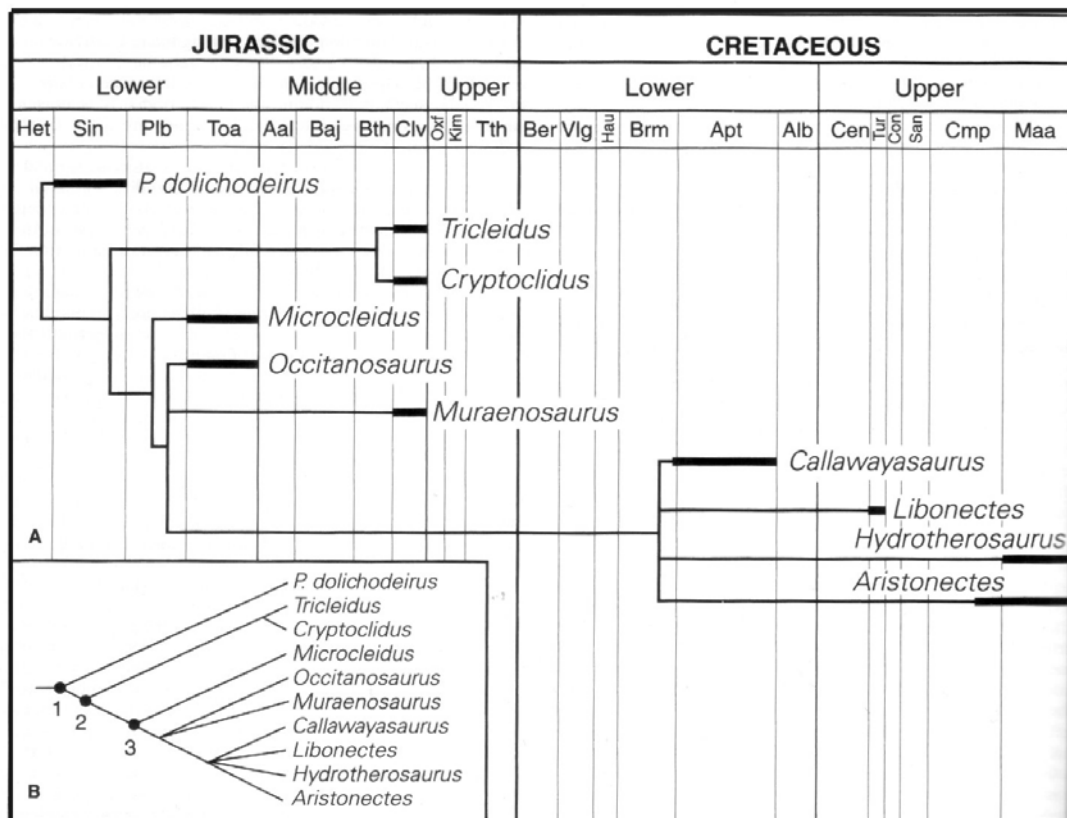
Text-fig 2.9. Cladogram of plesiosauroid relationships expressed in a stratigraphic context (from Gasparini *et al*. 2003). The authors attribute the weak resolution of Cretaceous elasmosaurids to a poor Lower Cretaceous plesiosaur fossil record. Note how cryptoclidids are monophyletic and in a basal position, congruent with Carpenter (1999).
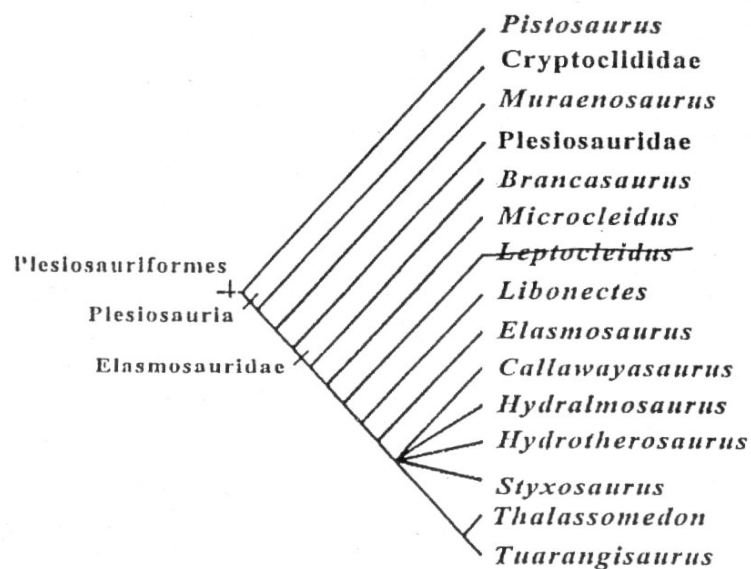
Text-fig 2.10. Cladogram produced from a cladistic analysis of long-necked plesiosauroids including nine elasmosaurid genera. Cryptoclidids occur in a rather basal position within the superfamily (From Carpenter, 1999).
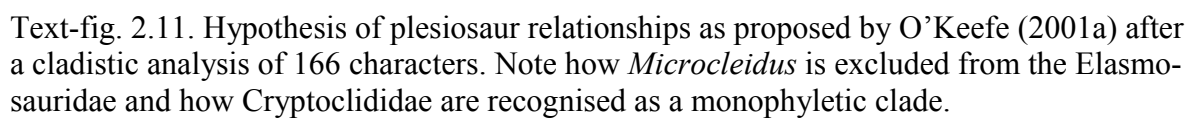
Text-fig. 2.11. Hypothesis of plesiosaur relationships as proposed by O'Keefe (2001a) after a cladistic analysis of 166 characters. Note how *Microcleidus* is excluded from the Elasmosauridae and how Cryptoclididae are recognised as a monophyletic clade.

3.2. Stratigraphy and quality of the plesiosaur fossil record

As Gingerich (1990, p. 437) points out, "time is important [in reconstructing phylogenies] because genealogy is sequential". The relationship between stratigraphy and phylogeny is bi-directional in that phylogenies provide implicit data on quality (stratigraphy completeness) and sampling intensity of the plesiosaur fossil record (e.g. by implying gaps) (Wagner, 1998), and conversely the stratigraphic fit may be used to provide data on the accuracy of the phylogenies. Of four possible topologies for a three-taxon case (Sober, 1983), cladograms are restricted to only one (the Y-spur topology). Stratophenetic methods may therefore be invoked to explore both stratigraphy and also other possible topologies (Gingerich, 1990).

3.3. Cranial versus postcranial characters

Detailed reviews of plesiosaur skull anatomy are provided in Andrews (1896), Bakker (1993) and, Brown and Cruickshank, (1994). The plesiosaur neurocranium is described and discussed in detail by Maisch (1998). Detailed and critical accounts of the plesiosaur postcranium are largely absent from the literature, although a review is currently being performed by Forrest (pers. comm. 2002). It is commonly stated that cranial characters are more reliable for determining phylogenetic relationships within the Plesiosauria (Bakker, 1993; Carpenter, 1997; Storrs, 1999). This project seeks to determine the validity of these observations.

4. Systematic palaeontology and valid taxa

4.1. Materials and Methods

Herein, previously excluded and many newly discovered taxa are included in a cladistic analysis and the phylogenetic relationships are resolved to species level. All 44 taxa were scored for 171 characters (Appendices 2 and 3). The matrix was constructed from existing literature, compiled first in Microsoft Excel 2000 and then transferred to PAUP version 4.0 (Swofford, 2000). Four heuristic searches (all random, 1000 replicates, no max trees limit) were performed. These will be referred to as 'unweighted, unreduced', 'weighted unreduced', 'unweighted, reduced' and 'weighted, reduced' throughout. Character partition homogeneity tests and Templeton tests (Templeton, 1983) were used to analyse cranial versus postcranial data. Permutation tests (Archie, 1989) and evaluation of random trees were performed. Tree robustness was tested via decay analyses (Bremer support) (Bremer, 1988; Lee and Hugall, 2003), and jacknife/bootstrap analyses (Efron, 1979). MacClade (Maddison and Maddison, 2000) was employed to draw trees and trace characters (to determine clade synapomorphies and homoplastic characters). RadCon (Thorley and Page, 2000) was used to compute leaf stabilities and reduced consensus (Wilkinson and Thorley, 2003) trees, overcoming the limitations of popular consensus techniques (Wilkinson, 1995). All processes performed in PAUP, MacClade and RadCon are outlined in appendix 4 for easy replication.

4.2 Choosing taxa: the data threshold

To give confidence when assessing patterns of plesiosaur evolution, it has been the aim of this study to include all valid taxa. However, for one reason or another many have been omitted, in the most part due to inadequacy of material/descriptions (Table 1). This maintains the quality and accuracy of the phylogenetic hypothesis. A character completeness threshold of 30% is considered sufficient; taxa with less than this may have detrimental effects to the analysis (Wilkinson, 1995). All taxa within this threshold but excluded from the analysis are presented in table 1.

The most incomplete taxon included in O'Keefe's (2001a) analysis was *Kronosaurus* at 41% (text-fig 3.1). A revision of this genus is near completion but as yet unpublished (McHenry pers. comm. 2003). The five most complete taxa represent every major clade; hence all clades are thoroughly represented. The 30% completeness threshold is not applied to one species, *Pachycostasaurus dawni*, because the few codeable characters are sufficiently diagnostic. However the 30% threshold is still used as an objective guideline. Appendix 5 lists the systematic palaeontology for all of the included taxa with relevant comments.

Table 1. List of selected plesiosaurs including valid and some invalid taxa. All are excluded from the current cladistic analysis, the justification of which is provided.

Valid species	Reason for exclusion
Aphrosaurus furlongi	Material and description insufficient (Welles, 1943).
Bathyspondylus swindoniensis	Material insufficient, i.e. vertebrae only (Delair, 1982).
Bishanopliosaurus youngi	A revised diagnosis (Sato, 2002) confirms the validity of this taxon, however the material is insufficient for determining phylogenetic affinity (23% completeness of data). Also, the type specimen is a poorly preserved juvenile.
Cimoliasaurus	A wastebasket genus with over 40 species (Kear, 2002), all of which are *nomina dubia* or can be reassigned. This confirms observations made by Welles (1943, p.2099). The generic type material consists of only 13 vertebrae.
Colymbosaurus trochanterius	Material insufficient. Brown (1981) revised *Colymbosaurus* as a monotypic genus but later Brown *et al.* (1986) discussed the possibility that *C. trochanterius* is synonymous with *Kimmerosaurus langhami,* refraining from doing so "pending the description of more complete material". A complete mandible, supposedly pertaining to *C. trochanterius*, is figured by Owen (1869 plate IV) and reproduced in Benton and Spencer (1995, p. 189 fig. 7.5) but this actually belongs to a large crocodilian (Tarlo, 1960).
Cryptoclidus richardsoni	Differs from *C. eurymerus* (included herein) only in the shape of the humerus (Martill, 1991).
Elasmosaurus platyurus	Material insufficient (Carpenter, 1999; Storrs, 1999).
Fresnosaurus drescheri	Material and description insufficient (Welles, 1943). Also, the type material is a juvenile, therefore poorly representative.
Georgiasaurus penzensis	Insufficient material. Reviewed by Storrs *et al.* (2000) who also note how the holotype specimen (POKM 11658) is poorly preserved.
Hydralmosaurus serpentinus	Although a referred skull (AMNH 5835) is complete, a description is limited "owing to poor preservation" (Carpenter, 1999).
Hydrotherosaurus alexandrae	The material is certainly sufficient (Welles, 1943), but published accounts are in need of review.

Kronosaurus boyacensis	Insufficient description (Hampe, 1992).
Leptocleidus clemai	Inclusion is unwarranted because the species is so similar to *L. capensis* (included herein) (Cruickshank and Long, 1997).
Leptocleidus superstes	Although the material is reasonably sufficient (Andrews, 1922), inclusion is unwarranted because the species is so similar to *L. capensis* (included herein) (Cruickshank, 1997; Persson, 1963),
Leurospondylus ultimus	Insufficient material (Brown, 1913) and of a juvenile nature (Creisler, 2003).
Liopleurodon rossicus	Halstead (1971) based this species on material confused by "inadequate collection management practices" (Storrs, *et al.* 2000, p. 191), thus many of the bones described may belong to 'Strongylokrotaphus', with only the damaged skull and pectoral girdles truly belonging to the type of *L. rossicus*. This is considered insufficient for inclusion.
Mauisaurus haasti	Material insufficient: the lectotype consists of just a paddle and pelvis (Cruickshank and Fordyce, 2002).
Mauisaurus gardneri	Insufficient material. Known elements figured by Seeley (1877), are reproduced (in part) in Benton and Spencer (1995).
Megalneusaurus rex	Insufficient material. Creisler (1998) also notes how the descriptions by Knight (1898) are unreliable and some of the type remains "appear to be lost" (paragraph 13).
Microcleidus macropterus	Material insufficiently distinct from *Microcleidus homalospondylus* to warrant inclusion.
Morenosaurus stocki	Insufficient description/material (Welles, 1943).
Muraenosaurus beloclis	Inclusion unwarranted because the species is so similar to *M. leedsii* (included herein) (Brown, 1981) and represented by insufficient material (Martill, 1991).
Plesiopleurodon	Insufficient material (Carpenter, 1996).
Plesiosaurus guilielmiiperatoris (*'Seeleysaurus'* of White, 1940)	Fraas (1910) describes this taxon. Recently, Storrs (1997) modified Persson's (1963) suggestion that *Plesiosaurus* contains only three valid species by proposing *P. brachypterygius* as a junior synonym of *P guilielmiiperatoris,* reducing the number to two. However, Maisch and Rucklin (2000, p. 38) justify retention of *P. brachypterygius* and as this species is currently the best documented, it is included herein. *P. guilielmiimperatoris* is omitted pending re-description of the type material. Some workers (Bakker, 1993) have retained the name *'Seeleysaurus'* for *P. guilielmiiperatoris.*
'Plesiosaurus' macrocephalus	An outdated description is given by Andrews (1896). This species is probably not *'Plesiosaurus'* and is under revision by Brown and Storrs (Creisler, 2003).
Pliosaurus (Strongylokrotaphus) irgisensis	Insufficient material (Storrs *et al.* 2000).

Pliosaurus andrewsi	Species proposed by Tarlo, (1960), the description is superficial. This species is possibly a large form of *Peloneustes* (Martill, 1991).
Polyptychodon interruptus (Lectotype species), *P. continuus*, *P. hudsoni*	*Polyptychodon* is the only valid Upper Cretaceous plesiosaur from Europe (Bardet and Godefroit, 1995). Creisler (2003) discusses the confusing history of this genus. It has important implication for the provenance of pliosauroids (presuming current diagnoses are correct), extending the range into the Late Cretaceous (Benton, 1993, Benton and Spencer, 1995). Unfortunately the lectotype material, comprising a skull roof and associated teeth (Milner, 1987) is insufficient for inclusion in cladistic analyses.
Rhomaleosaurus propinquus	The partly composite type of this "poorly known" (Taylor, 1992) but distinctive taxon is insufficient and insufficiently described.
Simolestes indicus	Incomplete material, comprising a partial vertebral column (Bardet *et al.* 1991).
Simolestes keileni	Incomplete material.
Sthenarosaurus dawkinsi	Incomplete material comprising a partial skeleton (Benton and Spencer, 1995). The only description is outdated and preliminary (Watson, 1909).
Sulcusuchus erraini	Insufficient material: incomplete skull and mandible of a polycotylid, originally described as a dyrosaurid crocodile (Gasparini *et al.* 2001).
Thalassomedon hanningtoni	Although represented by sufficient material (Carpenter, 1999), the existing descriptions (Welles, 1943; Carpenter, 1999) are insufficient or preliminary.
Trinacromerum kirki	Insufficient material.
Trinacromerum bonneri	Adams (1997) proposed this species in a paper written but not published before Carpenter (1996) diagnosed the same material as *Dolichorhynchops osborni*. The type specimen is not referred herein. It exhibits "Unique limb and vertebral structures" (Adams, 1997, p. 179) and may yet be a valid species.
Tuarangisaurus keyesi	The complete cranium is difficult to interpret "because of damage from crushing" (Wiffen and Moisley, 1986, p. 209). If studied in more detail this taxon, also known from throughout the southern hemisphere (Gasparini *et al.* 2003b) may well be included in future cladistic analyses.
Woolungasaurus glendowerensis	Insufficient material consisting of vertebrae, limb and girdle elements (Persson, 1963) and referred cranial material (Kear, 2003). Both the genus and species are recently considered *nomen dubuim* (Kear, 2003).
Yuzhoupliosaurus chenjiangensis	Insufficient material (Creisler, 2003).

4.3. Selecting Characters

An exhaustive suite of characters was compiled from existing descriptions, cladistic/phenetic studies and personal observations. All those of possible utility have been adopted for inclusion in the cladistic analysis. The analysis of O'Keefe (2001a) provided a sound base, however it has been beneficial to amend or delete some of these characters (see below) and in addition, six further characters were introduced. The combination of taxa and characters results in the largest data matrix ever constructed for plesiosaurs (appendix 3).

4.4. Character weighting and ordering

Brown (1981) divided his suite of characters into categories, each expressing a grade of phylogenetic significance. A similar approach can be utilised here to allow *a priori* weighting of characters, the only approach of weighting that does not invoke circular reasoning (Neff, 1986). Brown's Category A, ("…variation due …to ontogenetic growth") need not be invoked here either because the majority of taxa are known from "adult" or "mature adult" (*sensu* Brown, 1981) type/ referred material; or because such characters do not (for this very reason) enter the analysis. Category B characters are taxonomically reliable at low hierarchical levels but have little/no phylogenetic significance, or are poorly known and hence of dubious taxonomic value. Category C, ("…unidirectional evolutionary change which affects the entire order.") is particularly useful in assessing derivation but could be considered as representing homoplastic characters. Category D encompasses characters that "exhibit variants of an opposing nature that occur simultaneously" from which a "classification may be produced which reflects evolution". Tarlo (1960) groups characters into those changing universally with age and those that "persist through time and indicate possible phylogenetic relationships" (p. 149-150). This latter grouping is equivalent to Brown's (1981) Category D.

Here, two types of characters are recognised; (i) *Category A* (also equivalent to Category D of Brown): such characters are vital and make up the majority in this analysis. (ii) *Category B*: All other characters (equivalent to categories A, B and C of Brown). Experimentally, all category B characters (8, 11, 26, 52, 54, 57, 77, 107, 109, 111, 113, 121, 131, 135, 137, 138, 146, 151, 154, 166, 167, 168, 169) were weighted at half the value of category A characters. Character weighting is often dismissed as too subjective but can be justified "in resolving difficult instances of homoplasy" (Wheeler, 1986, p. 102). The following characters were ordered throughout the analysis: 9, 10, 64, 108, 109 and 124.

4.5. Amendments to O'Keefe's character suite

Taxa and characters already scored by O'Keefe (2001a) were reviewed, amended or deleted where necessary and taxa then scored for additional characters.

4.5.1. Character amendments

Character numbers refer to appendix 2.

Text-fig. 3.1. Graph to show the % of complete data entries for all taxa
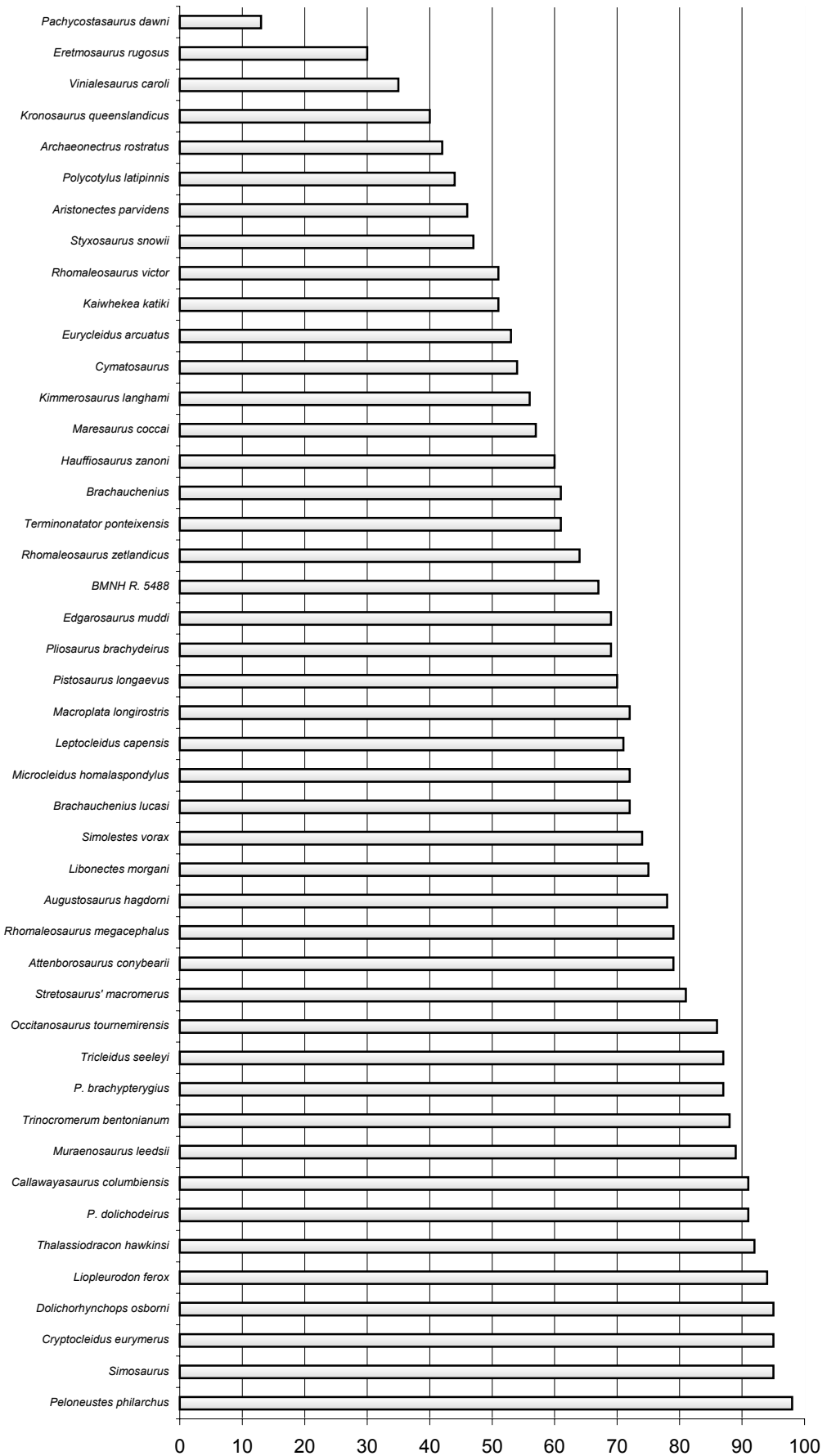
Char 11. Temporal emargination (original coding: present = 0, absent = 1). This character is uninformative under the definition and as coded by O'Keefe because an excavated cheek is present in all taxa. Nevertheless, the *degree* of emargination is a useful character because it is variable within plesiosaurs, e.g. Brown and Cruickshank (1994) employ the character, "deep ventral excavation of cheek margin" as synapomorphic for Cryptoclididae. This character is also used by Bardet *et al.* (1999) (char. 4) and Gasparini *et al.* (2002) (char. 4). However, therein the polarity is reversed, their justification being that *Plesiosaurus* shows a plesiomorphic weakly excavated cheek. However, the majority of stem-group sauropterygians show very deep emargination (Carroll, 1988) agreeing with the polarity of O'Keefe, at least with respect to the current analysis. In accord with the above, this modified character is coded as follows: (strongly emarginated = 0, weakly emarginated = 1). Strongly emarginated cheeks are recognised by a distinct 'U' shaped excavation and a postero-ventral corner formed by the jugal/maxilla (text-fig 3.4.b, d & f). Weakly excavated cheeks are shallowly arced and lack any angle at their anterior margin (text-fig 3.4.c.e).

Char. 21. Frontal contacts external naris (original coding: does contact = 0, does not contact = 1). Confusion over the polarity of this character arises because in O'Keefe's matrix, taxa are coded in reverse to the definition. For example, *R. megacephalus* shows a clear contact (Cruickshank, 1994) but is coded as 1. As frontal-naris contact is absent in all stem-group taxa including pistosaurids (Carroll, 1988) the matrix polarity is actually right and the coding polarity should be reversed: (does not contact = 0, does contact = 1).

Char. 31. Jugal extends anteriorly along ventral orbital margin' (see text-fig 3.4.c) and character 32 'Jugal contacts orbit margin'. Character 31 can only be scored for taxa with a positive state for character 32. This modification follows the inclusion of taxa, which show positive states for character 31 rendering this previously uninformative character informative.

Char. 34. Jugal forms narrow bar between orbit and temporal emargination. The following addition is included in the definition: 'and/or is small and vertically orientated' (after Brown and Cruickshank, 1994) (text-fig 3.4.e).

Char 41. Prefrontal and postfrontal exclude frontal from dorsal orbit margin. With the deletion of character 22 (see below), this character requires rewording. Revised definition: 'frontal excluded from the dorsal orbit margin'. Now, positive identification of a prefrontal need not preclude this character.

Char. 59. Squared lappet of pterygoid underlies quadrate pterygoid flange. There are three states shown in O'Keefe's matrix (0,1,2) but only two are described in the character description (original coding: 0 = absent, 1 = present). Personal observation indicates that where present, the flange occurs in one of two morphologies. The character definition is worded accordingly (0=absent, 1= extensive flanges form large plate, margin with postero-lateral corners i.e. lappet strictly squared, 2= restricted flange, margin curved/straight, may meet behind posterior interpterygoid vacuity to form pointed process).
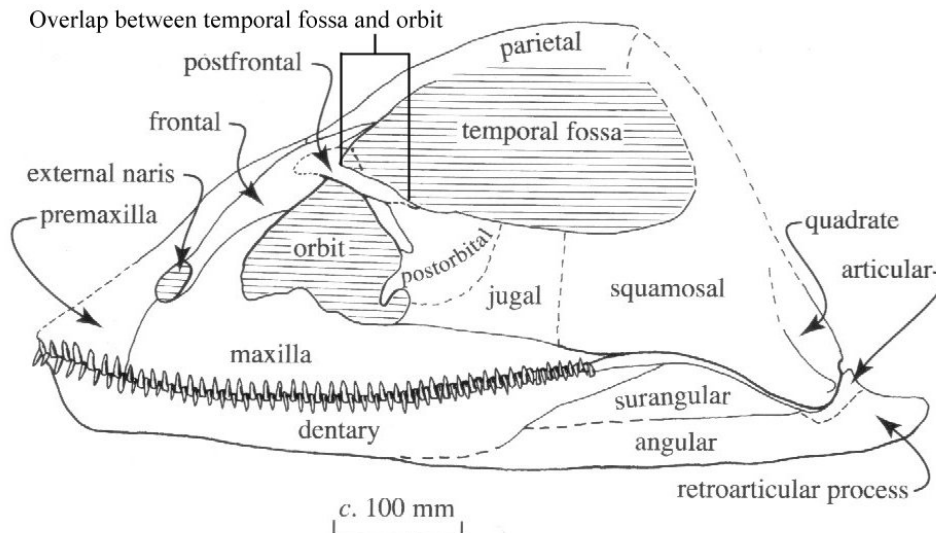
Text-fig. 3.2. Skull of *Kaiwhekea katiki* from the Upper Cretaceous of New Zealand, illustrating overlap between the orbit and temporal fenestra, a positive state for the new character 11. This character, plus the tiny form and abundance of teeth, comprise some cranial characteristics diagnostic of the Family Cimoliasauridae. (Modified from Cruickshank and Fordyce, 2002).

Text-fig. 3.3. Anterior cervical vertebrae from two cimoliasaurid plesiosauroids. A. *Aristonectes parvidens* in anterior view and B. left lateral view (mirrored for easy comparison); C. *Kaiwhekea katiki* in anterior view and B. left lateral view. (A and B modified from Gasparini *et al*. (2003); C and D from Cruickshank and Fordyce (2002)).
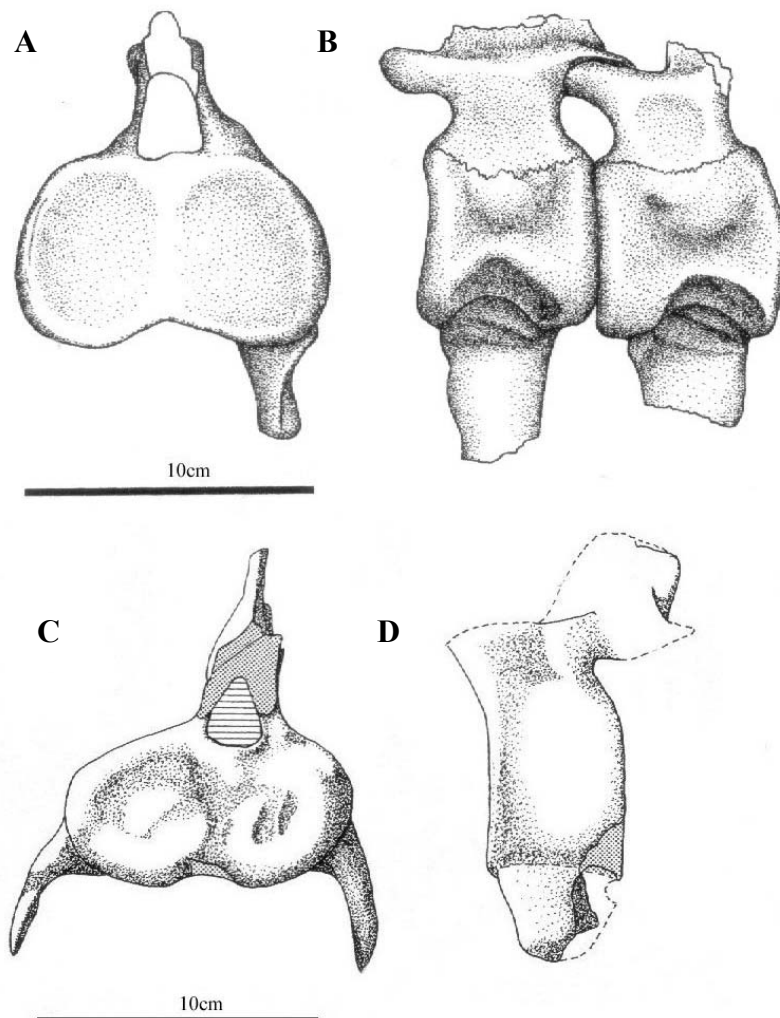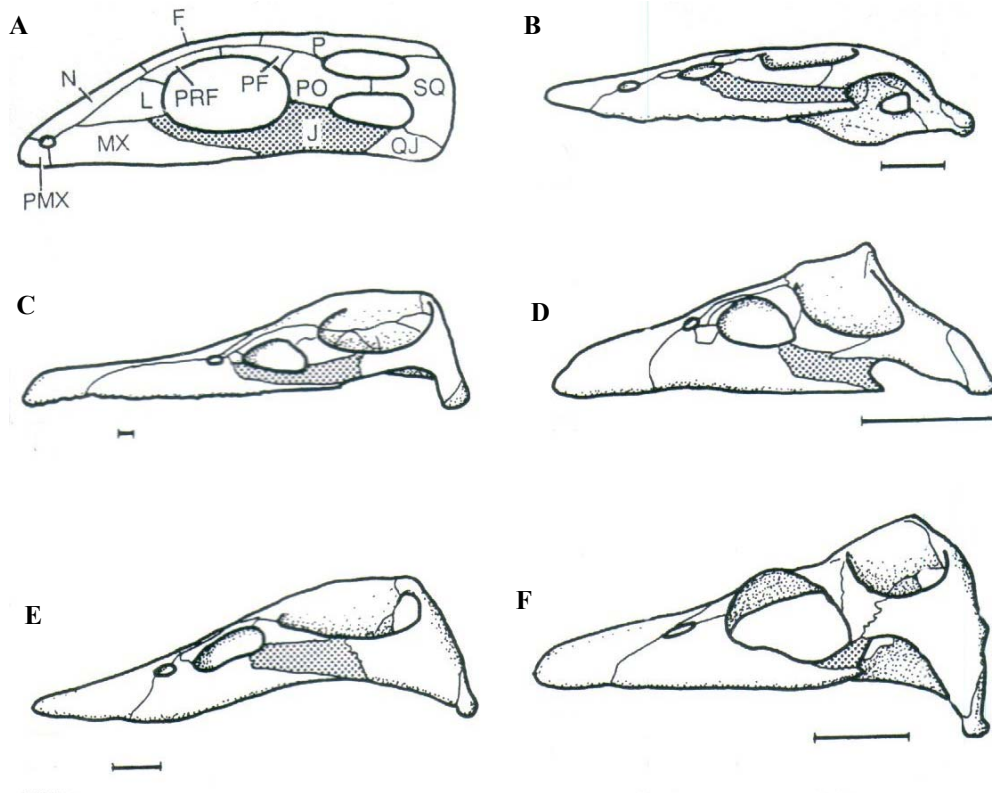
Text-fig. 3.4. Selection of sauropterygian skulls illustrating the variation in size, orientation and morphology of the jugal (stippled) and the degree of temporal emargination. A Generalised primitive diapsid; B, *Simosaurus*, a nothosaur; C, *Pliosaurus brachyspondylus*; D, *Plesiosaurus brachypterygius*, a pliosaurid; E, *Styxosaurus snowii*, an elasmosaurid; and F, *Cryptoclidus eurymerus*, a cryptoclidid. Scale bar = 50mm. Abbreviations: F, frontal; J, jugal; L, lachrymal; MX, maxilla; N, nasal; P, parietal, PMX, premaxilla; PO, postorbital; PF, postfrontal; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal. (From Brown and Cruickshank (1994)).
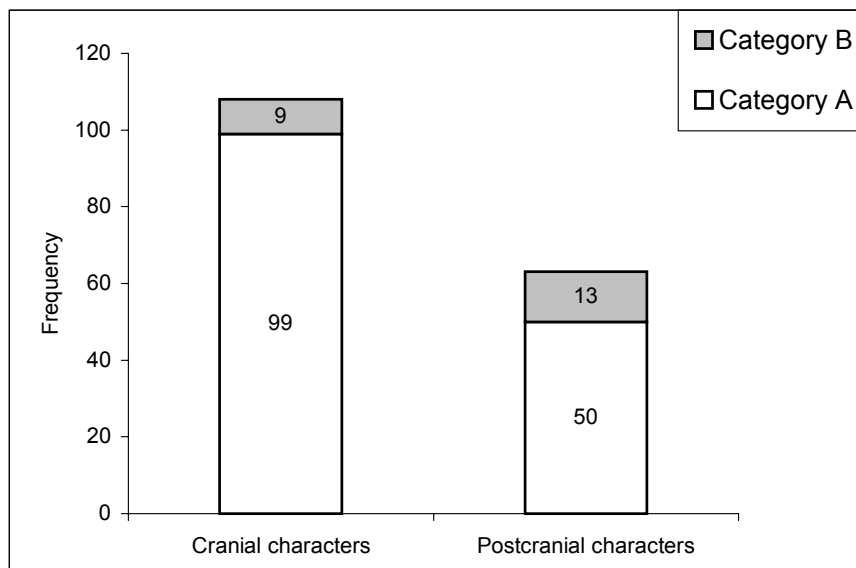
Text-fig. 4.1. Graph to show composition of data matrix in terms of numbers of postcranial/cranial characters and distribution of category A and B characters. The number of cranial characters exceeds postcranial characters by about 1/3. A relatively larger proportion of postcranial characters belong to category B. This suggests that cranial characters are more useful in terms of abundance and relative reliability.

Char. 94. Long lingual coronoid process (original coding: 0=absent, 1=present). With the recent observation of a high, narrow coronoid process in the plesiosauroids *Terminonatator* (Sato, 2003), *Muraenosaurus* (Evans, 1999) and *Vinialesaurus* (Gasparini *et al*. 2002), introduction of a third character state seems justified. Accordingly, the state for *Muraenosaurus* is changed. Revised definition: Coronoid process (0=absent, 1=long lingual, 2=high and narrow).

Char. 136. Dorsal process of scapulae (original coding: 0= Tapers to a blunt tip, 1= ventrally expanded posteriorly). A revised definition accommodates the larger suite of taxa (0= long slender, 1= short and broad, 2= distally expanded).

Char. 162. Ulna shape (0=narrow distally 1=broad distally). O'Keefe comments that "a broad distal ulna is thought to be a synapomorphy of *Augustasaurus* and *Pistosaurus…*" but then codes these taxa as having narrow ulnae and the majority of the other taxa as broad. Personal observation indicates that the quote is correct. To maintain consistency, the polarity and wording of this character is corrected: a distally broad or *flared* ulna is here considered the plesiomorphic condition (as seen in the majority of basal sauropterygians) whereas a narrow *un-flared* distal ulna (as seen in the majority of plesiosaurs) is derived. (0= broad distally 1= narrows distally). This new character differs from Storrs (1993) (char. 83), which refers to *overall* breadth of ulna.

4.5.2. Deleted characters

Uninformative characters are not included in this analysis; accordingly a number of characters included by O'Keefe were modified (see above) or deleted altogether.

Char. 22. Prefrontal present or absent. This character is difficult to score because this region of the skull is often poorly preserved or missing. Gasparini *et al*. (2002) use loss of the prefrontal as a synapomorphy of Cryptoclididae. However the type material they investigated is insufficient for *positive* scoring of the respective taxa (Brown, 1981). Indeed, O'Keefe (2001a) observes a postfrontal in *all* specimens with sufficient preservation. The loss of prefrontal as a diagnostic character should be treated as dubious; the character is presently uninformative and is excluded from this analysis.

4.5.3. Additional Characters

Char. 3. Relative size of orbit/postemporal fenestra. 0= subequal 1= orbit larger 2= fenestra larger. After Bardet *et al*. (1999) char. 5. Category A.

Char. 20. Temporal opening extends anterior to posterior orbit margin. 0=absent 1=present. Some derived plesiosauroids have temporal openings that extend anteriorly between the orbits (text-fig 3.2.). Category A

Char. 61. Foramen incisivum (= premaxillary fenestrae, vomeronasal fenestra of Carpenter, (1997). All three terms are used in the literature). 0=absent, 1=present. This character shared by some pistosaurids and plesiosaurids is believed to be a recurrence in some elasmosaurids, polycotylids, and cimoliasaurids. This character is therefore only applicable to Plesiosauria. Category A.

Char 110. Maxillary teeth extend posterior of orbit 0=present, 1=absent. A maxillary dentition restricted anterior to the posterior orbit margin is derived with respect to stem-group sauropterygians, *Simosaurus* shows state 0 (Rieppel, 2000). However the derived state seems to have arisen independently in some members of the Pistosauridae, Pliosauridae, and Cryptocleidoidea. Also, aspects of dentition have distinct connotations with ecology (i.e. feeding strategy) (Massare, 1987) and are therefore included as Category B.

Char 111. Number of dentary teeth. 20-30=0, <20=1, >30=2. There are two trends from a basal state: decrease in number is common to most elasmosaurs (*sensu* Bardet *et al*. 1999) and some other plesiosauroids. Increase in number of dentary teeth is a character distributed variably among the Plesiosauria. Number of teeth vary in modern lizards and may be taxonomically unreliable (Sato, 2003); therefore this character and character 109 (maxillary teeth) are placed in Category B.

4.5.4. Modified taxa
Three of the taxa used by O'Keefe (2001a) are removed. *Plesiosaurus* and Pistosauridae are removed reflecting a refinement of both these taxa to their constituent species, and *Morturneria* is removed following recent synonymisation (see discussion under *Aristonectes* appendix 5).

4.6. Stratigraphic approaches
Four approaches are utilised to incorporate the important temporal aspect absent from cladistics. 1. Simple presentation of cladograms calibrated to stratigraphy. 2. Stratophenetic linking of taxa, combining their cladistic relationships and stratigraphic position to produce a 'phylogenetic tree' (Pearson, 2001). 3. Calculation of various stratigraphic consistency indices, including SCI (Huelsenbeck, 1994), RCI, (Benton and Storrs, 1994) (by calculating ghost lineages (Norell, 2001)); GER, (Wills, 1999); and also sampling intensity (R) (Wagner, 1998) can be calculated. 4. Combination of phylograms (number of character changes) with stratigraphy.

The latter requires plotting the number of character changes per taxon (herein termed 'derivation'), against time. The resulting scatter-plot yields information about whole-organism morphologic rates of evolution (see Simpson, 1949 for clarification). Such analysis is often discouraged because it "involves too many separate characters for ready analysis and combination" (Simpson, 1949, p. 207) although there have been a few attempts (see Westoll, 1949; Benton, 1990b). By allowing PAUP to determine the number of character changes or degree of 'derivation' for each taxon, this problem is overcome. Usually presented as a phylogram (text-fig 4.4) this data can be converted to a figure (here as % of the maximum possible derivation) suitable for one axis of a graph. Real time (in Ma) was adopted for the second axis to avoid biases of unequal stage duration. For long ranging taxa a mean age was calculated. For taxa of vague provenance, a mean *stage* age was calculated (data from Gradstein, 1995). The same process is then applied to all internal nodes, with the point on the time axis taken as the minimum possible divergence time i.e. equal to the oldest taxon (Wagner, 1998), minus an arbitrary amount to maintain easy interpretation, aesthetic properties and to omit the presence of horizontal lines (which would imply *infinite* rate of morphological derivation).

The topology of the original cladogram can then be superimposed onto the resulting scatter-plot (taxon derivation against stratigraphic position). This method of presenting a phylogeny is herein termed a 'stratophylogeny'. It is important to note that the method makes assumptions as to the relative importance of characters. A fifth, and *a priori* method if incorporating stratigraphic data into phylogenies, stratocladistics (Fisher, 1994), is discussed but reserved for future analyses.

5. Results

5.1. Cladistic analyses and tree support
The final matrix comprises 43 taxa and 171 characters. The composition of the matrix is elaborated in text-fig 4.1 An heuristic search of 1000 replicates including all taxa yielded 17 MPT's each 595 steps long, the strict consensus of which brakes down into a poorly resolved polytomy and prompted reduction (see below). Following manual reduction (exclusion of *Eretmosaurus*), an heuristic search resulted in 16 MPT's each steps 586 steps long. When weighted *a priori*, the same searches yielded only 15 MPT's, each 555 steps long (unreduced) and 4 MPT's each 547 steps long (minus *Eret*). The cladistic indices calculated for each set of MPT's are presented in table 2. Permutation tests (reduced, unweighted) of 1000 replicates gave a P value of 0.030000 indicating that the cladogram fits the data significantly better than random trees.

A strict and 50% majority rule consensus of the original 'unweighted, reduced' MPT's is presented in text-fig 4.2. However, a consensus tree is unsatisfactory for the purposes of this study and the single remaining polytomy was resolved using the 50% majority rule consensus from the 'reduced weighted' search. This final most parsimonious and fully resolved hypothesis of plesiosaur interrelationships is presented in text-fig 4.3 with support indices and as a phylogram in text-fig 4.4. Text-fig. 4.5. shows the cladogram calibrated to stratigraphy and text-fig 4.6 illustrates SRL, MIG and other range data.

5.2. Description of final cladogram
The gross topology is balanced with the tree splitting into two roughly equal divisions, Plesiosauroidea and Pliosauroidea respectively (as defined by O'Keefe 2001a). The relationships within these clades are strongly asymmetrical and form a step series (Pearson, 2001) or 'Hennigian comb', as described by Panchen (1982). Within Pliosauroidea there are three taxa, Rhomaleosauridae and Pliosauridae form a sister relationship which together form a sister relationship with *Thalassiodracon* occupying a basal position. Within Plesiosauroidea, *Plesiosaurus dolichodeirus*, *Plesiosaurus brachypterygius* and *Occitanosaurus* form a basal stem group with the latter forming a sister relationship with Euplesiosauria (Elasmosauridae + Cryptocleidoidea). Within Cryptocleidoidea, *Terminonatator, Vinialesaurus, Muraenosaurus* and *Cryptoclidus* form a stem group leading to Tricleidea, itself containing *Tricleidus* in a basal position and Cimoliasauridae and Polycotylidae as sister taxa in a crown position.

Text-fig 4.2. Strict and majority rule (50%) consensus trees from an unweighted reduced (minus *Eretmosaurus*) search.

Text-fig 4.3. Cladogram depicting the most likely real evolutionary tree for plesiosaurs, annotated with support indices and clade names. The topology is derived from the majority rule consensus tree from the unweighted search, with further nodes resolved via referring to the weighted analysis. Figures to left of node represent: plain text = bootstrap value (uweighted analysis); plain text underlined = jacknife value (unweighted analysis); bold text = bootstrap value (weighted analysis); bold text underlined = jacknife value (weighted analysis). Figures above node represent: italicised = decay index value (unweighted), bold italicised = decay index from weighted analysis. N.B. Figures derived from the weighted analysis are only applied to nodes that gained no value from the unweighted analysis.

Text-fig 4.4. Final cladogram represented as a phylogram. The horizontal distance represents number of character changes, data that can be combined with temporal data to create a 'stratophylogeny' (see text-fig. 4.7).

Majority rule

Strict
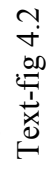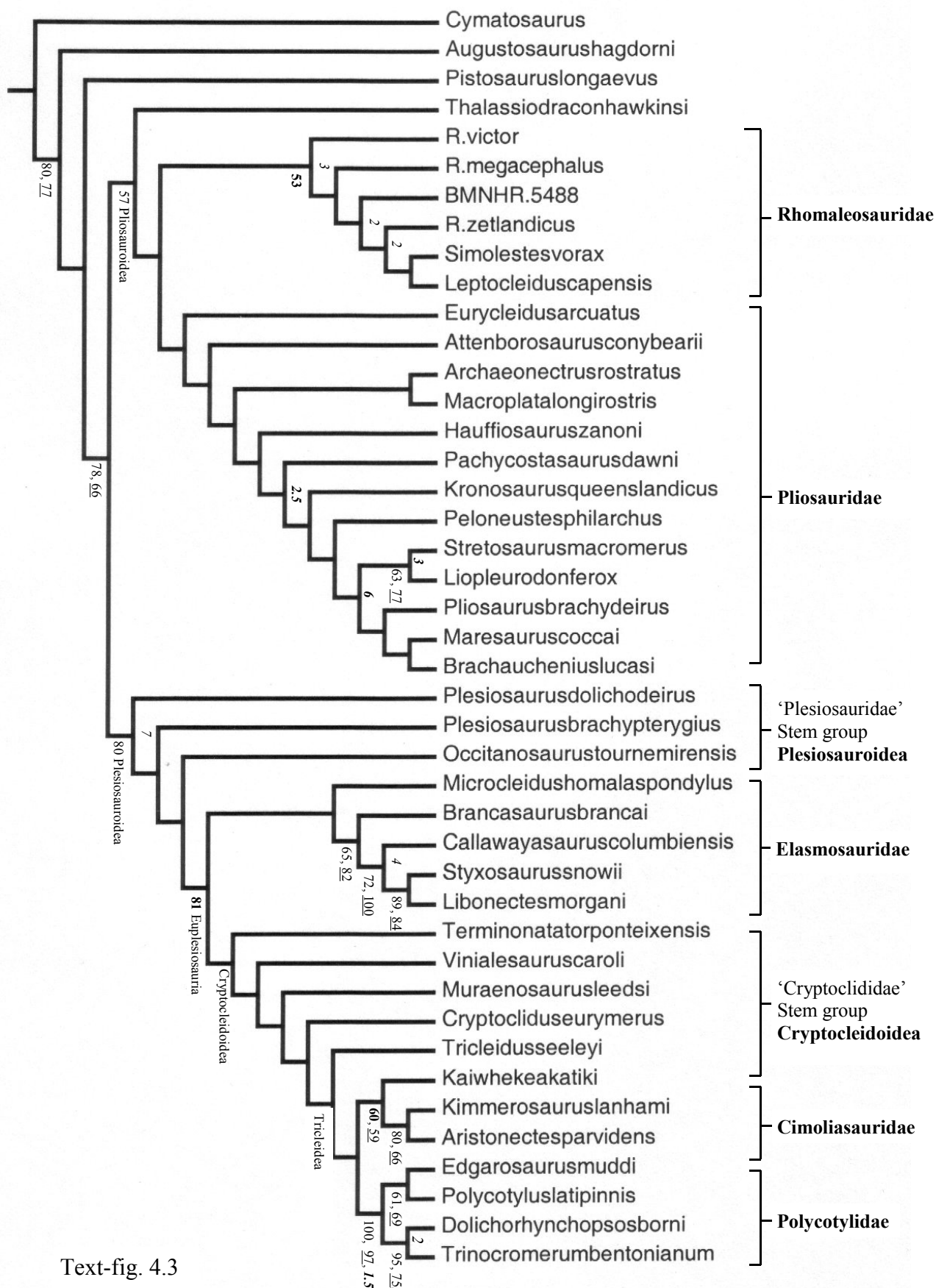
Text-fig 4.2

Text-fig. 4.3

Text-fig 4.4.

— 5 changes
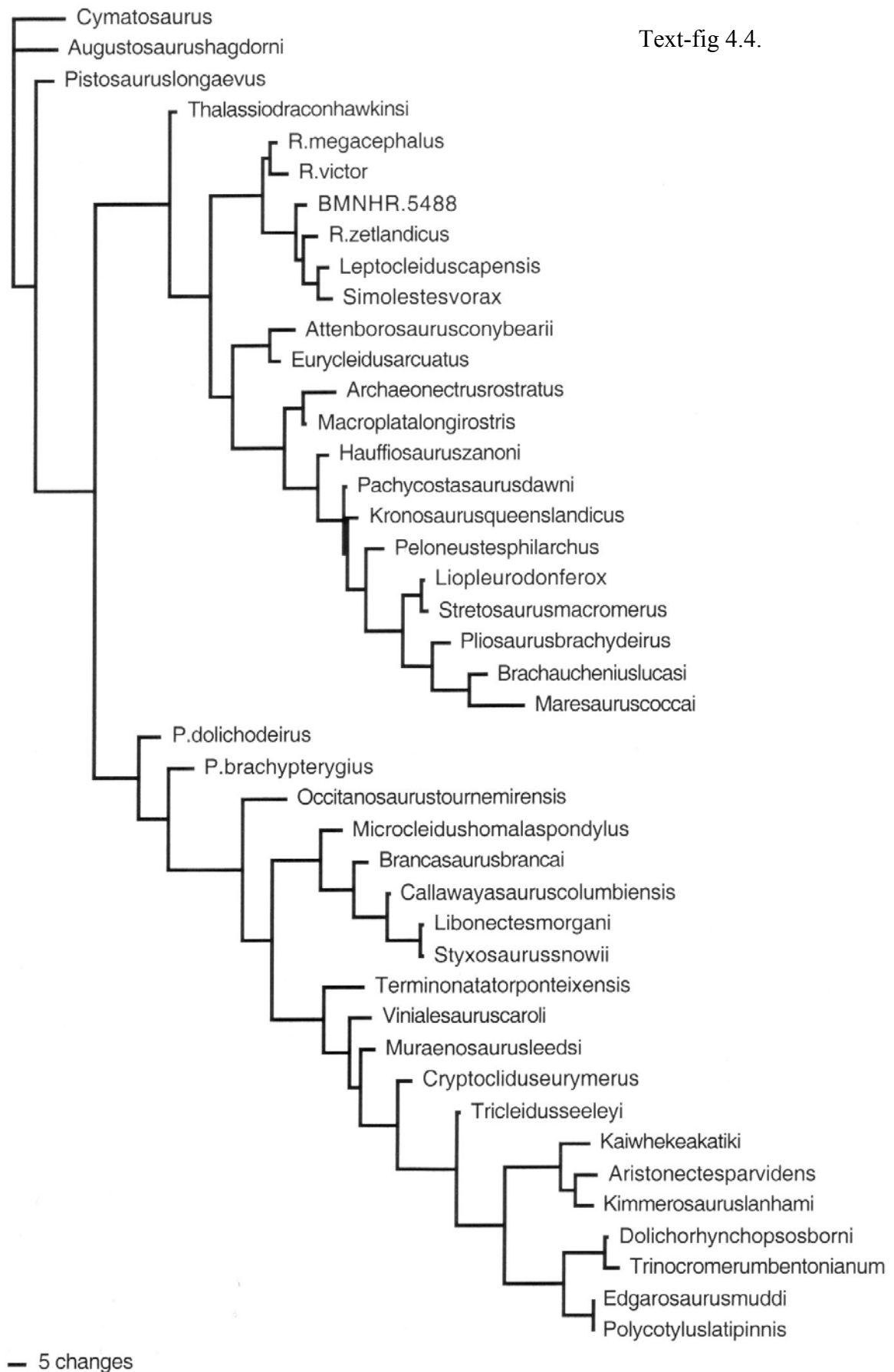
Text-fig. 4.5 Plesiosaur phylogeny plotted against stratigraphy (for type specimens only)

Age (Ma) Regular interavals denote 5 Ma, irregular intervals denote upper age of successive stages

Text-fig. 4.6. Range and ghost range (MIG) data for genera (solid boxes, dotted lines) and families (large open boxes, solid lines) within the Plesiosauria

Polycotylidae
Trinacromerum
'Dolichorhynchops'
Polycotylus
Edgarosaurus

Cimoliasauridae
Arristonectes
Kimmerosaurus
Kaiwhekea

'Cryptoclididae'
Tricleidus
Cryptoclidus
Muraenosaurus
Vinialesaurus
'*Terminonator*'

Elasmosauridae
Styxosaurus
Libonectes
Callawayasau-
Brancasaurus
Microcleidus

Stem-group Plesiosauroidea
Occitanosaurus
P. brachypterygius
P. dolichodeirus

Pliosauridae
Maresaurus
Brachauchenius
Pliosaurus
'*Stretosaurus*' = *Liopleurodon*
Liopleurodon
Peloneustes
'*Kronosaurus*'
Pachycostasaurus
Hauffiosaurus
Archaeonec-
acroplata
Attenborosau-
Eurycleidus

Rhomaleosauridae
Simolestes
Leptocleidus
R. zetlandicus
'*R. megacephalus*'
'*R. victor*'
Thalassiodracon

Pistosaurus
Augustasaurus

65
85.8
89
93.5
98.9
112
121
127
132
137
144.2
150.7
154.1
159.4
164.4
169.2
176.5
180.1
189.6
195.3
201.9
205.7
209.6
220.7
227.4
234.3
241.7

Age (Ma) Regular interavals denote 5 Ma, irregular intervals denote upper age of successive stages

Text-fig. 4.7. Stratophylogeny to show rate of character change (derivation) against time within the Plesiosauria

(Colour for ease of interpretation only)

Cryptocleidus eurymerus
Liopleurodon ferox
Tricleidus seeleyi
Occitanosaurus tournemirensis
Augustosaurus hagdorni
Macroplata longirostris
Pliosaurus brachydeirus
Pistosaurus longaevus
Terminonatator ponteixensis
Brancasaurus brancai
Maresaurus coccai
Kimmerosaurus langhami
Eurycleidus arcuatus
Rhomaleosaurus victor
Aristonectes parvidens
Vinialesaurus caroli
Pachycostasaurus dawni
Kronosaurus queenslandicus
Polycotylus latipinnis
Styxosaurus snowii
Kaiwhekea katiki
Hauffiosaurus zanoni
Edgarosaurus muddi
Microcleidus homalaspondylus
Leptocleidus capensis
Libonectes morgani
Rhomaleosaurus megacephalus
Simolestes vorax
Peloneustes philarchus
Dolichorhynchops osborni
Thalassiodracon hawkinsi
P. dolichodeirus
Callawayasaurus columbiensis
Muraenosaurus leedsii
Trinocromerum bentonianum
P. brachypterygius
Attenborosaurus conybearii
Brachauchenius lucasi
Archaeonectrus rostratus
Rhomaleosaurus zetlandicus
Stretosaurus' macromerus

Text-fig 4.8. Scatter graph of taxa to show derivation (in terms of percentage number of character changes) against stratigraphy with lines of best fit representing the relative average rate of character changes for the two monophyletic superfamilies Pliosauroidea and Plesiosauroidea.
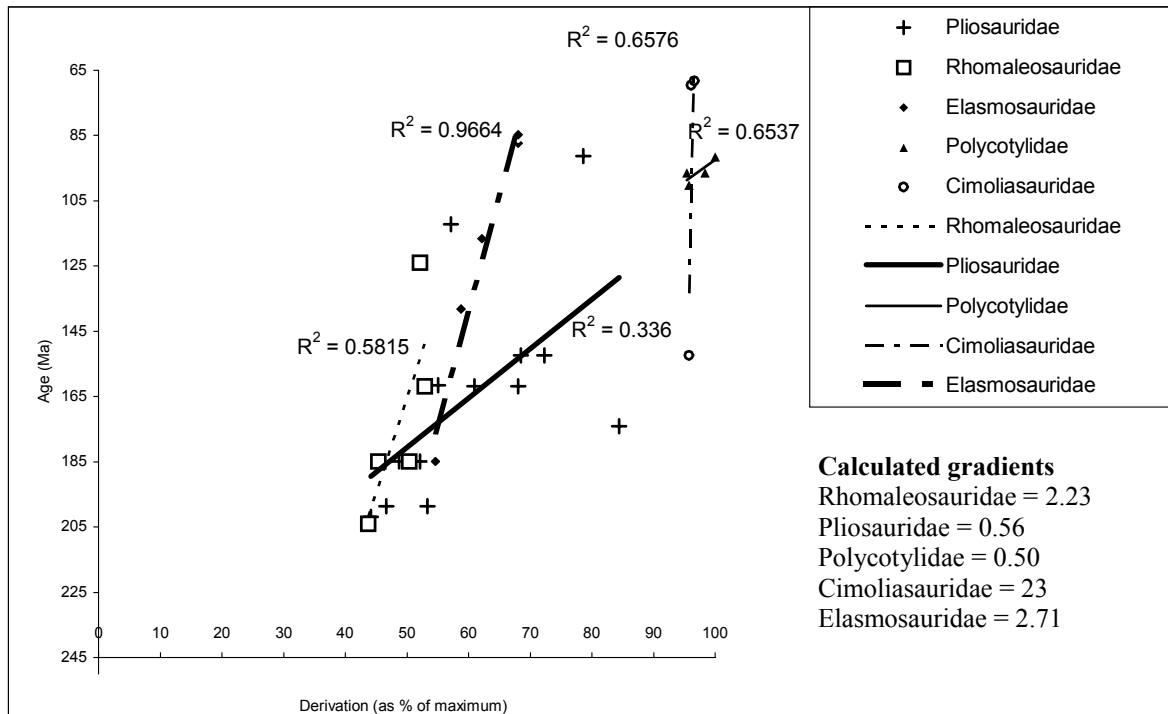
Text-fig 4.9. Scatter graph of taxa to show derivation (in terms of percentage number of character change against stratigraphy with lines of best fit representing the relative average rate of character changes in five monophyletic plesiosaur families.

Text-fig. 4.10. Hypothetical plesiosaur stratigraphic phy-logeny (for type specimens only) indicating the most likely ancestor descendent relationships based on i. cladistic analy-sis and ii. stratigraphic position (stratophenetic linkage).

Age (Ma) Regular interavals denote 5 Ma, irregular intervals denote upper age of successive stages
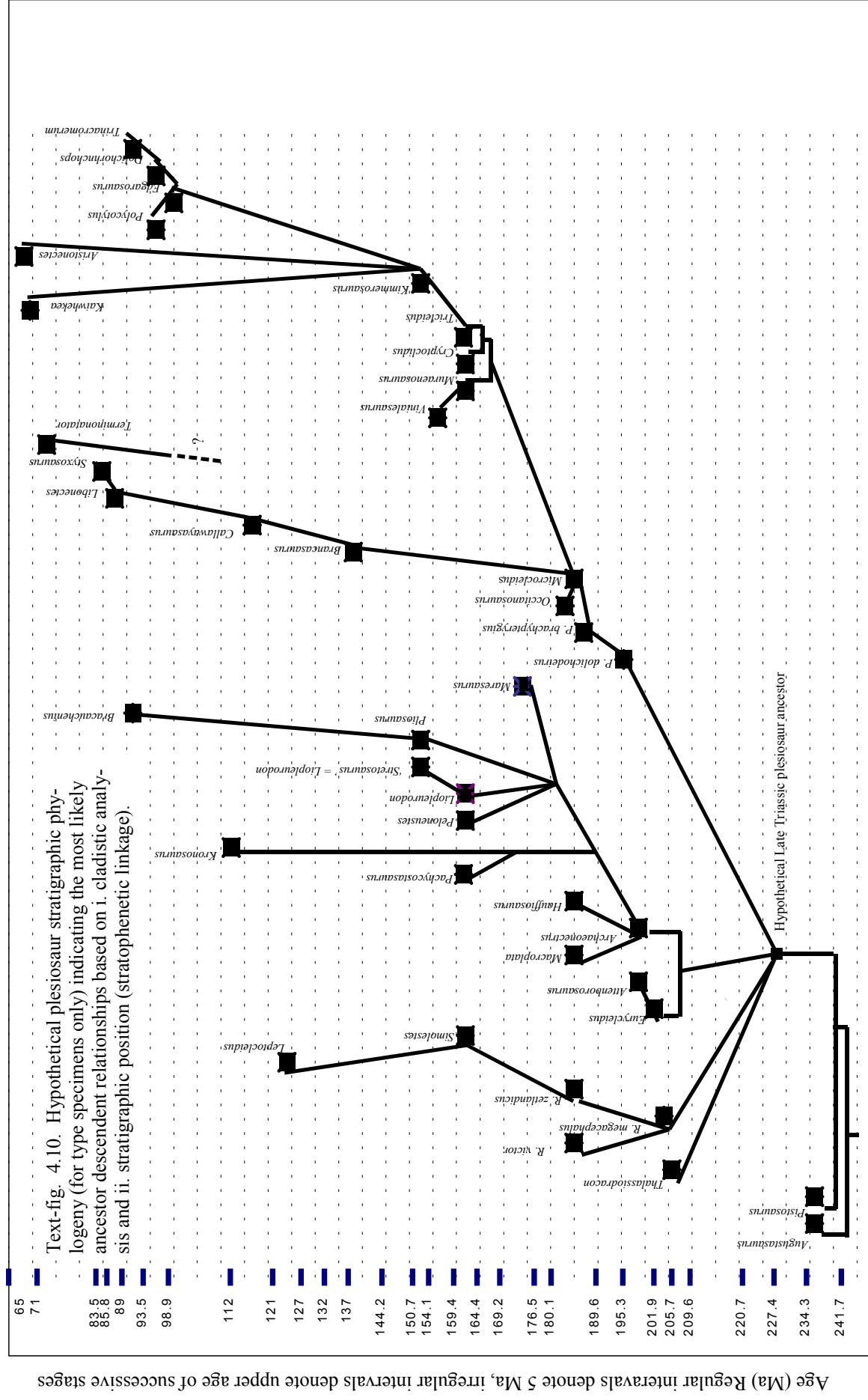
5.3. Stratigraphy and rate of morphologic evolution

All indices calculated to test the fit of phylogeny with stratigraphy are presented in table 2. The plesiosaur lineage has an SCI of 0.62, a level on a par with other accurate phylogenies (Huelsenbeck, 1994) and marginally exceeding the mean SCI for other trees with Mesozoic origins (0.60) (Benton *et al.* 2000). RCI value varies considerably with taxonomic level (general level, -40.9; familial level, 71.1). GER gives higher values (general, 0.78; familial, 0.89), by taking into account maximum possible ghost range. Notably inconsistent taxa include: *Terminonatator* [but see notes added in proof]*, Kaiwhekea* and *Aristonectes, Kronosaurus,* and *Maresaurus.* Analytical estimates of sampling intensity (R_{Ana}) (Wagner, 1998) of Plesiosauria, implicit to this analysis, vary with the size of the stratigraphic sampling unit (table 2). At 5Ma intervals, pliosauroids and plesiosauroids have R_{Ana} of 0.20 and 0.15 respectively, indicating that the pliosauroid record is more completely sampled. All indices make the assumption that the phylogeny is correct.

The average number of character changes occurs at a marginally greater *rate* in pliosauroids relative to plesiosauroids; the gradients are 0.60 and 0.79 respectively (lower gradients imply a more rapid acquisition of characters state changes) (text-fig 4.8.). The rate of character changes varies considerably between families (text-fig 4.9), with Pliosauridae and Polycotylidae exhibiting the greatest rates, with elasmosaurids and especially cimoliasaurids showing slow rates. The same patterns are present on the stratophylogeny (text-fig 4.7) but it is clearer here how the rapid rate of character change at the Jurassic Cretaceous boundary is followed by relative stasis in all surviving clades: Tricleididae (minus Polycotylidae), Elasmosauridae, and some Pliosauridae.

5.4. Cranial versus postcranial data

The character suite is more or less exhaustive and so it is clear that cranial characters are more abundant than postcranial characters (text-fig 4.1). However, the statistics calculated disagree with the observations of Bakker (1993), Carpenter (1997) and Storrs (1999), showing that cranial characters are actually no more reliable in reconstructing phylogenies.

The partition-homogeneity test compared the relative fit of cranial/postcranial characters, to the MPT's they produced when combined. It yielded a P-value of 0.030000 indicating no significant difference (at a 0.05 threshold). Templeton tests comparing the relative goodness of fit between two sets of MPT's (the results of two searches using cranial/postcranial characters respectively) yielded a P-value of 0.0588, a value approaching a significantly better fit of cranial characters to the data. Indeed, there are observable (yet insignificant) differences between the two sets of MPT's, for example in the strict consensus for postcranial characters polycotylids are supported in a pliosauroid position and the clade Brachaucheniidae Williston, 1925 ((*Brach, Kron*)) as accepted by Hampe (1992) and McHenry (pers. comm. 2003) is also recognised but not supported by bootstrap values.

Cladistic indices for sets of MPT's

	Unreduced Unweighted	Reduced Unweighted	Unreduced Weighted	Reduced Weighted
N° of MPT's	17	16	15	4
Length	595	586	554.5	547
CI	0.346	0.352	0.352	0.353
RI	0.652	0.655	0.658	0.660
RC	0.226	0.230	0.231	0.233
HI	0.645	0.648	0.647	0.647

Stratigraphic indices for the final hypothesis of plesiosaur phylogeny (text-fig 4.3)

		Family level	Genus level
SRL (in Ma)	-	562	365
MIG (in Ma)	-	168	893
SCI	0.62	-	-
RCI	-	71.1%	-40.9
G-max (in Ma)	-	460	3530
G-min (in Ma)	-	130	150
GER	-	0.89	0.78
R_{Ana}	5 Ma. = 0.17, 10 Ma = 0.35, 20 Ma = 0.45.		

Table 2. Cladistic and stratigraphic indices indicate tree robustness and fit to stratigraphy.

5.5 Revised diagnoses
Figures in parentheses denote character numbers.

Pistosauria Baur 1887-90
Definition as in Rieppel (2000)
Revised diagnosis: A monophyletic taxon including *Augustasaurus*, *Pistosaurus* and the Plesiosauria.

Plesiosauria de Blainville, 1835
Nasals absent (36); or if present do enter the nares margin (39); lappet of pterygoid underlies quadrate pterygoid flange (59); posterior interpterygoid vacuity present (63); dorsal neural arch height less than centrum height (131); accessory articulations on vertebrae absent (132); postero-lateral coracoid wings typically present (146); contact between pubis and ilium lost (147); ulna broad distally (162); intertrochanteric fossa rudimentary or absent (165); fifth metapodial shifted into distal mesopodial row (170).
Revised definition: A monophyletic taxon including Pliosauroidea and Plesiosauroidea.

Pliosauroidea Welles, 1943
Revised diagnosis: frontal contacts external naris margin (convergent with Cryptocleidoidea) (21); nasal absent (36); prefrontal does not contact external naris margin (40); occipital condyle always hemispherical with groove (44); paraoccipital process articulates with squamosal exclusively (character shared with Cimoliasauridae) (48); posterior bulb typically formed at the squamosal arch apex (56); pterygoids meet between anterior and posterior interpterygoid vacuities (65); ectopterygoid never contacts the postorbital bar (68); cristae ventrolaterales present (75); palatines approach closely or meet at the midline (82); suborbital fenestrae usually present (84); meckelian canal closed on the medial surface of the mandible (89); splenial participates in symphysis but angulars do not extend anterior of symphysis (92); long lingual coronoid process (96); point of jaw articulation usually at collinear with tooth row (100); axis with two ribs (112); cervical ribs usually dicranopleurous (double headed) (121) and centra usually with ventral keel (118); neural spines on cervical vertebrae never possess posterior articulations for the succeeding neural spine (125) but are angled backwards (129); cervical rib articulations and cervical ribs circular in cross section (126).
Revised definition: a monophyletic taxon including *Thalassiodracon*, Rhomaleosauridae and Pliosauridae.

Rhomaleosauridae (Khun, 1961)
Revised diagnosis: distinct groves anterior to external nares (character shared with *Maresaurus*) (38); contact between maxilla and squamosal but no flange as in Polycotylidae (42); paraoccipital process contacts quadrate pterygoid flange at lateral articulation only (convergent with derived elasmosaurids) (50); deep supraoccipital with sigmoid suture between exoccipital and prootic (60); anterior pterygoid vacuity broad with rounded ends (62); pterygoids meet posterior to posterior interpterygoid vacuity and exposed ventrally (convergent with derived pliosauids) (64); parasphenoid with a sharp continuous ventral keel (73); lateral palatal fenestration bordered by palatine and pterygoid (80); bowed mandible (88); ventral mandibular ridge (90); premaxilla and dentary fangs present (103); width of zygapophyses subequal to width of centrum (124); long slender dorsal process of scapulae (136); longitudinal pectoral bar formed by clavicle and coracoid (141); dorsal median foramen in premaxilla ((BMNH(*Zet(Sim,Lept)*)) (13); posterior premaxilla process contacts anterior extension of parietal ((*Zet(Sim,Lept)*)) (12).
Revised definition: a monophyletic taxon including *Rhomaleosaurus victor, R. megacephalus,* unnamed taxon BMNHR.5488, *Rhomaleosaurus zetlandicus, Simolestes* and *Leptocleidus.*

Pliosauridae Seeley, 1974
Revised diagnosis: No contact between external naris margin and premaxilla (13); frontal excluded from dorsal orbit margin (41); quadrate lacks process for articulation with pterygoid flange (52); lappet underlying quadrate pterygoid flange is restricted, margin curved/straight, may meet behind posterior interpterygoid vacuity to form pointed process (59); ectopterygoid and pterygoid form lateral flanges ventro-lateral to posterior pterygoid vacuity (71); dorsal process of scapulae short and broad (136); parasphenoid keeled anteriorly only (73); longitudinal pectoral bar always absent (141).

Revised definition: A monophyletic taxon including *Eurycleidus, Attenborosaurus, Macroplata, Archaeonectrus, Hauffiosaurus, Pachycostasaurus, Kronosaurus, Peloneustes, Liopleurodon* (inc. 'Stretosaurus' *macromerus*), *Pliosaurus, Maresaurus* and *Brachauchenius*.

Unnamed taxon. 1
Diagnosis: Pliosauroids in which the number of maxillary teeth is 20-30 (109) and the humerus shaft is straight and not angled (155).
Definition: A monophyletic taxon including *Macroplata, Archaeonectrus, Hauffiosaurus, Pachycostasaurus, Kronosaurus, Peloneustes, Liopleurodon* (inc. 'Stretosaurus' *macromerus*), *Pliosaurus, Maresaurus* and *Brachauchenius*.

Unnamed taxon. 2
Diagnosis: Pterygoids meet and are exposed ventrally, posterior to posterior interpterygoid vacuity (convergent with Rhomaleosauridae) (64) prominent pterygoid flange or ectopterygoid boss (convergent with Rhomaleosauridae);
 Ectopterygoid and pterygoid form lateral flanges ventro-lateral to posterior pterygoid vacuity, which may meet in midline (71).
Definition: a monophyletic taxon including *Hauffiosaurus, Pachycostasaurus, Kronosaurus, Peloneustes, Liopleurodon* (inc. 'Stretosaurus' *macromerus*), *Pliosaurus, Brachauchenius* and *Maresaurus.*

Unnamed taxon. 3
Humerus relatively longer than femur (6); dorso-median process of premaxilla contacts anterior extension of parietal (12); No notch on squamosal for articulation with paraoccipital process (46); No anterior process on cervical ribs (127); Expanded posterior flange of ischia (convergent with Polycotylidae) (150).
Definition: a monophyletic taxon including *Peloneustes, Liopleurodon* (inc. 'Stretosaurus' *macromerus*), *Pliosaurus, Brachauchenius* and *Maresaurus.*

Unnamed taxon. 4
Diagnosis: Constriction at premaxilla-maxilla suture and second constriction in maxilla (10) no contact between squamosal and postorbital (shared with cimoliasaurids and derived elasmosaurids) (29); robust paraoccipital process (shared with Rhomaleosauridae)(47) parasphenoid keeled anteriorly (71); palatine excluded from the external nares from vomer-maxilla contact (81); foramina subcentralia reduced and laterally positioned or lost in derived forms (123); propodials relatively elongate with narrow distal head (160).
Definition: a monophyletic assemblage including: *Brachauchenius, Pliosaurus, Liopleurodon* (inc. 'Stretosaurus' *macromerus*) and *Maresaurus.*

Plesiosauroidea, Welles, 1943
No constriction at the maxilla-premaxilla suture (10); nasals absent (36); prefrontal contacts margin of external naris (40); cristae ventrolaterales absent (75); palatines do not approach closely or meet at the midline (82); meckelian canal open anteriorly on the medial surface of the mandible (89); usually single axis rib (112); usually no ventral keel on cervical vertebrae (118); parietals fused posteriorly (except *Plesiosaurus dolichodeirus*)(16).

Revised definition: a monophyletic taxon including *Plesiosaurus dolichodeirus, P. brachypterygius, Occitanosaurus* and Euplesiosauria.

Unnamed taxon. 5
Diagnosis: Squamosal produces a long thin process covering the quadrate laterally (27); Columnar ectopterygoid contacts postorbital bar (68); pterygoid boss absent (86); cervical ribs cercidopleurous (single headed) (121); humerus shaft straight (convergent with unnamed taxon occ+) (155); at least two distinct planes on distal end of humerus (157).
Revised definition: a monophyletic taxon including *Occitanosaurus* and the Euplesiosauria).

Euplesiosauria O'Keefe, 2001a
Revised diagnosis: Jugal contacts orbit but is restricted to posterior margin of orbit (31); quadrate pterygoid flange straight and narrowing posteriorly (58).
Revised definition: a monophyletic taxon including Elasmosauridae and Cryptocleidoidea.

Elasmosauridae Cope, 1870
Revised diagnosis: relative length of scapula and coracoid become subequal ((*Call(Lib,Styx)*)) (5); Dorsal process of parietal meets parietal at pineal foramen ((*Lib,Styx*)) (12); Postfrontal excluded from the orbit margin due to frontal-postorbital contact (*(Call(Lib,Styx)*))) (18); frontal enters margin of temporal fenestra ((*Micro(Branc(Call*(-,-)) (19); paraoccipital process contacts quadrate pterygoid flange at lateral articulation only ((*Call(Lib,Styx)*))) (50); caniniform tooth developed on maxilla ((*Lib-Styx*)) (104); number of cervical vertebrae increased and may exceed 50 ((*Call(Lib-Styx)*)), never less than 30 (115); length of cervical vertebrae centra exceeds height (116) zygopophyseal angle changes along cervical vertebral column (117); cervical vertebrae binocular shaped (character convergent with Cimoliasauridae) (120), distinct lateral ridges on cervical vertebrae are present in many taxa but not diagnostic (119).
Revised definition: a monophyletic clade consisting of *Microcleidus, Brancasaurus, Callawayasaurus, Libonectes* and *Styxosaurus*.

Cryptocleidoidea Williston, 1925
Revised diagnosis: coronoid exposed in lateral view (97) (N.B. Although I follow O'Keefe's personal observations for some taxa, in some respects the existing literature seems to contradict those observations concerning this character (e.g. Carpenter, (1997); Brown and Cruickshank, (1994)); prearticular shelf groove (with the exception of *Aristonectes*) (99).
Revised definition: a monophyletic assemblage including paraphyletic Cryptoclididae (*Terminonatator, Vinialesaurus, Muraenosaurus, Cryptocleidus*) and Tricleidea.

Tricleidia O'Keefe, 2001a
Revised diagnosis: reduced basioccipital tubers, parasphenoid and basioccipital contact on the midline, distinct pterygoid median process contacts parasphenoid; clavicle median symphysis separated by scapula and coracoid (138).
Revised definition: a monophyletic taxon including: *Tricleidus*, Cimoliasauridae and Polycotylidae.

Cimoliasauridae Delair, 1959
Revised diagnosis: rostrum unconstricted and hooplike (9); temporal opening extends anterior to posterior orbit margin (20); exoccipital-opisthotic participates in formation of the occipital condyle (43); paraoccipital process articulates with squamosal exclusively (character shared with Pliosauroidea) (48); Coronoid absent (needs verification) (95); teeth tiny and needle-like (105); number of premaxillary teeth seven or more (108); number of maxillary teeth more than 30 (109), number of cervical vertebrae exceeds 40 (115) but length of individual cervical vertebrae does not exceed their height (116); vertebrae are bi-lobed in some members (convergent with Elasmosauridae) (120) but lack the distinct lateral ridges typical of many elasmosaurids (119).
Revised definition: A monophyletic taxon including *Kaiwhekea, Kimmerosaurus* and *Aristonectes.*

Polycotylidae Williston, 1908
Revised diagnosis: maxilla contacts squamosal in an expanded posterior flange (42); pterygoids are dished (69); Splenial participates in symphysis and angulars may extend anteriorly past symphysis (92); Axis rib confined to axis centrum (does not extend onto atlas centrum) (113); Median coracoid perforations (144). Expanded posterior flange of ischium (convergent with some pliosauroids) (150); pisiform and propodial supernumeracies present (167); distal phalanges interlock (170).
Revised definition: A monophyletic taxon including *Edgarosaurus, Polycotylus, Dolichorhynchops* and *Trinacromerum.*

The revised classification does not accommodate the following previously recognised clades, Pistosauridae, Plesiosauridae, and Cryptoclididae. However, there are characters synapomorphic for Cryptoclididae.

Cryptoclididae Williston, 1925
Jugal forms narrow bar between orbit and temporal emargination/ small and vertically orientated (possibly shared with *Kimmerosaurus*) (34); premaxilla enters anterior border of internal nares (83).
Revised definition: paraphyletic assemblage of stem group cryptocleidoids including *Terminonatator, Vinialesaurus, Muraenosaurus* and *Cryptoclidus.*

6. Discussion
The cladogram shape should come as no surprise; there is a significant trend for trees based on palaeontological data to be asymmetrical (Pearson, 2001; Harcourt-Brown *et al.* 2001). Unfortunately, such topologies have taxonomical repercussions in that clades become nested within clades. The cladistic indices offer poor support but this need not imply inaccuracy (Sober, 1983) and here probably reflects high homoplasy as already recognised in the lineage (Bakker, 1993; Storrs, 1993; O'Keefe 2001a, 2002).

6.1 Rogue Taxon - *Eretmosaurus*

Eretmosaurus is something of a rogue taxon in the current analysis (*sensu* Wilkinson 1995). In both the unweighted and weighted analyses, the consensus trees form a significantly unresolved polytomy: this is because *Eretmosaurus* rests with equal parsimony in apomorphic (derived) positions within both the Pliosauroidea (Pliosauridae) and Plesiosauroidea (sister to Cimoliasauridae). This is not entirely surprising, past workers have been in disagreement as to the taxonomic affinities of *Eretmosaurus*. The taxon has been included in:

- Rhomaleosauridae, based on the girdle bones according to Persson (1963).
- Pliosauridae according to Brown (1981).
- Elasmosauridae according to Bardet (1995) and Bardet *et al*. (1999).

The latter authors (Brown and Bardet) give no specific justification for their diagnoses. The holotype lacks a head, so considering that cranial characters make up 63% of the character matrix (text-fig 4.1), the rogue nature of *Eretmosaurus* can be confidently attributed to abundant missing data (Wilkinson, 1995). This hints towards unreliability of postcranial characters. Reduced consensus methods (Thorley and Page, 2000) removed *Eretmosaurus* in two of three reduced trees. Also, a strict consensus of heuristic searches minus *Eretmosaurus,* were more resolved. *Eretmosaurus,* last described by Owen (1865), is here referred to Plesiosauria *incertae sedis* pending revision of this taxon and/or the discovery of more complete, especially cranial material.

6.2. Pliosauroid- plesiosauroid dichotomy and neck length

The pliosauroid-plesiosauroid sisterhood is well supported with Cretaceous elasmosaurid plesiosaurs and cryptocleidoid plesiosaurs (including short-necked polycotylid 'pliosaurs') forming a sister relationship within the typically long-necked plesiosauroid clade. Bakker's (1993) suggestion that Cretaceous elasmosaurid-type plesiosaurs and polycotylid 'pliosaurs' evolved from a common *pliosauroid* (text-fig 2.5) stock is unlikely, although observations of pliosauromorph homoplasticity are confirmed. Similarly, *Attenborosaurus* has an elongate neck (Sollas, 1881) but Persson's (1963) allocation of this taxon to Plesiosauridae is unjustified and the genus is actually pliosauroidean. O'Keefe (2002) discusses the evolution of plesiosaur morphotypes in detail and discusses significant evolutionary trends in the palate, mandible, braincase, and postcranium (2001a).

6.3. Pistosaurid monophyly

Although in all previous cladistic analysis, *Pistosaurus* and *Augustasaurus* (Sander *et al*. 1997; Rieppel *et al*. 2002) unite in a monophyletic family (Pistosauridae), there are not enough synapomorphies to warrant such a relationship in the current analysis. While some MPT's (e.g. strict consensus using cranial data only) ally *Pistosaurus* and *Augustasaurus* with the Plesiosauroidea and hence Plesiosauria due to the presence of posterior interpterygoid vacuities and definite absence of nasals (Rieppel *et al*. 2002), a situation agreeing with some previous authors (e.g. White, 1940; Persson, 1963), the majority of trees followed the existing consensus i.e. pistosaurids as a sister group to the Plesiosauria (Rieppel, 2000).

6.4. Origin of Elasmosauridae

Past estimates of elasmosaurid divergence are Late Jurassic – Early Cretaceous (Persson, 1963) but these are too young. Maisch (1998) suggested "a very early divergence" (p.216) for elasmosaurids if, as advocated by Welles (1943), the quadratojugal was retained. It is not (Carpenter, 1999), nevertheless, the stratigraphic phylogeny (stratophenetic linkage) (text-fig 4.10) and stratophylogeny (text-fig 4.7) show how elasmosaurids diverged and became established early in plesiosaur history, followed by minimal character acquisition. Even Williston (c.1914) noted how the rather intermediate state of elasmosaurids contrasts with their late stratigraphic position. Furthermore, possible elasmosaurid remains have been reported in strata as old as the Triassic-Jurassic boundary (Forrest, 1998), complementing the notion of an early divergence followed by a period of relative stasis.

The earliest diagnostic elasmosaurid is *Microcleidus,* a taxon excluded from Elasmosauridae *sensu* O'Keefe (2001a). *Occitanosaurus* is not an elasmosaurid as proposed by Bardet *et al*. (1999) being primitive in various aspects (see definition of Euplesiosauria, Elasmosauridae, Cryptocleidoidea). It is an unusual that in terms of clade rank (Benton and Storrs, 1994) cryptocleidoids are derived with respect to elasmosaurids, the commonly held view is opposite (Welles, 1943; Benton, 1990a; Bakker, 1993; Carpenter, 1999; Bardet *et al*. 1999).

6.5. Cryptoclidid monophyly

The most recent cladistic analysis of cryptoclidids (Gasparini *et al*. 2002) concluded monophyly (*Tricleidus*, *Cryptoclidus, Vinialesaurus* and *Kimmerosaurus*) supported by three characters: large internal nares, absence of prefrontal, and strongly emarginated cheek. The character 'size of external nares' included by (char. 2 therein) is not adopted here because there is a lack of a significant/quantifiable variation in this character. The identification of the character 'absence of prefrontal' (char. 3 therein) suffers from a poor understanding of the constituent bones of the immediate preorbital region, making the positive dismissal of a prefrontal bone an uncertainty. Monophyly conflicts with the results presented here; Cryptoclididae as traditionally recognised represents a paraphyletic assemblage, or stem group of increasingly apomorphic cryptocleidoids as well as some cimoliasaurids (text-fig 4.4). The most basal cryptoclidid stem here, *Terminonatator*, was previously interpreted as an elasmosaurid (Sato, 2003). Some concern arises from the conflicting stratigraphic position of *Terminonatator* (text-figs 4.5, 4.7 & 4.10) [but see notes added in proof] Benton (2000) notes that classifications are utilitarian. In view of this, the term 'Cryptoclididae' should be retained to formalise this stem group.

6.6. Plesiosaurid monophyly

Previous work has suggested that *Plesiosaurus* is paraphyletic (Bardet *et al*. 1999) and perhaps even polyphyletic (Smith, 2003a, appendix 1) and this analysis agrees with such a paraphyletic relationship. Taxonomic procedure requires that *P. dolichodeirus,* as the type specimen, should retain the generic name and *P. brachypterygius* be allocated a new generic name, should this relationship be confirmed.

6.7. 'Stretosaurus' *macromerus: Pliosaurus or Liopleurodon?*
The species *macromerus* has something of a quirky history. Tarlo (1959) proposed the new genus *Stretosaurus* for *Pliosaurus macromerus,* based on an unusually diagnostic scapula. This was later recognised as a rather un-extraordinary iliac blade (Halstead [Tarlo], 1989) and the species was transferred to *Liopleurodon.* Disagreeing with this diagnosis, Hampe (1992) returned *macromerus* back to *Pliosaurus.* By including the species *macromerus* in this analysis, the '*Liopleurodon* or *Pliosaurus*?' dispute has been resolved. The species *macromerus* is congruent with *Liopleurodon* but not *Pliosaurus.* However, Noè (pers. comm. 2003) considers the species *macromerus* as sufficiently distinct from *Liopleurodon* and it therefore requires further study. Trihedral tooth form, a character shared by *L. macromerus* and contemporary species of *Pliosaurus* is a derived homoplastic character. In fact this character varies within *Pliosaurus* (Tarlo, 1960) and *Liopleurodon* (Halstead, 1971) as currently defined. The young *Liopleurodon rossicus* (Volgian [Tithonian]) also shares trihedral teeth with *L. macromerus*.

6.8. *Kaiwhekea*
Kaiwhekea is not a cryptoclidid as previously proposed (Cruickshank and Fordyce, 2002). The taxon falls most parsimoniously into the Cimoliasauridae. *Kaiwhekea* provides important character information previously absent for diagnosing the Cimoliasauridae because it is the only member of the group known from significant cranial and postcranial material. Synapomorphies uniting *Kaiwhekea* with other Cimoliasaurids include tooth form (small and needle like), number of maxillary teeth and number of premaxillary teeth (seven or more) (this is synapomorphic except for the presence of this state in the pliosaur *Hauffiosaurus*); temporal openings extending anterior to posterior orbit margin. Derived features excluding the taxon from 'Cryptoclididae' include: increasingly robust and weakly excavated cheek region, increased number of cervical vertebrae and vertebrae bi-lobed in outline. Although a long-necked form, *Kaiwhekea* lacks the following synapomorphies typical of elasmosaurids: elongate cervical vertebrae (length greater than height) with lateral ridge (text-fig 3.3), epipodials wider than long, heterodont dentition with maxillary fangs, large horizontal jugal with long straight contact with postorbital. Additionally, the close kinship of *Kaiwhekea* and *Aristonectes* is reflected in their similar provenance, both being Uppermost Cretaceous species with a southern hemisphere distribution.

6.9. Cimoliasauridae
In a recent re-description, Gasparini *et al.* (2003a) place *Aristonectes* within the Elasmosauridae. Removal from Cryptoclididae is justifiable but replacement into the Elasmosauridae is unwarranted and strongly incongruent with the results presented here. One character used by Bardet *et al.* (2003a) to unite *Aristonectes* with elasmosaurids, 'lateral keels on cervical vertebrae' has been identified as "not comparable" (Brown, 1993, p. 14). Here *Aristonectes* is retained in the family Cimoliasauridae as recently reintroduced by O'Keefe (2001a), a clade whose ancestors were more closely related to 'cryptoclidids' than to the earlier diverging elasmosaurids (fig 4.5).

Bi-lobed cervical vertebrae are convergent between members of the Cimoliasauridae (not *Kimmerosaurus*), and Elasmosauridae. This character is also observed in Oligocene Cetacea (Cruickshank and Fordyce, 2002) so convergence should come as no surprise. Nevertheless, the degree of similarity between cervical vertebrae of *Kaiwhekea* and *Aristonectes* is noteworthy (fig 3.3) and can be employed to recognise members of Cimoliasauridae, given that the bi-lobed character occurs alongside vertebrae whose height exceeds length (*contra* Elasmosauridae). Should *Colymbosaurus* resolve to be a synonym of *Kimmerosaurus* (Brown *et al.* 1986; see also table 2) this would compliment the definition of Cimoliasauridae, allying *Kimmerosaurus* and *Kaiwhekea* with a count of cervical vertebrae exceeding 40 (Brown, 1981, 1993; Cruickshank and Fordyce, 2002). Cretaceous Cimoliasaurids have a decidedly southern hemisphere distribution, although the relatively poor cimoliasaurid record should not be overlooked when interpreting distribution. Plesiosaur basicranial remains from Australia, allocated to Elasmosauridae (Kear, 2001) possess an exoccipital-opisthotic that participates in the occipital condyle, herein a synapomorphy of Cimoliasauridae. Indeed, following the revised definition, it seems probable that many indeterminable elasmosaurid specimens, especially from the southern hemisphere (Gasparini *et al.* 2001, fig 3.5 & 6; Wiffen and Moisley, 1986, fig, 34, 35, 51-55; Chatterjee and Small, 1989, fig. 11.) are actually cimoliasaurids.

6.10 Palaeobiogeography and stratophylogeny

The stratophylogeny confirms the observation of a complicated radiation amongst cryptocleidoids (Cruickshank and Fordyce, 1998) but extends it back to the Jurassic-Cretaceous boundary rather than to the Late Cretaceous as therein proposed. The distribution of cimoliasaurids as a primarily southern hemisphere group also implies that the southern hemisphere "was invaded… via the western Tethyan Seaway sometime in Late Jurassic or Early Cretaceous times" (Cruickshank and Fordyce, 1998, p. 50). This would have been via the so-called Hispanic Corridor, which is suggested to explain the similarity between stem-group cryptoclidids in Callovian South American deposits (Gasparini *et al.* 1993) and European deposits. A second corridor to the south of Africa, the Rocas Verdes Seaway, possibly opened up a link between the Tethys and Pacific Oceans during the Jurassic- Cretaceous boundary (Shultz *et al.* 2003).

Thus, a coincidental geographical and evolutionary radiation of cryptocleidoid plesiosaurs occurred at the Jurassic-Cretaceous boundary with polycotylids diversifying worldwide (Sato and Storrs, 2000) and cimoliasaurids and perhaps elasmosaurids (Gasparini *et al.* 2003b) more specifically to the south. The cimoliasaurids show very little change through time (text-fig 4.9) indicating that they met little competition in their specialized feeding guild: all cimoliasaurids share a dentition of small, uniform, interlocking pin-like teeth (the 'trap guild' was proposed (Chatterjee and Small, 1989) and successfully adopted (Martill *et al.* 1994) as an additional guild in Massare's (1987) scheme).

The pliosauroid extinctions during the Cretaceous coincide with the radiation of the mosasauroids, the earliest of which are Turonian (mosasaurids) (Martin and Stewart, 1977) and Late Jurassic (aigialasaurids) (Carroll, 1988) in age. This is significant because there is a considerable overlap between the feeding guilds of mosasaurids and pliosauroids (Massare, 1987) and this may exemplify competitive exclusion. As Cruickshank and Long (1997) point out, "large, open-water, sarcophagous forms [pliosauroids] appear to have died out at the end of the Turonian and are replaced by the mosasaurs". They later point out that "*Leptocleidus* -like forms seem to have been restricted" (Cruickshank and Long, 1997). In fact, even the youngest and most derived rhomaleosaurid (*Leptocleidus*) remains plesiomorphic with respect to pliosaurids (text-fig 4.7). It is possible that these forms sought shelter in near-shore/freshwater habitats away from the domain of the large pliosaurids and perhaps the appearing mosasauroids. Confirmation of fresh-water refugia for rhomaleosaurids comes from sedimentological evidence (Cruickshank, 1997; Sato, 2002; Sato *et al*. 2003). It is also possible that this period of pliosauroid-mosasauroid turnover initiated or contributed to the cryptocleidoid radiation. The pattern is also congruent with Bakker's (1993) observations of Jurassic-Cretaceous and mid-Cretaceous extinctions and re-radiations. The demise of the ichthyosaurs began at the Jurassic-Cretaceous boundary due to biological causes (Lingham-Solier, 2003) and could have encouraged the cryptocleidoid radiation, with polycotylids evolving more or less directly into the open ichthyosaur niche.

6.11 Stratigraphic indices, stratophenetics and phylogenetic trees

The stratophenetically linked phylogenetic tree (text-fig 4.10) is useful for speculating on the nature of possible plesiosaurs not yet known from specimens, for example it appears likely that there was a Late Triassic plesiosaur ancestor, as yet unknown. It is also interesting to create alternative tree topologies but the method is generally crude for organisms with such a poor record. It is clear that the plesiosaur fossil record suffers from biases of various sources: the majority of plesiosaur history is known from taphonomical and geographical windows, most notably the Early and Late Jurassic of Europe (see Tarlo 1960, Brown, 1981,) and the Late Cretaceous of North America (Welles, 1943, Carpenter, 1996, 1999).

An increasing quantity of Lower Cretaceous plesiosaur remains (e.g. Cruickshank, 1997; Carpenter, 1999; Druckenmiller, 2002; Haggart, 2003; Lazo and Cichowolski, 2003) are being discovered and it is only a matter of time before the gaps in the record are filled. The poor RCI value for genera represents bias against low taxonomic levels (Benton and Storrs, 1994), i.e. most genera are known from a single specimen/horizon. The good RCI value at family level and GER values confirm this bias. Generally, the stratigraphy shows a good fit and all indices herein are equal to, or exceed the average (Benton *et al*. 2000). This supports the validity of the cladogram as an accurate reconstruction of plesiosaur interrelationships.

Stratocladistic methods (Fisher, 1994) are claimed to be twice as effective as cladistics in recovering true phylogenies (Fox *et al*. 1999) and have been successfully implemented (Bodenbender and Fisher, 2001). However this *a priori* method of including stratigraphic data prevents independent assessment and falsifiability of the tree with stratigraphy (Benton, *et al*. 1999; Sumrall and Brochu, 2003) and introduces other problems such as the obscuration of character information. This method is therefore not included in the present study.

6.12 Cranial versus post-cranial data

Cranial and postcranial data do support different topologies when used separately, but overall this is insignificant despite the greater abundance of cranial characters. This may reflect the relative completeness of the data: cranial characters such as those of the braincase are often delicate or obscure (personal observation). This study shows that the only way of determining a phylogeny accurately, involves a combination of cranial and postcranial characters.

7. Conclusions

- The largest cladistic analysis of plesiosaurs to date is performed confirming the validity of five plesiosaur families, Rhomaleosauridae, Pliosauridae, Elasmosauridae, Cimoliasauridae and Polycotylidae.
- Pistosauridae, Plesiosauridae and Cryptoclididae are recognised as paraphyletic assemblages.
- A distinct dichotomy within Plesiosauria, into pliosauroids and plesiosauroids is confirmed.
- The taxonomic affinity of several genera is determined cladistically for the first time, *Kaiwhekea* is re-identified as a cimoliasaurid, *Terminonatator* is re-identified as a stem-group cryptocleidoid [but see note added in proof], *Maresaurus* is identified as a pliosaurid, and *Pachycostasaurus* and *Archaeonectrus* are confirmed as pliosaurids whereas *Eretmosaurus* is a rogue taxon and is allocated to Plesiosauria *incertae sedis*.
- The taxonomic position of some taxa differs from previous cladistic analyses, *Occitanosaurus* is re-identified as a sister taxon to Euplesiosauria, *Microcleidus* is included within the Elasmosauridae, *Vinialesaurus* is part of stem-group cryptocleidoids, and *Eurycleidus* and *Attenborosaurus* are included in Pliosauridae.
- *'Stretosaurus' macromerus* is a determined to be more likely a species of *Liopleurodon* rather than *Pliosaurus*.
- A method of combining total character change data and stratigraphic data is applied to plesiosaurs indicating that rate of character change evolution was roughly equal in the two superfamilies.
- A Late Jurassic - Early Cretaceous event in plesiosaur history is represented by rapid diversification (within Cryptocleidoidea) and extinction (amongst Pliosauroidea) and can be attributed to palaeobiogeographical activities and the appearance of new top predators including the mosasaurs.
- The cryptocleidoid radiation can be attributed to the demise of the ichthyosaurs during the Early Cretaceous.
- The long stratigraphic duration of plesiomorphic rhomaleosaurids can be explained by their occupancy of secluded freshwater habitats.
- Cranial characters are more abundant but are not significantly more reliable than postcranial characters in determining the phylogeny of plesiosaurs.
- The hypothesis of plesiosaur phylogeny shows a convincing fit with stratigraphy adding confidence to its accuracy.

8. Future possibilities

Numerous new specimens and novel taxa from around the world are in preparation or awaiting publication. A new plesiosaur of possibly elasmosaurid affinities (Forrest, pers. comm.), recently unearthed from Speeton, UK, awaits preparation and a second new taxon from the UK is under current investigation by Mark Evans but remains undisclosed for the time being (Evans, pers. comm.). A very recently described cryptocleidoid plesiosaur from America is in press (O'Keefe pers. comm. 2003). The so-called 'Monster of Aramberri', from the Kimmeridgian of Mexico appears to be a novel pliosaurid taxon (Frey *et al.* 2001) but diagnosis awaits further study/relocation of lost material (Buchy *et al.* 2003). A new specimen *cf. Leptocleidus superstes* from the English Wessex Basin (Turner pers. comm. 2003) may shed further light on rhomaleosaurid characteristics. Specimens from the Maastrichtian of Chile include an almost complete specimen of a plesiosauroid (Suarez and Smith, in press). New plesiosaur material from the Portlandian (uppermost Jurassic) of Lincolnshire (Forrest and Oliver, in press) is stratigraphically important but of little use in cladistics (Oliver pers. comm. 2003). Specimens of adult plesiosauroids with foetuses in the abdomens awaiting description from the Upper Cretaceous of Kansas (Everhart, pers comm. 2003) are the first real evidence of viviparity in plesiosaurs and will provide valuable information on ontogeny and thus the importance of certain characters in phylogeny. Future analyses should incorporate all of these additional taxa/specimens.

It is important to point out that the bulk of this study is based on existing literature and future analysis should incorporate direct observation of specimens to ensure uniform interpretation. The cladistic statistics and indices are useful internally but without objective meaning "do not offer a test against reality" (Benton *et al.* 2001. p. 581). Whilst simulation studies may in the future allow controls for comparison of indices, these only exist for microorganisms on the "scales of months rather than millennia" (Hillis, 1995) and as Huelsenbeck (1995) notes, it may be impossible to overcome the biases inherent in such studies. The method of combining character change and stratigraphic data into 'stratophylogenies' can easily be applied to any group of organisms.

Phylogenetic trees and taxon ranges will become evermore complete as sampling continues (Benton, 1994), especially at rates implied here (text-fig. 2.1). This will enable future hypotheses and subsequent interpretations to gain greater robustness and support. Unfortunately all reports of extant plesiosaurs are unsubstantiated (Kuban, 1997) so molecular or soft-part data is unobtainable for the group at hand.

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Appendix 1 - Abstract from Smith (2003b)

ABSTRACT. A concise phylogenetic hypothesis concerning the interrelationships between 11 plesiosaur taxa is re-evaluated and subjected to various statistical tests. The revised results contrast with those in the original analysis in numerous aspects, most notably in terms of tree length: the revised tree is actually longer by eleven steps. The results question the taxonomic affinity of the genus *Thalassomedon* and the monophyly of the genus *Plesiosaurus*. Partition homogeneity tests fail to identify greater reliability of cranial or post-cranial characters. The finalised consensus tree is presented as a phylogram and compared against a stratigraphic background, illustrating a convincing fit. Clade synapomorphies are tentatively proposed based on character tracing, however, it is recommended that further analyses to include an expanded range of characters and taxa be undertaken before these hypotheses be fully accepted. The data set as it stands is insufficient to make any robust conclusions.

Appendix 2 - List of characters

CHARACTER	STATES & CODING	CITATION
1. Relative skull length	Basal ('nothosaurian) =0, large =1, Small =2	Brown (1981), char. 2; O'Keefe (2001), char. 1
2. Relative neck length	Basal = 0, elongate =1, short =2	Storrs (1991), char. 2; O'Keefe (2001), char. 2
3. Relative size of orbit/postemporal fenestra	Subequal =0, orbit larger =1, fenestra larger =2	Bardet *et al.* (1999) char. 5
4. Relative length of ischium/pubis	Subequal =0, ischium longer =1, pubis longer =2	Brown (1981), char 29; O'Keefe (2001), char. 3
5. Relative length of scapula/coracoid	Subequal =0, coracoid longer =1	Welles, 1962; O'Keefe (2001), char.4
6. Relative length of humerus/femur	Subequal =0, humerus longer =1, Femur longer =2	Brown, 1981, char.32; Bardet *et al.* (1999), char. 28; O'Keefe (2001), char. 5
7. Preorbital and postorbital skull length	Subequal =0, preorbital longer =1, preorbital shorter =2	O'Keefe (2001), char. 6
8. Fin aspect ratio	High =0, low =1	O'Keefe (2001), char. 7
9. Elongate rostrum	Absent =0, premaxilla only =1, very long and including maxilla, =2, unconstricted, elongate and hoop-like =3.	O'Keefe (2001), char. 8
10. Consricted snout at premaxilla-maxilla suture	Unconstricted =0, constricted =1, additional constriction in maxilla =2	Storrs, 1991, char. 13; O'Keefe (2001), char. 9
11. Temporal emargination	Strong =0 Weak =1	Modified from Storrs (1991), char 6; Brown and Cruickshank (1994); Bardet *et al.* (1999), char. 4; O'Keefe (2001), char.10; Gasparini *et al.* (2002), char. 4
12. Dorso-medial process of premaxilla	Contacts forntal =0, contacts anterior extension of parietal =1, contacts parietal and pineal foramen =2	Carpenter (1999), char. 8; modified from Bardet *et al.* (1999), char. 9; O'Keefe (2001), char. 11
13. Premaxilla/external naris contact	Present =0, absent =1	O'Keefe (2001), char. 12
14. Dorsal median foramen in premaxilla	Absent =0, present =1	O'Keefe (2001), char. 13. modified from Cruickshank (1997)
15. Frontals paired/fused in adult	Paired =0, fused =1	O'Keefe (2001), char. 14
16. Parietals paired/fused in adult	Paired =0, fused posteriorly =1, fused =2	O'Keefe (2001), char. 15
17. Frontals with or without distinct postero-lateral process	Without process =0, with process =1	Storrs (1991), char. 30; O'Keefe (2001), char. 16

18. Postorbital bar	Both postorbital and postfrontal contact orbit margin =0, postfrontal excluded by frontal/postorbital contact =1	O'Keefe (2001), char. 17
19. Frontal enters margin of temporal fenestra	Does not contact =0, does contact =1	O'Keefe (2001), char. 18
20. Temporal opening extends anterior to posterior orbit margin.	Absent =0, present =1	New character
21. Frontal contacts external naris	Does not contact =0, does contact =1	Modified from O'Keefe (2001), char. 19
22. Pineal foramen location	Middle of parietal =0, anterior of parietal =1	Sues, 1987; Modified from Bardet *et al*. (1999), char. 10; O'Keefe (2001), char. 20
23. Pineal foramen bordered anteriorly by frontals on dorsal skull surface	Not bordered by frontal =0, bordered by frontal =1	O'Keefe (2001), char. 21
24. Accessory fenestra above orbits	Absent =0, present =1	Carpenter (1996); O'Keefe (2001), char. 23
25. Frontal process projects into orbit	Absent =0, present =1	Carpenter (1996); O'Keefe (2001), char. 24
26. Parietal skull table	Unconstricted =0, constricted =1, sagittal crest =2	Brown (1981); O'Keefe (2001), char. 25
27. Squamosal produces long, thin process covering quadrate laterally	Absent =0, present=1	Carpenter, 1996; O'Keefe (2001), char. 26
28. Squamosal dorsal processes meet at midline	Do not meet =0, meet in arch =1	Sues (1987); O'Keefe (2001), char. 27
29. Squamosal/postorbital contact	Contact =0, no contact =1	O'Keefe (2001), char. 28
30. Jugal/squamosal contact	No contact =0, contact =1	O'Keefe (2001), char. 29
31. Jugal extends anteriorly along ventral orbital margin	Reaches anterior margin =0, reaches middle of orbit =1, restricted to posterior margin =2. Code taxa as 'x' if character 32 (below) shows a positive state.	Modified from Storrs (1991) char 24 and O'Keefe (2001), char. 30
32. Jugal contacts orbit margin	Contacts orbit =0, excluded from orbit =1.	Modified from Storrs (1991) char 24; Bardet *et al*. (1999), char.3; O'Keefe (2001), char. 31.
33. Jugal/prefrontal suture anterior to orbit	Absent =0, present =1	O'Keefe (2001), char. 32.
34. Jugal forms narrow bar between orbit and temporal emargination and/or is small and vertically orientated	Absent =0, present =1	Modified from Bardet *et al*. (1999), char. 1; O'Keefe (2001), char. 33
35. Quadratojugal	Present =0, absent =1	Storrs (1991), char. 7; Sues (1987); O'Keefe (2001), char. 34

36. Nasal	Not reduced =0, reduced =1, absent =2	Storrs (1991), char. 34; Sues (1987); Carpenter (1999), char. 1; O'Keefe (2001), char. 35
37. Location of nasal relative to external nares	Posterior to external nares =0 anterior to external nares	O'Keefe (2001), char. 36
38. Distinctive grooves anterior to external nares	Absent =0, present =1	O'Keefe (2001), char. 37
39. Nasal enters margin of external naris	Enters margin =0 excluded from margin =1	Storrs (1991), char. 36; Sues (1987); O'Keefe (2001), char. 38.
40. Prefrontal contacts margin of external naris	No contact =0, contact =1	O'Keefe (2001), char. 39
41. Frontal excluded from dorsal orbit margin	Excluded from margin =0, enters margin =1	Modified from O'Keefe (2001), char. 40
42. Maxilla/squamosal contact	No contact =0, contact =1, expanded posterior flange =2	O'Keefe (2001), char. 41
43. Exoccipital participates in formation of occipital condyle	Do not participate =0, do participate =1	Brown (1981), char. 7; Cruickshank (1994); Bardet *et al.* (1999), char. 14; O'Keefe (2001), char. 42; Gasparini *et al.* (2002), char. 7.
44. Occipital condyle morphology	Hemispherical with groove =0, short with no groove =1	Brown (1981), char. 12; O'Keefe (2001), char. 43
45. Paraoccipital process/ formation of posttemporal fossa margin	No process =0, process =1	Rieppel (1997b), char 31; O'Keefe (2001), char. 44
46. Distinct squamosal notch for articulation of paraoccipital process	Absent =0, present =1	Rieppel (1997b), char 32; O'Keefe (2001), char. 45
47. Paraoccipital process morphology	Gracile =0, robust =1	Brown (1981), char. 11; O'Keefe (2001), char. 46
48. Paraoccipital process articulation	Squamosal exclusively =0, quadrate exclusively =1, both squamosal and quadrate =2	O'Keefe (2001), char. 47
49. Ventral extent of paraoccipital process	Do not extent ventrally past the occipital condyle =0, extend past condyle =1	O'Keefe (2001), char. 48
50. Nature of paraoccipital process/ quadrate pterygoid flange contact	No contact =0, contact at lateral articulation only =1, long contact along process bodies =2	O'Keefe (2001), char. 49
51. Quadrate flange of pterygoid/quadrate articulation	Quadrate flange articulates with quadrate only =0, articulates with quadrate and squamosal =1	Modified form Brown (1981), char. 10; Cruickshank, 1994b, char. 3; O'Keefe (2001), char. 50
52. Quadrate with process for	No process =0, process present =1	O'Keefe (2001), char. 51

articulation with pterygoid flange		
53. Dorsal wing of epipterygoid	Broad columnar =0, reduced =1	Rieppel (1997b), char 39; O'Keefe (2001), char. 52
54. Epipterygoid dorsal process contacts parietal	Contact =0, no contact =1	O'Keefe (2001), char. 53
55. Quadrate embayed/ dished shaped anteriorly	Massive quadrate =0, dished anteriorly =1	O'Keefe (2001), char. 54
56. Posterior bulb formed at the squamosal arch apex	Absent =0, present =1	O'Keefe (2001), char. 55
57. Supraoccipital morphology	Round =0, median process =1	O'Keefe (2001), char. 56
58. Shape of the quadrate pterygoid flange	Curved with raised lateral margin =0, straight and narrowing posteriorly =1, large and sigmoid with rolled margin =2	O'Keefe (2001), char. 57
59. Squared lappet of pterygoid underlies quadrate pterygoid flange	Absent =0, extensive flanges form large plate, margin with postero-lateral corners =1, restricted flange, margin curved/straight, may meet behind posterior interpterygoid vacuity to form pointed process =2	Modified from O'Keefe (2001), char. 58
60. Supraoccipital depth/sigmoid suture	Shallow =0, deep antero-posteriorly with a sigmoid suture between exoccipital and prootic =1	O'Keefe (2001), char. 59
61. Foramen incisivum (premaxillary fenestrae, vomeronasal fenestra).	Absent =0, Present =1	New character. Carpenter (1996, 1997, 1999 (char. 7); modified from Gasparini *et al*. (2003), char. 10
62. Anterior interpterygoid vacuity	Absent =0, slit like =1, broad with rounded ends =2	Modified from Bardet *et al*. (1999), char. 13; O'Keefe (2001), char. 60; Modified from Gasparini *et al*. (2002), char. 6
63. Posterior interpterygoid vacuity	Absent =0, present =1	Storrs (1991), char. 11; Sues, 1987; O'Keefe (2001), char. 61
64. Pterygoids meet posterior to posterior interpterygoid vacuity	Do not meet =0, do meet =1, meet but are covered by posterior parasphenoid process =2	Modified from Bardet *et al*. (1999), char. 12; O'Keefe (2001), char. 62
65. Pterygoids meet between anterior and posterior interpterygoid vacuities	Do not meet =0, meet =1	O'Keefe (2001), char. 63
66. Basioccipital exposed posterior to posterior pterygoid suture	Exposed =0, not exposed =1	Carpenter (1999), char.3; O'Keefe (2001), char. 64
67. Ectopterygoid reaches medially to lateral margin of posterior interpterygoid vacuities	Does not =0, does =1	O'Keefe (2001), char. 65
68. Columnar ectopterygoid contacts postorbital bar	No contact =0, contact =1	O'Keefe (2001), char. 66

69. Dished pterygoids	Absent =0, present =1	O'Keefe (2001), char. 67
70. Posterior pterygoid/parasphenoid contact	Absent =0, distinct pterygoid median process forms contact =1	O'Keefe (2001), char. 68
71. Ectopterygoid and pterygoid form lateral flanges ventro-lateral to posterior pterygoid vacuity	Do not =0, form flanges =1, flanges meet in short dished contact at midline =2 meet in broad contact =3	O'Keefe (2001), char. 69
72. Parasphenoid morphology	Long tapering anteriorly =0, short and blunt =1	O'Keefe (2001), char. 70
73. Parasphenoid keel	No keel =0, sharp keel =1, keeled anteriorly =2.	Modified from Carpenter (1999), char. 5.; O'Keefe (2001), char. 71
74. Parasphenoid exposure anterior to posterior interpterygoid vacuities	Anterior parasphenoid not exposed on palate surface =0, exposed via extension of posterior interpterygoid vacuities =1, exposed with lateral pterygoid sutures =2	O'Keefe (2001), char. 72
75. Possession of cristae ventrolaterales	Present =0, absent =1	O'Keefe (2001), char. 73
76. Parasphenoid/basiocciput contact on midline	Absent =0, present =1	O'Keefe (2001), char. 74
77. Possession of basal articulation (between basisphenoid and pterygoid)	Present =0, absent =1	O'Keefe (2001), char. 75
78. Basioccipital tubers reduced	Not reduced =0, reduced/ tuber facets confluent with basisphenoid articulation =1	O'Keefe (2001), char. 76
79. Jugal has small exposure on palate surface	No exposure =0, exposure =1	O'Keefe (2001), char. 77
80. Lateral palatal fenestration bordered by palatine and pterygoid	Absent =0, present =1	O'Keefe (2001), char. 78
81. Palatine/ internal naris	Palatine enters internal nares border =0, excluded by vomer-maxilla contact =1	O'Keefe (2001), char. 79
82. Palatines approach closely or meet at the midline	Do not meet =0, closely approach or meet on midline =1	O'Keefe (2001), char. 80
83. Premaxilla/anterior border of internal naris	Premaxilla enters anterior border =0, is excluded by vomer-maxilla contact =1	Rieppel (1994a, 1997b) chars. 35, 45; O'Keefe (2001), char. 81
84. Sub-orbital fenestration	Absent =0, present =1	Storrs (1991), char. 9; O'Keefe (2001), char. 82
85. Vomers extend far posterior to internal nares midline	Do not =0, extent posteriorand meet pterygoids in wide	O'Keefe (2001), char. 83

	interdigitating suture =1	
86. Prominent 'pterygoid flange'/ectopterygoid boss	Absent = 0, present =1	Rieppel, (1994a, 1997b) chars. 35, 44; Storrs, 1997; O'Keefe (2001), char. 84
87. Ectopterygoid boss has wide contact with jugal/squamosal	Contact absent =0, contacts jugal =1	O'Keefe (2001), char. 85
88. Bowed mandible	Absent = 0, present =1	Modified from O'Keefe (2001), char. 86
89. Meckelian canal open anteriorly	Closed =0, open =1	O'Keefe (2001), char. 87
90. Ventral mandibular ridge/ pedestal like symphysis	No ridge =0, ridge =1	O'Keefe (2001), char. 88
91. Mandibular symphysis	Short =0, somewhat enforced =1, scooplike =2, long =3	Tarlo, (1960); Brown (1981), char 5; O'Keefe (2001), char. 89
92. Splenial participates in symphysis	Does not =0, participates =1, angulars extend past symphysis =2	O'Keefe (2001), char. 90
93. Lingual mandibular fenestra	Absent =0, present =1	O'Keefe (2001), char. 91
94. Mophology of dentary/ angular-surangular suture	Angular projects forward of surangular in lateral view =0, surangular anterior process =1	O'Keefe (2001), char. 92
95. Coronoid	Present =0, absent =1	Cruickshank (1994b), char 9. O'Keefe (2001), char. 93
96. Coronoid process	Absent =0, long and lingual =1, high and narrow =2	Modified from O'Keefe (2001), char. 94 and Gasparini *et al*. (2003) char. 12
97. Coronoid eminence on lateral jaw surface	No eminence =0, eminence =1	Modified from O'Keefe (2001), char. 95
98. Prearticular	Present =0, absent =1	Cruickshank (1994b), char 9. O'Keefe (2001), char. 96
99. Prearticular shelf/groove	Absent =0, present =1	O'Keefe (2001), char. 97
100. Jaw articulation in relation to tooth row	Above or at collinear with toothrow =0, lower than tooth row =1	O'Keefe (2001), char. 98; Gasparini *et al*. (2003), char . 11
101. Diastemma at maxilla/premaxilla suture	Absent =0, present =1	Modified from Storrs (1991), char. 37; O'Keefe (2001), char. 99
102. First tooth after diastema	Large =0, reduced =1	Modified from Carpenter (1999) char. 10 and Bardet *et al*. (1999), char. 17; O'Keefe (2001), char. 100
103. Premaxilla and dentary fangs	Absent =0, present =1	Brown (1981), char. 8; Storrs (1991), char. 39; Rieppel (1994a, 1997b) chars. 44, 55; modified from Bardet *et al*. (1999), char. 17; O'Keefe (2001), char. 101

104. One or two caniniform teeth on maxilla	Absent =0, present =1	Rieppel (1994a, 1997b) chars. 45, 56; Storrs (1991), char. 41; O'Keefe (2001), char. 102
105. Tooth form	Gracile, small root, narrow =0, robust, large root =1, very small/needle like =2	Brown, 1981, char 3. Tarlo (1960), O'Keefe (2001), char. 103
106. Teeth round or with reinforced planar face/trihedral	Round =0, planar face/trihedral =1	Tarlo (1960); O'Keefe (2001), char. 104
107. Longitudinal striations on teeth	Striations all around =0, striationa lingually only =1, none =2	Tarlo (1960); Modified from Bardet *et al.* (1999), char. 18; Keefe (2001), char. 105; Modified from Gasparini *et al.* (2002), char. 9.
108. Number of premaxillary teeth	5 =0, 6=1, 7 =2, >7 =3	Brown (1981) char. 7; Cruickshank (1994b), char. 1; Bardet *et al.* (1999), char. 15; Carpenter (1999), char. 11; O'Keefe (2001), char. 106; Gasparini *et al.* (2002), char. 8.
109. Number of maxillary teeth	<20 =0, 20-30 = 1, >30 = 2	Cruickshank (1994b), char. 1; O'Keefe (2001), char. 107
110. Maxillary teeth extend posterior of orbit	Present =0, absent =1	New character
111. Number of Dentary teeth	20-30=0, <20=1, >30=2.	New character. Modified from Bardet *et al.* (1999), char. 16
112. Number of axis rib heads	2 =0, 1 =1	O'Keefe (2001), char. 108
113. Articulation of axis rib	broad articulation including contact with atlas centrum =0, head confined to axis centrum =1	O'Keefe (2001), char. 109
114. Atlas-axis morphology	No lateral exposure of atlus centrum on cup face =0, lateral exposure =1, no lateral exposure but atlas and axis intercentra exclude atlas centrum ventrally =2	Brown (1981), char. 13; O'Keefe (2001), char. 110
115. Number of cervical vertebrae	Primitive =0, increased = 1, reduced =2, greater than 50 =3	Brown (1981), char 14; modified from Bardet *et al.* (1999), char. 19 and Carpenter (1999), chars. 12, 13, 14 & 15; O'Keefe (2001), char. 111
116. Proportions of cervical centra	Length and height subequal =0, length exceeds height =1 length less than height =2	Brown (1981), char. 15; Bardet *et al.* (1999), char. 10; O'Keefe (2001), char. 112
117. Distinct change in zygopophyseal angle along cervical column	No change in angle =0, change =1	O'Keefe (2001), char. 113
118. Ventral keel on cervical vertebrae in adults	Absent = 0, present =1	Tarlo (1960), O'Keefe (2001) char. 114
119. Lateral ridge on anterior cervical vertebrae in adults	Absent =0, present =1	Brown (1981) char.16; Bardet *et al.* (1999), char. 22; Carpenter (1999),

		char. 17; O'Keefe (2001), char. 115
120. Binocular shaped anterior cervical centra	Absent =0, present =1	Welles (1943), Bardet *et al.* (1999), char. 23, O'Keefe (2001), char. 116
121. Number of cervical rib heads	Dicranopleurus (two) =0 Cercidopleurus (one) =1	Persson (1963); Sander *et al.* (1997); Brown (1981) char 21 O'Keefe (2001), char. 117
122. Ventral foramina (foramina subcentralia) in cervical vertebrae	Absent =0, present =1, lost =2	Sander *et al.* (1997); Storrs (1991), char. 47; O'Keefe (2001), char. 118
123. Foramina subcentralia reduced and lateral	Medial and large =0, lateral and reduced =1	Tarlo (1960); O'Keefe (2001), char. 119
124. Width of cervical zygopophyses	Wider than centrum =0, subequal with centrum =1, more narrow than centrum =2	Sander *et al.* (1997); Storrs (1991,) char. 48; O'Keefe (2001), char. 120
125. Posterior articulation for succeeding neural spine, cervical vertebrae	Absent =0, present =1	O'Keefe (2001), char. 121
126. Cervical rib articulation greatly elongate/ cervical ribs expanded and blade like	Circular or subcircular =0, elongate =1	O'Keefe (2001), char. 122
127. Anterior process of cervical ribs	Present =0, absent =1	Sander *et al.* (1997), Storrs (1997); O'Keefe (2001), char. 123
128. Anterior neural flange on cervical neural spines	Absent =0, present =1	O'Keefe (2001), char. 124
129. Neural spines, cervical vertebrae	Angled backwards =0, not angled backwards =1	Brown (1981), char. 20; O'Keefe (2001), char. 125
130. Distal end of transverse processes, dorsal vertebrae	No diameter increase =0 thickened/flared =1	O'Keefe (2001), char. 126
131. Dorsal neural arch height	Subequal to centrum height =0, shorter than centrum height =1	Sander *et al.* (1997); O'Keefe (2001), char. 127
132. Zygosphene/ zygantrum accessory articulations	Present =0, absent =1	Sander *et al.* (1997); O'Keefe (2001), char. 128
133. Height of neural spines, dorsal vertebrae	Low =0, low and rugose, =1, high =2	Sander *et al.* (1997); O'Keefe (2001), char. 129
134. Lateral compression of dorsal spines	Not compressed =0, compressed and blade-like =1	Sander *et al.* (1997); O'Keefe (2001), char. 130
135. Interclavicle posterior process	Present =0, absent =1	Storrs (1991), Char. 58; O'Keefe (2001), char. 131
136. Dorsal process of scapulae	Long slender =0, short and broad =1, distally expanded =2	Modified from O'Keefe (2001), char. 132

137. Presence of clavicles and interclavicles	Present=0, interclavicle absent =1, both absent=2	Brown (1981); O'Keefe (2001), char. 133
138. Clavicle median symphysis	Symphysis =0, separated by interclavicle =1, meet only behind notch =2	O'Keefe (2001), char. 134
139. Scapulae meet in anterior median symphysis	Separated by clavicles/interclavicles =0, meet medially but leave a notch for dermal elements =1, meet in long symphysis without notch =2	Brown (1981), char 4; Bardet *et al.* (1999) char. 24; O'Keefe (2001), char. 135
140. Anterior intrascapular fenestra	Absent =0, present =1	O'Keefe (2001), char. 136
141. Longitudinal pectoral bar	Absent =0, formed by clavicle and coracoid =1, formed by scapular and coracoid =2	Storrs (1991), char. 66; Brown (1981), char. 25; modified from Carpenter (1999), chars. 18 & 19; O'Keefe (2001), char. 137
142. Supracoracoid foramen/ notch	Present =0, absent =1	Storrs (1991), char 64; O'Keefe (2001), char. 138
143. Coracoid shape	Rounded contours/ not plate-like =0, expanded median symphysis =1	Storrs (1991), char 63; O'Keefe (2001), char. 139
144. Median coracoid perforations	Absent =0, present =1	O'Keefe (2001), char. 140
145. Posterior coracoid extention with deep median embayment (intercoracoid foramen)	Absent =0, present =1	Brown (1981), char. 27; Bardet *et al.* (1999), char. 27; O'Keefe (2001), char. 141
146. Posterio-lateral coracoid wing (cornua)	Absent = 0, present =1	Brown (1981), char. 26; Bardet *et al.* (1999), char. 25; O'Keefe (2001), char. 142
147. Contact between ilium and pubis	Present =0, absent =1	Storrs (1991) char 68; Sues (1987); O'Keefe (2001), char. 143
148. Pubis ventral (medial) margin	Concave =0, convex =1	Storrs (1991) char. 69; Brown (1981) char. 28; O'Keefe (2001), char. 144
149. Large, ventral pubo-ischiatic plate	Absent =0, present =1	Sues (1987); O'Keefe (2001), char. 145
150. Ischia shape: expanded posterior flange	Absent = 0, present =1	New character. Modified from Tarlo (1960)
151. Median pelvic bar	Absent =0, present =1.	Brown (1981), char. 30; Carpenter (1999), char. 20; O'Keefe (2001), char. 146
152. Thyroid fenestra closed or open in adult	Closed =0, open =1	Storrs (1991), char. 71; O'Keefe (2001), char. 147
153. Obturator foramen	Present =0, absent =1	Storrs (1991), char. 70; O'Keefe (2001), char. 148
154. Iliac blade	Well developed =0, reduced =1	Storrs (1991), char. 67; Brown (1981), char. 31; Sues (1987); O'Keefe (2001),

		char. 149
155. Angled humerus	Present =0, absent =1	Storrs (1991), char. 73; O'Keefe (2001), char. 150
156. Expanded distal propodials with dorsal trochanter/ tuberosity	Absent =0, present =1	O'Keefe (2001), char. 151
157. Distal end of humerus has two distinct planes in adult	Absent =0, present =1	O'Keefe (2001), char. 152
158. Distinct facet on distal humerus for supernemery ossification	Absent =0, present =1	O'Keefe (2001), char. 153
159. Gracile or massive	Gracile/constricted =0, massive =1	Brown (1981), char. 32; O'Keefe (2001), char. 154
160. Propodials relatively elongate	Not elongate =0, elongate with narrow distal head	O'Keefe (2001), char. 155
161. Deltopectoral crest	Present =0, absent =1	O'Keefe (2001), char. 156
162. Ulnar shape	Narrow distally =0, broad distally =1	Sander *et al*. (1997); Storrs (1991), char. 83; O'Keefe (2001), char. 157
163. Distinctly lunate ulna	Absent =0, present =1	O'Keefe (2001), char. 158
164. Internal trochanter	Well developed =0, reduced =1	O'Keefe (2001), char. 159
165. Inter-trochanteric fossa	Deep =0, distinct but reduced =1, rudimentary or absent =2	O'Keefe (2001), char. 160
166. Epipodial morphology	Longer than broad =0, equal or broader than long =1	Brown (1981), char. 35; Sues (1987); O'Keefe (2001), char. 161
167. Supernumeracy ossifications, forelimb	None =0, epipodial row/pisiform =1, propodial =2, both =3	Modified from Storrs (1991), char. 84, Brown (1981), char. 37; O'Keefe (2001), char. 162
168. Fifth metapodial	In line with metapodial row =0, shifted into distal mesopodial row =1	Brown (1981), char. 37; O'Keefe (2001), char. 163
169. Hyperphalangy	No increase =0, present =1	Storrs (1991), char. 80; O'Keefe (2001), char. 164
170. Interlocking distal phalanges anterior to fifth phalangeal row	Absent =0, present =1	O'Keefe (2001), char. 165
171. Median gastral rib element	Always one =0, sometimes two = 2	O'Keefe (2001), char. 166

Appendix 3 - data matrix

Character Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Cymatosaurus	0	?	0	?	?	?	2	x	0	1	1	0	?	0	0	2	1	0	1	0	?
Archaeonectrusrostratus	1	0	0	0	?	2	1	1	2	0	1	?	?	1	?	x	?	0	?	0	?
Aristonectesparvidens	?	?	?	?	?	?	1	?	3	0	1	?	?	?	?	?	1	?	?	1	1
Attenborosaurusconybearii	1	0	1	1	1	2	0	0	1	1	0	0	?	?	0	0	?	0	?	0	?
Augustosaurushagdorni	0	0	0	?	1	?	0	x	1	1	1	0	0	0	0	1	1	0	1	1	0
BMNHR.5488	1	0	?	1	1	0	0	1	1	1	?	?	0	1	0	?	?	0	0	?	1
Brachaucheniuslucasi	1	2	0	?	?	1	1	?	2	1	1	1	1	0	x	x	0	0	0	0	0
Brancasaurusbrancai	2	1	1	2	1	?	0	0	0	0	?	0	0	0	1	x	0	0	1	0	?
Callawayasauruscolumbiensis	2	1	0	2	0	?	0	0	0	0	0	0	0	0	0	x	0	1	1	0	?
Cryptocliduseurymerus	2	0	2	0	1	0	0	1	0	0	0	0	0	0	0	x	0	0	0	?	1
Dolichorhynchopsosborni	1	2	2	1	1	2	1	1	2	0	1	1	0	0	x	x	0	0	0	0	?
Edgarosaurusmuddi	0	2	0	?	?	?	0	1	1	0	1	0	1	0	0	x	0	0	0	0	1
Eretmosaurusrugosus	?	1	?	2	1	0	?	1	?	?	?	?	?	?	?	?	?	?	?	0	?
Eurycleidusarcuatus	0	?	?	0	?	0	0	0	1	1	1	0	?	0	0	0	1	0	0	?	?
Hauffiosauruszanoni	1	0	0	2	1	?	1	0	2	1	1	?	?	?	?	?	?	?	?	0	?
Kaiwhekeakatiki	2	1	0	?	?	?	2	0	0	0	1	1	0	0	x	x	0	0	1	1	1
Kimmerosauruslanhami	?	?	2	?	?	0	2	?	3	0	0	0	?	?	0	x	0	?	0	1	?
Kronosaurusqueenslandicus	1	2	?	2	1	?	1	?	2	?	?	?	?	?	?	?	?	?	?	?	?
Leptocliduscapensis	?	2	?	?	1	?	0	1	1	1	1	1	0	1	x	x	0	0	0	?	?
Libonectesmorgani	2	1	0	?	0	?	0	0	0	0	1	2	0	0	x	x	?	1	?	0	?
Liopleurodonferox	1	2	0	1	1	1	1	1	2	2	1	1	1	0	x	x	0	0	0	0	1
Macroplatalongirostris	1	0	0	2	1	0	1	0	2	0	1	?	1	0	x	0	0	?	?	0	0
Maresauruscoccai	1	2	0	?	?	?	1	?	2	2	1	0	0	0	1	2	0	?	?	?	1
Microcleidushomalaspondylus	2	1	0	0	1	0	0	0	0	0	0	0	0	0	?	?	0	?	1	1	?
Muraenosaurusleedsi	2	1	1	0	?	2	0	1	0	0	0	0	0	0	x	0	0	0	0	0	0
Occitanosaurustournemirensis	2	1	0	0	1	0	1	?	0	1	1	0	0	0	0	2	0	0	0	0	0
Pachycostasaurusdawni	1	2	0	?	?	?	?	?	2	?	1	?	?	?	?	?	?	?	?	?	?
Peloneustesphilarchus	1	2	0	1	1	1	1	1	2	1	1	1	1	0	x	x	0	0	0	0	1
Pistosauruslongaevus	0	0	0	?	1	?	0	x	1	0	1	0	0	0	0	1	1	0	1	0	0
P.brachypterygius	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0
P.dolichodeirus	0	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pliosaurusbrachydeirus	1	2	0	?	?	?	1	?	2	2	1	1	1	0	x	x	0	0	0	0	?
Polycotyluslatipinnis	?	2	?	1	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
R.megacephalus	0	0	0	0	1	0	0	0	1	1	1	0	1	0	0	x	1	0	0	0	1
R.victor	1	0	?	0	1	2	0	0	1	1	?	?	0	?	?	?	?	?	?	?	?
R.zetlandicus	0	2	0	?	?	0	1	?	1	1	1	1	0	1	x	?	0	0	0	0	1
Simolestesvorax	1	2	1	1	1	1	0	1	1	1	1	1	0	?	x	x	0	?	?	0	?
Stretosaurusmacromerus	1	2	0	1	1	1	1	1	2	2	1	1	1	0	x	x	0	0	0	0	?
Styxosaurussnowii	2	1	0	?	?	?	0	0	0	0	1	2	0	?	x	?	0	1	0	0	?
Terminonatatorponteixensis	2	1	1	?	?	0	0	?	0	?	1	1	0	0	x	?	0	?	0	?	0
Thalassiodraconhawkinsi	0	0	2	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1
Tricleidusseeleyi	2	0	2	?	1	0	2	1	0	0	0	0	0	0	0	x	?	?	0	1	?
Trinocromerumbentonianum	1	2	1	1	1	1	1	1	2	0	1	1	0	0	x	x	0	?	0	0	?
Vinialesauruscaroli	?	?	?	?	?	?	1	?	0	1	1	0	0	0	0	x	0	0	0	0	0

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0	?	?	1	1	?	?	?	?
?	?	0	0	2	?	?	?	?	?	?	?	?	1	0	1	0	?	?	?	?	0	?	?	?	?	?	?	?
1	1	?	0	?	0	1	1	?	?	?	?	0	1	2	x	0	x	x	x	0	1	0	1	1	0	0	1	?
1	0	0	0	2	0	1	0	1	1	0	0	0	?	1	0	?	0	?	0	0	?	?	1	?	0	?	?	?
1	0	0	0	2	0	1	0	1	1	0	0	0	1	2	x	0	x	0	1	0	0	0	1	0	0	?	?	?
1	?	0	0	2	?	1	?	1	0	0	?	0	?	1	0	1	?	0	0	?	0	1	1	?	1	?	0	?
1	0	0	0	2	0	1	1	1	0	0	1	0	1	1	1	0	x	1	0	0	?	?	1	?	1	?	0	?
1	1	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	1	0	0	1	?	0	?	0	0
1	1	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	1	1	1	0	0	1	1	0	2	0	1
1	1	0	0	2	1	1	0	1	2	0	0	1	1	2	x	0	x	1	1	0	1	1	1	?	0	1	0	0
1	0	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	?	1	1	2	0	0	1	1	0	1	1	1
1	0	0	0	2	1	1	0	1	2	0	0	0	1	2	x	0	?	1	1	2	0	0	1	1	1	?	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	0	2	0	1	0	1	x	1	?	0	1	?	?	0	?	0	?	?	1	1	1	1	0	0	?	?
?	?	?	?	?	?	?	?	1	?	?	?	0	1	?	?	?	?	?	?	0	?	1	?	?	?	?	?	?
1	0	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	?	?	1	?	?	?	?	?	?	?	?
1	1	0	0	2	1	1	?	1	?	?	?	?	1	?	x	?	?	?	1	?	1	1	1	1	0	0	0	0
?	?	?	?	0	1	?	1	?	?	1	?	1	?	?	?	?	?	?	?	?	?	1	1	1	0	2	0	1
1	0	0	0	2	0	1	0	1	0	0	?	0	1	?	?	?	x	0	?	1	0	?	1	?	?	?	?	1
1	1	0	?	2	1	?	1	1	2	0	0	0	1	2	x	0	0	1	1	?	0	0	1	1	0	2	0	1
1	0	0	0	2	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	?	1	1	0	1	0	0	1
1	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	x	0	?	?	0	1	1	1	0	0	0	0
1	?	0	0	2	1	1	?	?	?	?	0	?	1	?	?	1	?	1	?	1	0	0	1	0	0	?	0	2
1	1	0	0	2	1	1	?	1	?	?	0	0	1	2	x	0	x	?	1	1	?	?	?	?	?	?	?	?
1	1	0	0	2	1	1	?	1	2	0	0	?	1	?	x	0	0	?	1	?	0	1	1	?	0	?	0	?
x	x	0	0	2	1	1	0	1	x	1	0	0	1	2	x	0	x	1	1	1	0	0	1	x	1	1	?	2
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	0	x	0	0	0	0	1	1	0	0	0	0	1
1	?	0	0	2	0	1	0	1	x	1	0	0	?	2	x	0	x	0	1	0	?	?	?	?	?	?	?	?
1	1	1	0	2	0	0	0	1	x	1	0	0	1	2	x	0	x	1	0	0	0	1	?	0	?	?	?	?
1	0	0	1	1	0	1	0	1	1	0	0	0	1	2	x	0	x	1	1	0	0	0	1	?	0	?	?	?
1	0	0	0	2	?	1	1	1	0	0	1	0	1	1	?	0	?	?	0	0	0	1	1	?	1	?	?	1
?	?	?	?	?	?	?	?	?	?	?	?	?	x	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	0	2	0	1	?	1	0	0	?	0	1	1	0	1	0	0	1	1	?	1	1	1	1	?	0	1
?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
1	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	1	0	0	1	1	?	?	1	1	1	1	1	1
1	0	0	0	2	0	1	?	1	0	0	1	0	1	1	0	?	0	?	?	?	0	1	1	?	1	0	0	1
1	0	0	0	2	?	1	?	1	0	0	1	0	1	1	?	0	?	?	0	0	0	1	1	?	1	?	?	1
?	?	0	0	2	1	1	1	1	2	0	0	0	1	2	x	0	x	1	1	1	?	?	1	?	?	?	?	?
x	x	0	0	2	0	?	?	1	2	0	0	?	1	2	x	0	x	1	1	1	?	?	?	?	?	?	?	?
1	0	0	0	2	0	1	0	1	1	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0
1	0	0	0	2	1	1	?	1	2	0	0	1	1	2	x	0	x	?	1	0	0	0	1	1	0	1	1	0
1	?	0	1	2	1	1	0	1	2	0	0	0	1	2	x	0	x	1	1	2	?	0	1	?	0	1	1	?
1	0	0	1	2	?	?	?	?	2	0	0	1	?	2	?	0	?	?	1	0	?	?	?	?	?	?	?	?

51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
?	?	?	?	0	x	?	?	1	0	x	0	0	x	x	x	0	0	?	x	x	?	x	x	x	x	?	x	0	0
?	?	?	0	?	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	0	?	?	1	?	?	?	1	0	1	0	?		
?	?	?	?	1	1	?	?	2	0	?	?	1	0	1	x	0	0	0	0	1	0	0	2	0	0	0	0	1	?
0	0	1	1	0	1	0	1	0	?	x	0	1	0	x	x	0	0	0	0	0	?	1	0	?	?	?	?	0	0
?	?	0	0	?	1	1	0	1	?	?	?	1	1	1	?	0	0	0	0	0	0	0	2	x	0	?	0	?	?
?	?	1	1	1	1	?	?	1	0	?	0	1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	?	0
?	?	?	?	0	0	1	1	1	?	?	0	1	?	?	0	?	?	0	0	?	0	?	?	1	0	?	0	0	?
1	1	?	?	0	0	1	1	1	1	?	0	1	1	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	0
?	0	?	?	1	0	1	1	1	0	0	2	1	0	0	x	0	1	0	0	0	1	0	2	1	0	0	0	0	0
0	0	0	0	1	0	1	1	1	0	1	2	1	2	0	0	0	1	1	1	0	1	0	2	1	1	0	1	0	0
?	0	?	?	?	0	?	1	1	0	0	2	1	1	0	0	0	1	1	1	0	1	?	2	1	?	?	?	0	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	?	?	1	1	1	0	1	0	?	2	1	0	1	x	0	0	0	0	0	0	2	2	0	0	0	0	?	?
0	0	?	?	1	?	?	?	2	0	0	0	1	1	1	0	1	0	0	0	2	0	2	2	x	?	?	0	0	0
?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	0	?	?	1	0	1	1	1	0	?	2	1	0	0	x	0	?	0	1	0	?	0	2	1	1	?	1	?	?
0	0	?	?	?	1	?	?	2	0	?	0	1	1	?	0	?	?	0	2	?	?	?	x	0	?	0	0	?	
0	?	0	0	1	1	?	?	1	1	?	2	1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	1	?
1	1	1	?	0	0	1	1	1	1	1	0	1	2	0	0	0	1	0	0	0	0	1	2	1	?	0	0	0	?
1	0	0	1	1	1	?	0	2	0	0	1	1	1	1	0	0	0	0	0	3	0	2	2	x	0	?	0	0	1
0	0	?	0	?	1	?	?	1	0	?	0	1	0	1	x	?	?	0	0	0	0	2	2	0	0	?	0	?	?
2	0	0	1	1	0	?	2	1	?	0	0	1	1	x	0	0	0	0	0	3	?	0	1	?	?	?	0	?	0
?	?	?	?	?	0	?	?	?	1	0	0	1	0	1	0	0	?	0	0	0	0	?	2	1	0	0	?	?	0
0	1	?	?	1	0	?	1	1	0	0	2	1	0	0	x	0	1	0	0	0	1	0	1	1	0	0	0	0	0
0	0	?	?	1	0	?	0	0	?	0	0	1	0	1	x	0	1	0	0	1	0	1	0	?	0	?	0	0	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	1	1	1	1	0	2	0	?	0	1	1	1	0	1	0	0	0	2	0	2	2	x	0	0	0	1	0
?	0	?	?	0	0	?	?	0	0	x	0	1	0	x	x	0	?	0	0	0	?	?	0	?	0	?	?	0	0
?	1	?	?	1	x	0	0	1	0	1	0	1	1	x	0	0	0	0	0	0	?	1	?	0	0	0	1	0	
?	1	1	1	1	0	0	0	1	0	0	1	1	0	0	x	0	0	0	0	0	0	?	1	?	0	0	0	0	0
?	?	0	0	1	1	?	?	2	0	0	?	1	1	?	0	?	?	0	?	3	?	?	?	x	?	?	0	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?
0	1	0	0	?	1	?	?	1	1	?	2	1	1	1	1	0	0	0	0	0	0	1	2	x	0	0	0	?	1
?	?	?	?	0	0	?	?	0	0	?	2	1	1	1	1	0	?	0	0	?	?	1	1	x	?	?	0	?	1
0	1	0	0	1	1	?	?	1	1	?	2	1	?	1	?	0	?	0	0	0	0	?	2	x	0	?	?	?	?
?	?	0	0	1	1	?	0	1	?	?	?	1	1	1	?	0	0	0	0	0	0	?	2	x	0	?	0	?	1
?	?	0	?	1	1	?	?	2	0	0	?	1	1	?	0	0	?	0	?	3	?	?	?	x	?	?	0	0	1
?	1	1	0	0	0	1	1	?	?	0	?	?	?	?	0	?	?	?	0	?	?	?	?	?	?	?	?	0	?
?	1	?	?	1	?	0	?	?	1	0	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?
0	1	1	?	1	1	0	0	1	0	0	2	1	0	1	x	0	0	0	0	0	0	2	2	0	0	0	0	0	?
0	0	?	?	1	0	?	?	1	0	?	2	1	0	0	x	0	1	0	1	0	1	0	2	1	1	0	1	?	?
0	?	0	0	1	0	?	?	1	1	?	2	1	2	0	0	0	?	1	1	0	1	0	2	1	1	?	1	0	0
?	?	?	?	?	?	?	?	?	?	0	0	1	?	x	?	?	?	1	?	?	?	?	?	?	?	?	?	0	0

81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
0	1	1	0	1	1	0	0	?	?	2	?	?	?	?	?	?	?	?	?	1	?	1	1	0	0	?	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?
0	0	1	?	?	?	?	0	1	0	0	0	1	0	0	0	x	?	0	1	0	x	0	0	2	0	1	3
?	?	?	1	?	0	x	0	0	1	2	1	?	0	0	?	?	0	0	0	1	?	0	0	1	0	0	0
0	0	1	0	1	0	x	0	0	0	1	0	0	?	0	?	0	?	0	?	1	1	1	1	1	0	0	0
?	?	?	?	?	?	?	1	?	1	2	1	?	?	?	?	?	?	?	0	1	?	?	0	1	0	0	1
?	?	?	1	1	1	0	0	0	?	2	1	?	1	?	?	0	?	0	0	1	?	0	0	1	0	?	?
0	1	1	?	1	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	0	x	0	0	0	0	?	0
0	1	1	0	1	0	x	1	1	0	1	0	0	0	0	?	0	0	0	1	0	x	0	1	0	0	?	0
0	?	?	0	0	0	x	0	1	0	0	0	0	0	0	0	1	0	1	0	0	x	0	0	0	0	0	1
0	1	1	0	0	0	x	0	x	0	3	2	0	0	0	0	1	0	1	1	0	x	0	0	0	0	?	0
?	?	?	0	?	0	x	0	x	0	2	1	0	0	0	?	1	0	1	1	0	x	0	1	1	0	?	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	?	?	?	0	0	x	0	1	1	2	1	?	?	0	?	0	0	0	0	1	1	?	0	0	0	?	?
0	1	1	0	1	1	1	0	?	0	3	1	0	?	?	?	?	?	0	0	1	1	0	0	0	0	?	2
?	?	?	?	?	?	?	0	?	?	?	?	?	0	?	?	?	?	?	0	0	x	0	0	2	0	0	2
?	?	?	?	?	0	x	?	?	0	0	0	?	0	1	0	1	?	1	1	?	?	0	0	2	0	?	3
?	?	?	?	?	1	?	?	?	0	3	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?
?	1	1	1	0	1	0	1	?	?	2	?	0	1	0	1	0	0	0	0	1	1	1	0	1	0	0	0
0	1	1	0	1	0	x	?	1	0	1	0	1	0	0	0	0	0	0	1	0	x	0	1	0	0	?	0
1	1	1	1	1	1	1	0	1	0	2	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0
0	1	1	?	1	0	x	0	0	0	3	1	?	1	?	?	?	0	0	0	?	?	0	0	0	0	0	?
1	0	1	1	1	1	?	1	?	0	0	1	1	?	0	1	0	0	0	1	1	1	1	1	1	0	0	0
?	?	?	0	?	0	x	0	1	0	1	0	?	0	?	0	0	?	0	1	0	x	0	?	0	0	0	?
1	0	0	0	1	0	x	0	1	0	0	0	0	0	0	2	1	0	1	0	0	x	0	0	0	0	0	0
0	0	?	0	1	0	x	1	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0
?	?	?	?	?	?	?	?	?	?	3	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0
0	1	1	1	1	1	2	0	0	0	3	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	0	1
0	0	0	0	0	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	x	1	0	?	0	?	?
0	0	1	0	0	1	0	1	?	0	?	?	?	?	?	?	?	?	?	0	0	x	0	0	0	0	0	0
0	0	1	0	1	1	0	0	?	0	0	?	0	?	?	0	0	?	0	0	0	x	0	0	0	0	0	0
1	1	1	?	1	1	?	0	0	0	3	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	1	1
?	?	?	?	?	?	?	?	x	0	?	?	0	?	0	0	1	0	1	1	?	?	?	?	1	0	?	?
0	1	1	1	?	1	1	1	0	1	2	1	1	?	?	?	?	?	0	0	1	?	1	0	1	0	0	0
1	1	1	0	0	1	?	0	0	1	2	1	1	?	?	?	?	0	0	0	?	?	1	0	1	0	?	?
?	?	?	?	?	?	?	1	0	1	2	1	?	?	0	?	0	0	0	0	1	?	1	0	1	0	0	?
?	?	?	?	?	1	?	?	0	1	2	1	?	1	0	1	0	0	0	0	?	?	1	0	1	0	0	0
1	1	1	1	1	1	1	0	?	0	2	1	0	1	0	1	?	0	0	0	1	1	0	0	1	1	1	0
?	?	?	?	?	?	?	1	?	0	1	?	?	0	?	?	0	?	?	1	0	x	0	1	0	0	?	0
0	?	?	?	0	?	?	?	1	0	0	0	1	1	0	2	1	0	1	1	1	0	0	0	0	0	1	0
?	1	1	?	1	0	x	0	?	0	2	1	?	?	?	?	0	?	0	0	0	x	0	0	0	0	0	0
?	0	0	?	0	0	x	0	1	0	0	0	0	0	0	0	?	0	1	1	0	x	0	0	0	0	0	0
?	?	?	0	?	0	x	0	?	0	3	2	?	0	?	0	1	0	1	1	0	x	0	0	0	0	?	0
0	0	0	0	1	?	?	0	?	0	1	0	0	?	0	2	1	?	?	0	0	1	0	0	0	0	0	0

109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132
0	0	0	?	?	?	?	?	?	0	0	?	?	?	x	?	?	?	?	?	?	0	?	?
?	?	0	?	?	?	0	0	?	1	0	0	1	1	0	2	0	1	0	0	0	1	1	1
2	0	2	0	0	2	?	2	?	0	0	1	1	1	0	2	0	1	1	0	?	?	1	1
0	1	1	?	?	?	1	0	1	1	0	0	0	1	?	2	?	0	0	0	0	1	1	1
1	0	?	?	?	?	0	0	0	1	0	0	0	1	0	1	1	1	0	0	?	1	0	?
?	?	?	0	1	0	0	2	0	1	0	0	0	1	0	1	?	0	?	0	0	1	1	1
?	1	0	?	?	?	2	2	?	?	0	0	1	2	1	2	?	0	?	0	1	1	1	1
?	?	?	?	1	0	1	1	?	?	0	0	1	1	0	2	1	0	?	0	0	1	1	1
0	0	0	?	?	?	3	1	1	?	0	1	1	1	0	2	1	0	?	0	1	1	1	1
0	1	0	1	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	1	1	1	1	1
0	1	2	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1	1	1	1	1
0	1	2	1	1	2	2	2	?	1	0	0	1	1	0	?	?	0	?	?	?	?	1	1
?	?	?	?	?	?	1	0	?	1	0	0	1	1	0	2	0	0	?	0	1	1	1	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	?	?	?	0	0	0	?	0	0	0	?	0	2	?	0	?	?	?	?	1	1
2	0	2	?	?	?	1	0	0	0	0	1	1	1	0	2	0	1	1	0	1	1	1	1
2	0	2	1	?	?	?	2	?	0	0	0	1	1	0	2	?	1	1	?	1	?	?	1
?	?	?	?	1	?	2	2	?	?	?	?	1	2	?	2	?	0	?	0	0	?	1	1
0	?	?	?	?	?	2	2	0	1	0	0	1	1	0	2	0	0	?	0	0	1	1	1
0	0	1	1	?	0	3	1	1	?	1	1	1	1	0	2	1	1	?	0	1	?	1	1
1	0	0	?	?	?	2	2	0	0	0	0	1	1	2	1	0	1	0	0	1	1	1	1
1	?	2	0	?	0	0	0	?	1	0	0	0	1	0	2	0	0	?	0	0	?	1	1
0	?	0	1	?	0	?	2	?	?	0	0	1	1	0	2	?	0	?	0	1	?	1	1
?	0	0	0	?	?	1	1	1	0	1	1	0	1	0	2	?	1	0	0	1	1	1	1
0	1	0	1	0	1	1	1	0	0	0	?	1	1	0	2	1	1	1	1	1	1	1	1
0	0	1	1	0	1	1	1	0	0	1	0	1	1	0	2	0	1	0	0	0	1	1	1
?	?	?	?	?	?	?	2	?	?	?	0	0	1	0	2	0	?	?	?	0	1	0	?
1	1	2	0	0	0	2	2	0	1	0	0	0	1	0	2	0	0	1	0	0	1	1	1
0	1	?	?	?	?	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0
0	0	0	?	?	0	1	0	?	0	1	0	0	1	0	2	1	0	0	0	1	1	1	1
0	0	0	?	?	0	1	0	?	0	0	0	0	1	0	2	1	0	0	0	1	1	1	1
1	0	0	?	?	?	?	2	?	1	0	0	0	1	1	2	?	0	?	0	0	1	1	1
?	?	?	1	1	2	2	2	0	?	0	0	1	1	0	1	1	0	?	1	1	1	1	1
?	0	0	?	?	?	0	2	?	1	0	0	0	1	0	1	?	0	0	0	0	1	1	1
?	?	?	?	?	?	0	?	0	?	0	0	?	?	0	?	?	0	0	?	?	?	?	1
?	?	0	?	?	?	2	2	0	1	0	0	0	1	0	1	?	0	?	0	?	1	1	1
?	0	0	?	?	0	2	2	?	0	0	0	0	1	0	1	1	0	1	0	?	1	1	1
1	0	0	?	?	?	2	2	0	0	0	0	1	1	2	1	0	1	0	0	1	1	1	1
?	0	1	?	?	?	3	1	?	?	1	1	1	1	0	2	1	1	?	0	1	?	1	1
0	0	1	?	?	?	1	1	0	0	1	0	1	1	0	2	0	1	1	0	1	1	1	1
0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0	0	0	0	1	1	1
?	?	?	1	?	1	0	0	1	0	0	0	1	1	0	2	1	0	1	1	1	1	1	1
1	1	0	1	1	2	2	2	1	?	0	0	1	1	0	2	1	0	?	1	1	1	1	1
0	1	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156
?	?	?	0	?	?	?	?	?	?	?	x	?	?	?	1	?	0	?	1	?	?	0	0
1	0	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	?	?	?	1	1	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	?	1	0	0	0	0	0	1	1	0	0	1	1	1	1	0	0	1	1	1	0	1
1	0	?	0	0	?	0	?	0	1	1	0	0	0	?	?	?	?	?	?	?	?	1	0
?	0	?	?	0	0	0	0	1	1	1	0	0	0	1	1	1	?	1	1	1	1	0	1
2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
2	1	1	?	0	0	1	?	2	1	1	0	1	1	1	0	1	?	1	1	1	1	1	1
2	1	?	?	0	0	1	0	1	1	1	0	1	1	1	0	1	?	0	1	1	1	1	1
2	1	?	1	0	0	1	1	2	1	1	0	0	1	1	1	1	0	0	1	?	1	1	1
2	0	x	0	0	2	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1
0	1	?	?	?	?	?	?	?	?	1	0	0	0	1	0	1	1	1	1	1	1	1	1
?	?	?	?	?	?	?	?	?	?	0	?	?	1	1	1	0	0	1	1	1	?	?	1
?	0	?	?	?	?	0	0	?	1	1	0	0	1	1	1	1	?	?	1	1	?	1	1
2	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?	?	?	0	?	1
?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	0	?	?	?	?	0	?	0	1	1	?	0	?	?	1	1	?	1	1	1	?	?	1
?	0	0	0	0	0	0	0	1	1	1	0	?	1	?	?	?	?	?	?	?	?	1	1
?	1	?	1	0	0	2	0	2	1	1	?	1	1	?	?	?	0	?	?	?	?	?	?
2	0	?	1	?	?	0	?	?	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1
0	0	?	?	?	?	?	?	?	?	1	?	?	?	1	1	1	?	1	1	1	?	1	1
0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	1	?	1	?	?	1	?	2	?	1	0	0	1	1	1	1	0	1	1	1	1	1	1
2	1	?	1	0	1	1	1	2	1	1	0	0	1	1	1	1	0	0	1	1	1	1	1
2	1	0	0	0	?	0	0	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1
0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
2	0	0	1	?	?	0	0	0	1	1	0	0	1	1	1	1	1	0	1	1	1	1	1
2	0	?	1	?	?	0	0	0	1	1	0	0	0	0	?	1	0	?	?	1	1	0	0
2	1	?	0	1	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0
2	1	?	0	1	0	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0
?	0	?	1	?	?	?	?	?	?	?	0	?	?	1	1	1	1	0	1	1	?	1	1
2	0	x	0	0	2	0	1	1	1	1	1	?	?	1	1	1	1	0	1	1	1	1	1
2	0	?	?	?	?	?	?	?	?	1	?	0	?	1	1	1	?	?	1	1	1	0	1
2	?	?	?	0	?	0	0	1	1	1	0	0	1	?	1	1	0	1	1	1	?	0	1
?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	1
?	0	?	0	?	?	0	?	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1
2	0	?	1	?	?	?	?	?	1	1	0	0	1	1	1	1	1	1	1	1	0	1	1
2	1	?	2	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1
2	1	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	?	?	1	1	1	1
2	0	?	?	0	0	0	0	1	1	1	0	0	1	1	1	1	?	1	1	1	?	0	1
2	0	0	?	0	2	1	0	2	1	1	0	0	1	1	1	1	0	0	1	1	?	1	1
2	0	x	0	0	2	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

157	158	159	160	161	162	163	164	165	166	167	168	169	170	171
x	?	x	x	?	?	?	0	1	?	?	?	?	?	0
0	0	0	0	1	1	1	1	2	0	0	1	1	0	?
?	?	?	?	?	?	?	?	?	1	?	?	1	0	?
0	0	0	0	1	1	1	1	2	0	0	1	1	0	0
0	0	x	x	1	0	0	?	?	0	0	?	?	0	?
?	0	0	0	1	1	1	1	2	0	?	?	1	?	0
?	?	0	1	?	?	0	?	?	1	?	1	1	?	?
?	?	0	0	1	?	0	1	2	1	?	1	1	?	0
0	0	1	0	1	1	0	1	2	1	0	1	1	1	?
1	0	0	0	1	1	0	1	2	1	1	1	1	0	0
1	0	0	0	1	1	0	1	2	1	3	1	1	1	?
1	1	0	0	1	1	0	1	2	1	?	1	1	1	?
1	0	1	0	1	1	1	1	2	0	2	1	1	0	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	0	1	1	1	1	2	0	2	1	1	0	0
?	?	1	0	1	?	?	1	2	0	?	1	1	0	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
?	?	0	0	?	?	0	1	2	1	?	?	1	?	?
0	0	?	0	1	?	?	?	?	?	?	?	1	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	0	1	1	0	1	2	0	0	1	1	0	0
0	0	0	0	1	1	?	1	2	0	?	?	1	?	?
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	0	0	1	1	1	1	2	0	1	1	1	0	0
1	1	0	0	1	1	0	1	2	1	1	1	1	0	0
1	0	0	0	1	1	1	1	2	0	?	?	1	0	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
0	0	0	0	1	1	0	1	2	1	0	1	1	0	0
0	0	x	x	1	0	0	1	?	0	0	0	?	?	0
0	0	0	0	1	1	0	1	2	0	1	1	1	0	0
0	0	0	0	1	1	1	1	2	0	1	1	1	0	0
0	0	0	1	1	1	0	1	2	1	?	?	1	?	0
1	1	0	0	1	1	0	1	2	1	3	1	1	?	0
0	0	0	0	1	1	1	1	2	0	?	?	1	?	0
0	0	0	0	1	1	1	1	2	0	3	1	1	0	0
0	0	0	0	1	1	1	1	2	0	?	?	1	?	?
1	0	0	0	1	1	0	1	2	0	0	?	1	?	?
0	0	0	0	1	1	0	1	2	1	0	1	1	0	0
?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
1	0	1	0	1	1	0	1	2	1	1	1	1	0	?
0	0	0	0	1	1	1	1	2	0	0	1	1	0	0
1	1	0	0	1	1	0	1	2	1	2	1	1	?	0
1	0	0	0	1	1	0	1	2	1	3	1	1	1	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 4 - Processes performed in PAUP, RadCon and MacClade.

Processes using PAUP:

[DATA → SET CHARACTER TYPES → selection of characters → ORDERED]
[DATA → SET CHARACTER WEIGHTS → selection of characters weighted at 0.5]
[DATA → DEFINE OUTGROUP]
[ANALYSIS → HEURISTIC SEARCH → random, 1000 replicates, no max trees]
[TREES → COMPUTE CONSENSUS → non-default settings in dialogue box: ⌄ Show frequencies of all observed bipartitions, ⌄ show tree, ⌄ consensus indices].
[TREES → TREESCORES → PARSIMONY → ⌄ all in box titled 'Measures to show']
[BOOTSTRAP/JACKKNIFE ANALYSIS → ⌄ heuristic, 100 replicates].
[ANALYSIS → BOOTSTRAP/JACKKNIFE ANALYSIS → ⌄ heuristic, 50% deletion]
[ANALYSIS → PERMUTATION TESTS → ⌄ PTP].
[INCLUDE/EXCLUDE CHARACTERS → select characters for exclusion]
[ANALYSIS → PARTITION-HOMOGENEITY TEST]
[TREES → GET TREES FROM FILE → repeat for second treefile, making sure to select both files in the options dialogue box → TREES → TREESCORES → ⌄ non parametric]
[HEURISTIC SEARCH → ⌄ search constraints Trees NOT with constraint → the decay index is the difference between the length of the constrained tree and the MPT. Repeat for each node constraint]
[TREES → PRINT TREES → select phylogram in dialogue box]

Processes performed in RadCon:

[open tre. file of most parsimonious trees produced in PAUP → SOURCE → CONVENTIONAL CONSENSUS → STRICT BASIS REDUCED → ⌄ CIC strict reduced CTs]
[SOURCE → LEAF BOOTSTRAP → ⌄ Maximum ⌄ Difference ⌄ Entropy] N.B. this option was not functioning during the progress of this project.
[SOURCE → LEAF BOOTSTRAP STABILITY DECAY INDEX → INPUT → input MPT tree length → select the relevant tree file and log file]

Processes performed in MacClade:

[ASSUME → CHANGE TYPE → perform as necessary for each character] then [Σ → Tree Length, repeat for CI, RI, rescaled, CI, Σ maximum and Σ minimum]
[TRACE → trace characters]

Appendix 5 - Systematic palaeontology

The following 43 taxa were fully analysed. Taxa with a + prefix were not included in O'Keefe's (2001a) analysis but are included in cladistic analyses elsewhere. Those with an asterisk are treated cladistically here for the first time. Approx. mean ages are for plotting a stratophylogeny (text-fig 4.7).

+Taxon: *AUGUSTASAURUS HAGDORNI* Sander, Rieppel and Bucher, 1997
Type material: Holotype: FMNH PR 1974, complete skull and mandible, post-cranial skeleton consisting of posterior neck vertebrae, pectoral girdle, majority of forelimbs, dorsal vertebrae and associated fragmentary ribs and gastralia.
Type locality: Pershing County, Nevada.
Type horizon: Fossil Hill Member, Farvet Formation, Star Peak Group, *Rotelliformis* Zone, Late Anisian, Middle Triassic. Approx. mean age 236 Ma.
Referred material: None.
Remarks: The post-cranium of *A. hagdorni* is described by Sander *et al.* (1997) and the cranium is described by Rieppel *et al.* (2002). This taxon has great implications, being the second stem-group sauropterygian to be discovered in the New World, the more basal *Corosaurus alcovensis* being the first (Storrs, 1991).

+Taxon: *PISTOSAURUS LONGAEVUS* Meyer, 1839
Type material: Un-catalogued, Oberfränkisches Erdgeschichliches Museum, Bayreuth, skull.
Type locality: Lainecker Hohenzug, east of Bayreuth, southern Germany.
Type horizon: Lower Meißner Formation, Upper Muschelkalk, (*atavus* through to *postspinosus* biozone), Middle Triassic, Upper Anisian. Approx. mean age 236 Ma.
Referred material: SMF R 4041, postcranial skeleton.
Remarks: Some authors have considered *Pistosaurus* as a member of the Plesiosauria (e.g. White, 1940 p.459; Persson, 1963). Rieppel (2000) presents a concise summary of the unusual history of this genus.

Taxon: *THALASSIODRACON HAWKINSI* (Owen, 1839)
Type material: BMNH 2018, skull.
Type locality: Street, Somerset, England.
Type horizon: Rhaetian/Hettangian Boundary, Uppermost Triassic/Lowermost Jurassic. Approx. mean age: 205.7 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Thalassiodracon* for 166 characters. Additional characters were scored from Cruickshank (1994b).

Taxon: '*RHOMALEOSAURUS' VICTOR* (Fraas, 1910)
Type material: SMNS 12478, complete articulated skeleton.
Type locality: Holzmaden, Germany.
Type horizon: Posidonien-Schiefer, Toarcian, Lower Jurassic, Approx. mean age: 184.9 Ma.
Referred material: None.
Remarks: This genus is well figured in Fraas (1910) and possibly deserves generic status of it's own. O'Keefe (2001a) codes '*R' victor* for 166 characters.

Taxon: *RHOMALEOSAURUS MEGACEPHALUS* Stutchbury, 1846
Type material: Neotype, LEICT G221.1851, complete skeleton.
Type locality: Barrow-upon-Soar, Leicestershire, England.
Type horizon: Early Hettangian, Lower Jurassic. Approx. mean age: 204 Ma.
Referred material: None.
Remarks: Nicknamed the 'Barrow Kipper' (Taylor and Martin, 1990), the skull is described extensively by Cruickshank (1994b).

Taxon: Unnamed genus ('*Macroplata tenuiceps*')
Type material: BMNH R. 5488, complete skeleton.
Type locality: Harbury, Warwickshire, England.
Type horizon: Unknown.
Referred material: None.
Remarks: O'Keefe (2001a) discusses this undescribed specimen and scores it for 166 characters. Unfortunately the specimen could not be scored for additional characters, nevertheless, O'Keefe's scores are employed and the specimen is retained in the analysis.

Taxon: *RHOMALEOSAURUS ZETLANDICUS* Phillips, 1854
Type material: YORYM G503, almost complete skeleton.
Type locality: Whitby, Yorkshire, England.
Type horizon: Alum Shale, Toarcian, Lower Jurassic. Approx. mean age: 184.9 Ma.
Referred material: None.
Remarks: *R. thorntoni,* and *R. cramptoni,* were made junior synonyms of *Rhomaleosaurus zetlandicus* by Cruickshank (1996a). Material is described by Tayor (1992a, b).

Taxon: *SIMOLESTES VORAX Andrews 1909*
Type material: BMNH R.3319, complete skeleton.
Type locality: Peterborough, England.
Type horizon: Lower Oxford Clay, Callovian, Middle Jurassic. Approx. mean age: 161.9 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Simolestes* for 166 characters. Two additional species of *Simolestes* are omitted from the analysis (table 1).

Taxon: *LEPTOCLEIDUS CAPENSIS* (Andrews, 1911)
Type material: BMNH R.4828, Incomplete skull.
Type locality: Berwick, Sussex, England.
Type horizon: Barremian, Lower Cretaceous, Approx. mean age: 124 Ma.
Referred material: SAM-K5822.
Remarks: O'Keefe (2001a) codes *L. capensis* for 166 characters. Additional characters were scored from Cruickshank (1997). Other species of *Leptocleidus* are omitted (see table 1).

Taxon: *EURYCLEIDUS ARCUATUS* Andrews, 1922
Type material: BMNH 2030, partial mandible.
Type locality: Lyme Regis, Dorset, England.
Type horizon: Lower Lias, Hettangian/Lower Sinemurian, Lower Jurassic.
Referred material: OUM J.28585, disarticulated partial skull and associated skeleton. Approx. mean age: 201.9 Ma.
Remarks: O'Keefe (2001a) codes *Eurycleidus* for 166 characters. Additional characters were scored from Cruickshank (1994a).

Taxon: *ATTENBOROSAURUS CONYBEARI* (Sollas, 1881)
Type material: BMNH R. 1339 (cast of destroyed original), skull, neck, axial skeleton and proximal portion of limbs.
Type locality: Charmouth, Dorset, England.
Type horizon: Sinemurian? Approx. mean age: 198.6 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Attenborosaurus* for 166 characters. Additional characters were scored from Sollas (1881).

*****Taxon**: *ARCHAEONECTRUS ROSTRATUS* (Owen, 1865)
Type material: BMNH 38525, complete articulated skeleton including skull preserved in dorsal view.
Type locality: Charmouth, Dorset (further detail is unavailable).
Type horizon: Sinemurian, Lower Jurassic. Approx. mean age: 198.6 Ma
Referred material: None
Remarks: Genus proposed for *'Plesiosaurus' rostratus* by Novozhilov (1964) and diagnosed as a pliosauroid. Unfortunately Owen's (1865) original description is inadequate. Many characters have been coded via personal observation of the figures of the holotype (some tentatively) while other characters have been omitted due to poor resolution of said figures. Unfortunately a taxonomic revision of all pliosauroids is long overdue and such an undertaking does not fall within the scope of this project.

Taxon: *MACROPLATA LONGIROSTRIS* (Blake, 1876)
Type material: MCZ 1033, in collection of fossil reptiles and amphibians. Damaged skull, 85 vertebrae and 4 limbs.
Type locality: Whitby, Yorkshire, England.
Type horizon: Alum Shale, Upper Lias, *serpentinus* ammonite zone, Toarcian, Lower Jurassic. Approx. mean age: 184.9 Ma.
Referred material: MANUM 8004, Skull and associated skeleton proposed by O'Keefe.
Remarks: O'Keefe (2001a) scores the majority of the characters for *M. longirostris* via personal observation (MANUM 8004). Additional characters were scored from White (1940).

Taxon: *HAUFFIOSAURUS ZANONI* O'Keefe, 2001
Type material: *HAUFF* Uncatalogued, complete skeleton.
Type locality: Holzmaden, Germany.
Type horizon: Posidonien-schiefer, Toarcian, Lower Jurassic, Approx. mean age: 184.9 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) proposed this new taxon for a display-specimen in the Urwelt-Museum Hauff labelled '*Thaumatosaurus'* (personal observation, 2002).

*Taxon: *PACHYCOSTASAURUS DAWNI* Cruickshank *et al*. 1996.
Type material: PETMG R338, an almost complete skeleton including most of the skull and some of the mandible, almost complete vertebral column and associated ribs, left pelvis, right ilium, both humeri, three phalanges from a hindlimb.
Type locality: The King's Dyke Clay Pit at Whittlesey, near Peterborough, Cambridgeshire, UK.
Type horizon: Peterborough Member of the Oxford Clay Formation, *Jason* Subzone, Middle Callovian, Middle Jurassic. Approx. mean age: 161.5 Ma.
Referred material: None.
Remarks: Cruickshank *et al*. (1996) gives "a preliminary description" of this rare taxon, which exhibits pachyostosis. A detailed description is pending.

Taxon: *KRONOSAURUS QUEENSLANDICUS* Longman, 1924
Type material: Queensland Museum (unspecified)
Type locality: Army Downs, north of Richmond, Queensland, Australia.
Type horizon: Aptian-Albian, Approx. mean age: 112.2 Ma.
Referred material: None.
Remarks: The genus *Kronosaurus* is currently under revision (McHenry, pers. comm., 2003). Data for this taxon comes from O'Keefe (2001a) and from McHenry, pers. comm. 2003) [But see notes added in proof].

Taxon: *PELONEUSTES PHILARCHUS* (SEELEY, 1869)
Type material: CAMSM J.46913, almost complete skeleton.
Type locality: Peterborough, England.
Type horizon: Oxford Clay, Callovian, Upper Jurassic, Approx. mean age: 161.9 Ma.
Referred material: None.
Remarks: *Peloneustes* is often difficult to distinguish from *Pliosaurus* and some species may possibly be congeneric (Martill, 1991).

Taxon: *LIOPLEURODON FEROX* Sauvage, 1873
Type material: BMNH R.3536, a single tooth (but see below).
Type locality: Wast, Boulogne, France.
Type horizon: Callovian, Middle Jurassic. Approx. mean age: 161.9 Ma.
Referred material: Associated skeleton (also BMNH R.3536), "the teeth of which are indistinguishable from the type" (Tarlo, 1960, p.166) and BMNH R.2680 and GPIT 1754/2 (O'Keefe, 2001a).
Remarks: In addition to *L. ferox*, three other possible species are typically recognised. However, *L. pachydeirus*, also from the Callovian, has been recently recognised as a junior synonym of *L. ferox* (Noè, 1999). '*L.*'('*Stretosaurus*') *macromerus* is subjected to revision herein whereas the valid *L. rossicus* is omitted for reasons discussed in table 1. Noè *et al*. (2003) recently described an exoccipital-opisthotic bone, reducing the number of question marks in the data matrix for this taxon.

*Taxon: '*STRETOSAURUS' MACROMERUS* (Phillips, 1871)
Type material: Lectotype. OXFUM. J. 10441, Single vertebra.
Type locality: Shotover railway, Oxfordshire.
Type horizon: Kimmeridge Clay, Kimmeridgian, Upper Jurassic, Approx. mean age: 152.4 Ma.
Referred material: OXFUM. J. 35990, OXFUM. J. 10454.
Remarks: This 'giant pliosaur' (Tarlo, 1959 p. 39) known as the *Stretham Pliosaur* is actually a young species of *Liopleurodon* (see text).

Taxon: *PLIOSAURUS* Owen, 1841   [*P. brachydeirus* + *P. brachyspondylus* – *P. andrewsi*]
Type material: *P. brachydeirus* OXFUM J.9245 A.B., "teeth, lower and upper jaws, vertebral column, femur, tibia and fibula" (Tarlo, 1960, p. 152).
Type locality: Market Rasen, Lincolnshire, England.
Type horizon: Kimmeridge Clay, Kimmeridgian, Upper Jurassic. Approx. mean age: 152.4 Ma.
Referred material: BRSMG Cc332, *P. brachyspondylus,* the 'Westbury Pliosaur' (Taylor and Cruickshank, 1993a). Almost complete skull and mandible, some associated cervical vertebrae, phalanges and a rib.
Remarks: I have refrained from including both of the Kimmeridgian species of *Pliosaurus* because few characters separate them, many of questionable validity (Taylor and Cruickshank, 1993a). However the type specimens of *P. brachyspondylus* and *P. brachydeirus* are complementary and, combined, allow a greater degree of resolution for the genus. Accordingly, I have coded *Pliosaurus* to genus level only, albeit discounting characters of the Callovian species *P. andrewsi,* which is omitted from the analysis (see table 1).

Taxon: *BRACHAUCHENIUS LUCASI* Williston, 1903
Type material: USNM 4989, skull and mandible (palatal view) plus 37 ribs and associated vertebrae.
Type locality: Ottawa County, Kansas, USA.
Type horizon: Greenhorn Limestone, Turonian, Late Cretaceous Approx. mean age: 91.3 Ma.
Referred material: USNM 2361, skull and vertebrae; FHSM VP321, compete skull.
Remarks: This taxon is treated in Carpenter's (1996) revision of short-necked North American plesiosaurs.

*Taxon: *MARESAURUS COCCAI* Gasparini, 1997
Type material: MOZ 4386 V Museo Prof. Olsacher, Zapala, Neuquén, articulated skull and mandible, atlas-axis and first cervical vertebrae.
Type locality: Chacaico Sur, (39˚ 15' S, 70˚ 18' W), 70 km southwest of Zapala, Neuquén Province, Argentina.
Type horizon: Upper part of the Los Molles Formation, Cuyo Group, *Emileia giebeli* and *Emileia multiformis* subzone, Lower Bajocian, Middle Jurassic. Approx. mean age: 174 Ma.
Referred material: None.
Remarks: Diagnosed as a pliosaurid under the current limitations of poor understanding of pliosaur phylogeny.

+Taxon: *PLESIOSAURUS DOLICHODEIRUS* Conybeare 1824
Type material: BMNH 22656, complete skeleton.
Type locality: Lyme Regis, Dorset, England.
Type horizon: Uppermost Sinemurian, Lower Jurassic. Approx. mean age: 195.5 Ma.
Referred material: None.
Remarks: Text-fig 1.1. Extensively revised by Storrs (1997).

+Taxon: *PLESIOSAURUS BRACHYPTERYGIUS* von Huene, 1923
Type material: GPIT 'GPIT von Huene'; complete skeleton including skull.
Type locality: Steinbruch 29, Ohmden (near Holzmaden), Baden-Württemberg.
Type horizon: Lias epsilon II, 4 (Unterer Schiefer), *Harpoceras falcifer* Zone, Lower Toarcian. Approx. mean age: 187 Ma.
Referred material: None.
Remarks: This taxon can be confidently included, owing to the recent re-description of the holotype skull by Maisch and Rucklin (2000). The remainder of the skeleton is figured by Hauff (1953, Tafel [Plate] 30/31).

+Taxon: *OCCITANOSAURUS TOURNEMIRENSIS* (Sciau, Crochet and Mattei, 1990)
Type material: MMM J. T. 86-100, Musée Municipal de Millau, Aveyron, near complete skeleton including the skull, complete vertebral series with atlas-axis and associated ribs to the sacrum, complete pectoral and pelvic girdles, right forelimb and both hind limbs.
Type locality: Tournemire (43°56' 25''N, 3°1'14''E), Aveyron Department, southern France.
Type horizon: Marnes feuilletées, *Aalensis* Zone, *Pleydellia celtica* Subzone, Upper Toarcian, Lower Jurassic. Approx. mean age: 183 Ma.
Referred material: None.
Remarks: Described by Sciau *et al*. (1990) and Bardet *et al*. (1999), the genus was proposed for '*Plesiosaurus' tournemirensis* by Bardet *et al*. (1999). The taxon is diagnosed therein as an early elasmosaurid.

Taxon: *MICROCLEIDUS HOMALOSPONDYLUS,* Owen, 1865.
Type material: YORYM G. 502, complete skeleton.
Type locality: Whitby, England.
Type horizon: Alum Shale, Toarcian, Lower Jurassic Approx. mean age: 184.9 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Microcleidus* for 166 characters. Amended characters and additional characters were scored from Owen's (1865) original description and Watson (1911). As O'Keefe (2001a) correctly points out: "this genus is in need of redescription" (p. 14).

Taxon: *BRANCASAURUS BRANCAI* Wegner, 1914
Type material: GPMUM Unspecified, Münster.
Type locality: Gronau, Münster, Westphalia, west-central Germany.
Type horizon: Valanginian according to O'Keefe (2001a) but Berriasian according to Creisler (2003). Approx. mean age: 138.1 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Brancasaurus* for 166 characters. Additional characters were scored from Bakker (1993).

Taxon: *CALLAWAYASAURUS COLUMBIENSIS* (Welles, 1962)
Type material: UCMP 38349, complete skeleton.
Type locality: Columbia, South America.
Type horizon: Aptian, Lower Cretaceous Approx. mean age: 116.6 Ma
Referred material: UCMP 125328, partial skull.
Remarks: Genus proposed for '*Alzadosaurus' columbiensis* by Carpenter (1999). O'Keefe (2001a) codes *Callawayasaurus* for 166 characters. Additional characters were scored from Carpenter (1999).

Taxon: *STYXOSAURUS SNOWII* (Williston, 1890)
Type material: KUVP 1301, Skull.
Type locality: Hell Creek, Logan County, Kansas, USA.
Type horizon: Niobrara Formation, Santonian, Upper Cretaceous. Approx. mean age: 84.7 Ma.
Referred material: AMNH 5835.
Remarks: O'Keefe (2001a) codes *Styxosaurus* for 166 characters. Additional characters were scored from Carpenter (1999) and Storrs (1999). *Styxosaurus snowii* is the only long-necked plesiosauroid taxon from the central USA based on diagnostic material (Storrs, 1999). Reasonably described by Welles (1943) and Welles and Bump (1949), the latter describes the type specimen of 'Alzadosaurus permbertoni', which has been referred to *S. snowii* (Carpenter, 1999)). Only the type is considered valid (Storrs, 1999), and this "is worthy of a renewed study" (p. 7).

Taxon: *LIBONECTES MORGANI* (Welles, 1949)
Type material: SMUSMP 69120, Skull.
Type locality: Near Cedar Hill, Texas, USA.
Type horizon: Britton Formation, Coniacian, Late Cretaceous Approx. mean age: 87.4 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) codes *Trinacromerum* for 166 characters. Additional characters were scored from Carpenter (1997, 1999).

*Taxon: *TERMINONATATOR PONTEIXENSIS* Sato, 2003
Type material: RSM P2414.1, skull, partly disarticulated vertebral column, incomplete pectoral and pelvic girdles, almost complete fore and hind limbs, disarticulated ribs and gastralia.
Type locality: Riverside cliff on the eastern side of Notukeu Creek (49˚ 46' 20" N, 107˚, 26' 20" W) Ponteix, southwestern Saskatchewan, Canada.
Type horizon: Bearpaw Formation, *B. cuneatus* or *B. reesidei* zone, Upper Campanian, Upper Cretaceous. Approx. mean age: 73 Ma.
Referred material: None.
Remarks: Sato (2003) diagnoses this taxon as an elasmosaurid: "one of the youngest plesiosaurs from the western interior".

+**Taxon**: *VINIALESAURUS CAROLI* (De la Torre and Rojas, 1949)
Type material: MNHNCu P3008, mostly complete skull and mandible with associated atlas-axis.
Type locality: Between Laguna de Piedra and La Palma, in the Sierra de Los Organos, Pinar del Río Province, western Cuba. Approx. mean age: 156 Ma.
Type horizon: Jagua Vieja Member, Jagua Formation, Middle-Late Oxfordian, Late Jurassic.
Referred material: None.
Remarks: Gasparini *et al*. (2002) propose the new genus *Vinialesaurus* for '*Cryptocleidus? Cuervoi caroli*', diagnosing the taxon as a cryptoclidid.

Taxon: *MURAENOSAURUS LEEDSII Seeley, 1874*
Type material: BMNH R.2421, almost complete skeleton.
Type locality: Peterborough, England
Type horizon: Lower Oxford Clay, Callovian, Middle Jurassic, Approx. mean age: 161.9 Ma
Referred material: BMNH R.2678, R.2864, R.2863, R. 2861, R. 3704, LEICT G.18.1996.
Remarks: Recent work on *M. leedsii* includes independent reviews of the cranial osteology by Maisch, (1998) and Evans (1999), both accounts contain some information overlooked by O'Keefe (2001a). A second valid species of *Muraenosaurus* (*M. beloclis*) (Brown, 1981) is omitted from this analysis (table 1).

Taxon: *CRYPTOCLIDUS EURYMERUS* Phillips, 1871
Type material: Neotype: BMNH R. 2860, complete skeleton.
Type locality: Unspecified brick pit near Peterborough, England.
Type horizon: Callovian, Upper Jurassic. Approx. mean age: 161.9 Ma
Referred material: PETMG R.283.412, almost complete skull and atlas-axis (figured by Brown and Cruickshank, 1994) plus associated skeleton.
Remarks: The neotype of *C. eurymerus* is "one of the most complete adult plesiosaur skeletons known" (Brown, 1981, p. 257). O'Keefe (2001a) codes *Cryptoclidus* for 166 characters. Additional characters were scored from Brown (1981), and Brown and Cruickshank (1994).

Taxon: *TRICLEIDUS SEELEYI* Andrews, 1909
Type material: BMNH. R. 3539, incomplete disarticulated skeleton, comprising most of the skull and about half of the postcranial skeleton.
Type locality: Pit adjacent to Woodston Lodge, Fletton, near Peterborough, England
Type horizon: Middle or Upper Callovian, Upper Jurassic. Approx. mean age: 161.5 Ma
Referred material: None.
Remarks: O'Keefe (2001a) codes *Tricleidus* for 166 characters. Additional characters were scored from Brown (1981, 1993).

*Taxon: *KAIWHEKEA KATIKI* Cruickshank and Fordyce, 2002

Type material: OU 12649, an almost complete skull, almost complete vertebral column minus the posterior caudals, almost complete ribcage, some gastralia, partial pelvic girdle and associated right hindlimb and fragmentary left hindlimb.

Type locality: Shore platform at Shag Point (45˚ 28' S, 170˚ 49'E) north of the Shag River Mouth, North Otago, South Island, New Zealand.

Type horizon: Lower to Middle Katiki Formation, *Dimitobelus hectori* Zone (for belemnites) *Palaeocystodinium granulatum* Subzone (for dinoflagellates), Boundary between Upper and Lower Maastrichtian, Upper Cretaceous. Approx. mean age: 69.5 Ma.

Referred material: None.

Remarks: Text-figs 2.1, 2.2 Cruickshank and Fordyce (2002) diagnose *K. katiki,* also known as the 'Shag Point Plesiosaur'*,* as a cryptoclidid.

Taxon: *KIMMEROSAURUS LANGHAMI* Brown, 1981

Type material: BMNH R.8431, disarticulated incomplete skull.

Type locality: Endcombe Bay (Egmont Bay) Dorset, England.

Type horizon: Kimmeridgian (*Pavlovia rotunda zone*), Upper Jurassic. Approx. mean age: 152.4 Ma.

Referred material: R. 1798 and R. 10042, additional skull and vertebrae fragments

Remarks: *Kimmerosaurus* may be synonymous with *Colymbosaurus* (Brown *et al,* 1986; Brown, 1993) (see also table 1). O'Keefe (2001a) codes *Kimmerosaurus* for 166 characters. Additional characters were scored from Brown (1981), Brown *et al.* (1986) and Brown (1993).

+Taxon: *ARISTONECTES PARVIDENS* Cabrera, 1941

Type material: MLP 40-XI-14-6; part of a skull and mandible, atlas-axis complex and 21 cervical vertebrae, 8 caudal vertebrae and an incomplete limb.

Type locality: Canadon del Loro, middle Chubut River (42˚ 40' S-70˚ 00' W), northwest Chubut Province, Patagonia, Argentina.

Type horizon: Paso del Sapo Formation, Fefipan Member, Maastrichtian. Mean Age 68.2 Ma.

Referred material: TTU P 9219, incomplete skull and mandible plus associated cervical material; SGO-PV-957, posterior cranium and incomplete mandible.

Remarks: Text-fig 2.2. O'Keefe (2001a) included '*Morturneria'* in his analysis, a taxon recently recognised as a junior synonym of *A. parvidens* (Gasparini *et al*. 2003). The affinities of *Aristonectes* have long remained in dispute. The taxon was first interpreted as elasmosaurid (Cabrera, 1941) and later also by Bardet *et al.* (1991) and most recently by Gasparini *et al*. (2003). However, it has also been variously interpreted as an 'aberrant pliosaur' (Welles, 1962), a cryptoclidid (Brown, 1981; Chatterjee and Small, 1989) and as 'cimoliasaurid' (Persson, 1963). The now redundant '*Morturneria'* is a member of the newly defined Cimoliasauridae of O'Keefe (2001a). The synonymy makes this species 11% more complete (text-fig 3.1) and we can thus regard its phylogenetic position with more accuracy. The recent observation (Gasparini *et al.* 2003) that the genus *Morturneria* is a junior synonym of *Aristonectes* and the description of a new skull from Chile (Suarez and Fritis, 2002) is of great value to this study: there is now sufficient material of this taxon for inclusion in analyses.

Brown (1981) noted the *possibility* that the occipital condyle of *Aristonectes* incorporates the exoccipital, a character shared only by the cryptoclidids (*sensu* Brown, 1981) and *Eurycleidus,* (Cruickshank, 1994b). This state can now be confirmed for *Aristonectes* as considered by Gasparini *et al*. (2003): the posterior protrusion at the base of the exoccipital (see Chatterjee and Small, 1989 fig. 8) when paired with the "very short [basioccipital], without a separating groove" (Brown 1981) would complete the occipital condyle.

Taxon: *EDGAROSAURUS MUDDI* Druckenmiller, 2002
Type material: MOR 761, Compete skull, 26 cervical vertebrae, 3 pectoral, five dorsal and an almost complete forelimb.
Type locality: Montana, USA.
Type horizon: Thermopolis Shale, Upper Albian, Lower Cretaceous. Approx. mean age: 100 Ma.
Referred material: None.
Remarks: O'Keefe (2001a) included specimen MOR 751; this specimen has since been named *E. muddi* (Druckenmiller, 2002).

Taxon: *POLYCOTYLUS LATIPINNIS* Cope, 1869
Type material: Holotype: USNM 27678, vertebrae, illium and metapodials.
Type locality: Fort Wallace, Kansas, USA
Type horizon: Niobrara Formation, Cenomanian, Late Cretaceous Approx. mean age: 96.2 Ma.
Referred material: Paratype: YPM 1125, nearly complete skeleton with skull fragments.
Remarks: O'Keefe (2001a) codes *Polycotylus* for 166 characters. Herein, additional characters were scored from Carpenter's (1996) revision.

Taxon: *TRINACROMERUM BENTONIANUM* Cragin, 1888
Type material: USNM 10945, almost complete skeleton.
Type locality: Osborne County, Kansas, USA.
Type horizon: Fencepost Limestone, Turonian, Late Jurassic. Approx. mean age: 91.3 Ma.
Referred material: USNM 10946, MCZ 1064, FHSM VP404, KUVP 5070, SM 3025.
Remarks: O'Keefe (2001a) codes *Trinacromerum* for 166 characters. Additional characters were scored from Williston (1908) and from Carpenter's (1996) revision.

Taxon: *DOLICHORHYNCHOPS OSBORNI* Williston, 1903
Type material: KUVP 1300, almost complete skeleton.
Type locality: Logan County, Kansas, USA.
Type horizon: Niobrara Formation, Cenomanian, Late Cretaceous. Approx. mean age: 96.2 Ma.
Referred material: MCZ 1064, FHSM VP404.
Remarks: O'Keefe (2001a) codes *Dolichorhynchops* for 166 characters. Herein, additional characters were scored from Carpenter's (1996) revision.

*Taxon: *ERETMOSAURUS RUGOSUS* (Owen, 1965)

Type material: BMNH 14435, almost complete skeleton with skull missing, almost complete vertebral column and associated ribs, complete pectoral girdle poorly exposed and complete pelvic girdle with all four limbs complete and in articulation.

Type locality: Granby, Leicestershire (further detail is unavailable).

Type horizon: *Ammonites stellaris* zone, Sinemurian, Lower Jurassic. Approx. mean age: 198.6 Ma.

Referred material: None.

Remarks: Genus named for '*Plesiosaurus*' *rugosus* by Seeley (1874). After confusion over the type material of this species, a formal petition was filed with the ICZN (Brown and Bardet, 1994). The skeleton described here (BMNH 14435) is now the official holotype (ICZN opinion 1831 (March 1996)) (Creisler, 2003). In a case of mistaken identity, Benton and Spencer (1995) discuss *Eretmosaurus macropterus,* (e.g. pp.115, 120) but this is actually a second species of *Microcleidus* as correctly pointed out on p. 116 (*ibid*).

Notes added in proof

During the closing stages of this project, a wealth of updated information was kindly provided on the pliosaurid species, *Kronosaurus queenslandicus*. When included in future cladistic analyses, this revised set of character states may affect the position of *Kronosaurus* relative to other pliosaurs or warrant the retention of the family Brachaucheniidae.

Terminonatator has since been included by the present author in a more detailed cladistic analysis of the Plesiosauroidea and occurs within the Elasmosauridae. This relationship fits the stratigraphy much more accurately than presented here, and also agrees with the original diagnosis of the taxon (Sato, 2003). The character 'coronoid forms high process' which united *Terminonatator* with some stem-group cryptoclidids is now considered unreliable.