A COMPUTER ASSISTED ANALYSIS OF THE RELATIONSHIPS OF THE HIGHER CATEGORIES OF TURTLES

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Abstract—A character matrix of 39 characters for 14 supregeneric categories of living and extinct turtles was examined using PAUP 2.41 and 3.0L. The Branch and Bound algorithm found a single most parsimonious cladogram of 55 steps, consistency index of 0.709, retention index of 0.848 and a rescaled consistency index of 0.601. The cladogram is identical to that proposed by Gaffney and Meylan (1988). The Pleurodira and Cryptodira are each shown to be monophyletic and are supported by synapomorphies involving complex structures of the basicranium and adductor musculature. These synapomorphies are judged to be relatively well-tested homologies. A paraphyletic Cryptodira occurs in 18% of 38 equally parsimonious trees 57 steps in length, but these trees are based on characters, such as absence of pterygoid teeth, that are susceptible to homoplasy in amniotes. We re-iterate the notion that it is better to choose fewer, well-analysed characters than large numbers of poorly analysed characters.

Introduction

In a recently developed phylogenetic hypothesis for turtles (Gaffney and Meylan, 1988) the authors combined a series of published hypotheses of relationships within turtles with several newly proposed sets of relationships to provide an extensive systematic analysis of turtles down to the generic level. Only limited portions of the combined hypothesis had been studied using computer algorithms designed to examine parsimony of such hypotheses. The purpose of the current paper is to continue this numerical examination with a restudy of the higher relationships among turtles.

The monophyly of the Testudines is firmly established (Gaffney, 1975, 1984, 1990); and the monophyly of the groups used as terminal taxa in this study is well supported (Gaffney and Meylan, 1988). Turtles are a good group for phylogenetic studies. They are morphologically diverse in characters and they have a relatively dense fossil record extending back to the late Triassic, which is useful in examining the utility of fossils in the formulation of hypotheses of relationship of living taxa.

Methods

A matrix of 39 characters for 14 turtle taxa and a hypothetical ancestor was compiled. It was examined using PAUP versions 2.41 and 3.0L by David Swofford. Analysis proceeded using the Branch and Bound algorithm of PAUP to find all most parsimonious trees. Farris optimization was used to optimize characters on the solution cladogram and two options (CSPOSS and BLRANGE) were utilized in version 2.41 to elucidate ambiguity in character optimization. The network produced by PAUP was rooted using a hypothetical ancestor for which character states were scored based on our knowledge of *Proganochelys* and non-testudine anapsid amniotes, particularly *Captorhinus*

except for characters of the shell (Gaffney, 1990). Although we have been particularly interested in using captorhinids as a close outgroup to turtles, substitution of procolophonids and *Owenetta* (based on information in Reisz and Laurin, 1991) does not alter any of the character distributions. In fact, the assertion of these authors that the use of *Owenetta* rather than captorhinids as the outgroup for turtles "...could alter considerably our concepts of turtle evolution" (Reisz and Laurin, 1991:326) is unfounded. For shell characters (which constitute less than 13% of our characters) we accept the hypothesis that *Proganochelys* is the sister group of all other turtles, because no reasonable outgroup has a shell.

The characters for extinct genera used in the analysis are based on first hand examination of the materials. Characters for higher taxa are scored on the basis of our understanding of the distribution of the features within the monophyletic groups. All the characters are binary. It would be possible to list some characters (e.g. 12, 13, 14) as states in one morphocline but we see no particular advantage to this and the results are the same. The inclusion of characters in the analysis depended upon their variation among higher taxa and relative uniformity within these taxa. Autapomorphies for terminal taxa were excluded. Missing values occupy 11.7% of the data matrix; all but five are for the Mesozoic taxa *Proterochersis* and *Platychelys*, known only from shells. The taxa utilized are the same representatives of turtle diversity that appear in fig. 5.1 in Gaffney and Meylan (1988), with two exceptions. The families Emydidae, "Butaguridae" and Testudinidae are treated as the monophyletic superfamily Testudinoidea, and the Pleurodira is broken down into four taxa (*Proterochersis*, *Platychelys*, Pelomedusidae and Chelidae) to allow testing of pleurodiran monophyly.

Basic Taxa

For purposes of this analysis the 14 basic taxa employed are assumed to be monophyletic. Four of them (*Progranochelys, Proterochersis, Platychelys* and *Kayentachelys*) are monospecific genera diagnosed in the literature indicated. The other taxa are higher taxa that have been hypothesized as monophyletic in the literature. All of these taxa are referred to and discussed in Gaffney and Meylan (1988), but important references published since that date are listed below. Our 14 basic taxa are listed in the order in which they appear in the data matrix (Table 1).

Living turtles are included in the families Pelomedusidae, Chelidae and Chelydridae, and superfamilies Chelonioidea (Cheloniidae and Dermochelyidae), Trionychoidea (Trionychidae, Carettochelyidae, Dermatemydidae and Kinosternidae) and Testudinoidea (Testudinidae, Emydidae and "Bataguridae"); the remaining taxa, *Proganochelys, Proterochersis, Platychelys, Kayentachelys*, Pleurosternidae, Baenidae, Plesiochelyidae and Meiolaniidae are all extinct. There are many named fossil turtle species that may represent unrecognized higher taxa but they are excluded because they are as yet too poorly known.

PROGANOCHELYS (2)

This Late Triassic turtle is one of the two oldest known turtles, the other being *Proterochersis. Proganochelys* is known from nearly complete skeletons. Information on characters in *Proganochelys* comes from a recently completed study of the osteology of the well-preserved German specimens (Gaffney, 1990). Gaffney (1985) concluded that the

Table 1

Data matrix for examination of higher turtle relationships. See text for explanation of characters

	1	2	3	4	5	6	7	8	9	10	11	12	13
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterochersis	?	?	?	?	?	?	?	?	?	?	?	?	?
Platychelys	?	?	?	?	?	?	?	?	?	?	?	?	?
Chelidae	1	1	1	1	1	0	0	0	0	1	1	0	0
Pelomedusidae	1	1	1	1	1	0	0	0	0	1	1	0	0
Kayentachelys	1	1	1	1	1	1	1	1	0	0	0	0	0
Pleurosternidae	1	1	1	1	1	1	1	1	1	1	1	1	0
Baenidae	1	1	1	1	1	1	1	1	1	1	1	1	0
Plesiochelyidae	1	1	1	1	1	1	1	1	1	1	1	1	1
Meiolaniidae	1	1	1	1	1	1	1	1	1	1	1	1	1
Chelydridae	1	1	1	1	1	1	1	1	1	1	1	1	1
Chelonioidea	1	1	1	1	1	1	1	1	1	1	1	1	1
Trionychoidea	1	1	1	1	1	1	1	1	1	1	1	1	1
Testudinoidea	1	1	1	1	1	1	1	1	1	1	1	1	1

	14	15	16	17	18	19	20	21	22	23	24	25	26
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterochersis	?	?	?	?	?	?	?	?	?	?	?	?	?
Platychelys	?	?	?	?	?	?	?	?	?	?	?	?	?
Chelidae	1	0	0	1	0	0	1	1	1	1	1	0	1
Pelomedusidae	1	1	0	1	1	1	1	1	1	1	1	0	1
Kayentachelys	0	0	0	0	0	0	0	0	0	0	1	?	0
Pleurosternidae	0	0	0	0	0	0	0	0	0	0	1	?	0
Baenidae	0	0	0	0	0	0	0	0	0	0	1	?	0
Plesiochelyidae	0	0	0	0	0	0	0	0	0	0	1	?	0
Meiolaniidae	0	0	1	0	0	0	0	0	1	0	1	?	0
Chelydridae	0	1	1	0	1	1	0	0	0	0	1	1	0
Chelonioidea	0	1	1	0	0	1	0	0	0	0	1	1	0
Trionychoidea	0	1	1	0	1	1	0	0	0	0	1	1	0
Testudinoidea	0	1	1	0	1	1	0	0	0	0	1	1	0

	27	28	29	30	31	32	33	34	35	36	37	38	39
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0
Proganochelys	0	0	0	0	0	0	0	0	0	0	0	0	0
Proterochersis	?	1	0	0	0	1	?	0	0	?	?	?	1
Platychelys	?	1	0	1	0	1	1	0	0	?	0	1	1
Chelidae	0	1	1	1	1	1	1	0	1	1	1	1	1
Pelomedusidae	0	1	1	1	0	1	1	0	1	1	1	1	1
Kayentachelys	0	1	1	0	0	0	0	0	0	0	0	0	0
Pleurosternidae	0	1	1	0	0	0	0	0	0	0	0	0	0
Baenidae	0	1	1	0	0	0	0	0	0	0	0	1	0
Plesiochelyidae	0	1	1	1	1	0	0	0	0	0	0	1	0
Meiolaniidae	0	1	1	1	1	0	1	0	0	0	0	0	0
Chelydridae	0	1	1	1	1	0	1	1	1	0	0	1	0
Chelonioidea	0	1	1	1	1	0	1	1	1	1	1	1	0
Trionychoidea	1	1	1	1	1	0	1	1	1	1	1	1	0
Testudinoidea	1	1	1	1	1	0	1	1	1	1	1	1	0

available material consists of one species, *Proganochelys quenstedti*. *Proganochelys* has repeatedly been hypothesized as the sister group to all other turtles (Gaffney, 1975, 1984, 1990; Gaffney and Meeker, 1983; Gaffney and Maylan, 1988).

PROTEROCHERSIS (3)

The other Triassic turle is *Proterochersis robustum*, best known from the work of Fraas (1913). *Proterochersis* is known only from the shell and pelvis, and yields only nine of our 39 possible characters. The reasons for including this taxon are discussed below. Characters are scored on the basis of re-examination of 20 specimens of this genus at the Staatliches Museum für Naturkunde in Stuttgart.

PLATYCHELYS (4)

Platychelys oberndorferi is based on six shells and a few vertebrae. Best described by Rutimeyer (1873) and Brâm (1965), it yields only 12 out of 39 possible characters. Characters are scored on the basis of study of six specimens from Solothurn and Basel, Switzerland.

The inclusion of the poorly known genera *Proterochersis* and *Platychelys* is an attempt to include some information from archaic pleurodires. Although it is notoriously difficult to judge the adequacy of a particular group's fossil record, it is easy to argue that in contrast to cryptodires, pleurodires are poorly represented in the early Mesozoic. These two taxa, *Proterochersis* and *Platychelys*, are the only pleurodires known from pre-Cretaceous horizons and no pre-late Cretaceous pleurodire skulls have been described. On the other hand, nearly complete cryptodire skeletons are known from one early Jurassic taxon and many late Jurassic and early Cretaceous forms. The identification of *Proterochersis* as a pleurodire shows that this group has a late Triassic minimum age. The relevance of this to phylogenetic analysis is that the living pleurodires, particularly pelomedusids, have some characters in common with living cryptodires that are, however, absent in cryptodires primitively. The inclusion of *Proterochersis* and *Platychelys* demonstrates the homoplasy of at least some of these characters. Gaffney (1988) and Gaffney and Meylan (1988) have argued that *Proterochersis* and *Platychelys* are sister taxa to all other pleurodires and those relationships are retested by their inclusion in the present study.

CHELIDAE (5)

Monophyly of the Chelidae, one of two living families of pleurodires, can be considered relatively well corroborated as argued by Gaffney (1977) and Gaffney and Meylan (1988). The best synapomorphies are in the unique structure of the cheek region.

PELOMEDUSIDAE (6)

Pelomedusids represent the second living pleurodire family. Monophyly and cladograms of included taxa are presented by Gaffney (1988) and Gaffney and Meylan (1988). Monophyly of this family is well corroborated but the existence of many as yet undescribed fossil pelomedusids may affect relationships within the family (Gaffney, 1988).

KAYENTACHELYS (7)

The early Jurassic *Kayentachelys aprix* is argued by Gaffney et al. (1987) to be the sister group to all other cryptodires, and accepted as such by Gaffney and Meylan (1988). Gauthier et al. (1989) dispute this hypothesis (discussed below).

PLEUROSTERNIDAE (8)

This family, as recognized by Gaffney and Meylan (1988), consists of only two genera sharing one synapomorphy, separation of the pterygoids by the basisphenoid. It is possible that as other non-eucryptodiran cryptodires become better known, this will be altered. Of all the basic taxa used in this analysis, this is the one terminal taxon most likely to be non-monophyletic. Even if this were true, however, it is unlikely that it would alter the basic results because the characters used here do not vary greatly among pleurosternids or their apparent nearest relatives, the baenids.

BAENIDAE (9)

Baenid monophyly and a cladogram of included taxa is discussed in Gaffney (1972) and revised by Gaffney and Meylan (1988). With the removal of *Neurankylus* this family has a number of synapomorphies (i.e. dorsal lappet of prefrontal small or absent, incisura columellae auris partly or completely enclosing stapes and eustachian tube) and its monophyly is well corroborated.

PLESIOCHELYIDAE (10)

This family of Mesozoic marine turtles is most recently treated in Gaffney and Meylan (1988) who present synapomorphies and a cladogram with three included genera. Considering that a number of probable plesiochelyids are excluded as *incertae sedis* by Gaffney and Meylan (1988) because they lack skulls, it is likely that the composition and characterization of this family may vary with more work. Esclusion of the prootic from the trigenimal foramen is a synapomorphy uniting the family.

MEIOLANIIDAE (11)

The monophyly of this highly autapomorphic family of three genera is well established and described in Gaffney (1983) and Gaffney and Meylan (1988). The most prominent synapomorphy is paired horns born on unusually large squamosals.

CHELYDRIDAE (12)

We follow Gaffney and Meylan (1988) by including *Platysternon* in the Chelydridae. A synapomorphy for the family is the anterior-most caudals procoelous, followed by on biconvex caudal, remaining caudals being opisthocoelous. Bickham and Carr (1983) question the inclusion of *Platysternon* in the Chelydridae but this would not affect the character distributions. There are a number of extinct taxa, termed Sinemydidae/ Macrobaenidae, that are very likely to be either members of the Chelydridae or its sister group (or both). This analysis ignores sinemydids, but as we understand them at present, their inclusion would not alter the distribution of the characters used here.

CHELONIOIDEA (13)

Gaffney and Meylan (1988) present a cladogram and synapomorphies for this taxon, consisting of the living and extinct sea turtles. We consider the monopoly of this taxon to be well corroborated, based on the modification of the forelimbs into flippers and an articular facet for the last cervical on the nuchal bone.

TRIONYCHOIDEA (14)

This taxon and the Testudinoidea contain most of the species diversity of the living turtles. The monophyly and relationships of included taxa of this large group has been the subject of much argument in the literature in the past (see Gaffney, 1984). The most recent analysis is in Maylan and Gaffney (1989) with a shorter version in Gaffney and Meylan (1988). Cladograms of included taxa are in Meylan (1987) and the two above-mentioned papers. We consider the monophyly of this taxon to be well corroborated, based on the small stapedial artery, palatine bone in the braincase, and other characters.

TESTUDINOIDEA (15)

This taxon is diagnosed and discussed in Gaffney and Meylan (1988). The monophyletic nature of the living representatives is supported by the absence of inframarginal scutes and the presence of large buttresses, but the placement of some fossil forms (e.g. *Echmatemys*, *Tsaeotenemys*) is in doubt. This does not affect the distribution of the characters used here.

The Characters

Almost all of the characters making up our character matrix have been used in published cladistic analyses of turtle relationships. We have tried to rely specifically on the characters in Gaffney and Meylan (1988) which is the most recent cladistic analysis of turtle higher categories. The distribution of several characters has been updated since that paper was prepared and one significant new character (39) from our on-going studies of the oldest pleurodires has been added. Most of the characters used are described in Gaffney (1975, 1984, 1990). For more information and descriptions of these characters, see the references indicated.

Our treatment of characters here is relatively "conservative" in terms of the various computer options available. We use no weighting (but see discussion under character 25), all characters are ordered and none are multistate. Attempts to weight characters reflect the nearly universal recognition that some characters are more accurate tests of relationships than others. The reasons can be complex but usually are resolved into assessments of homology hypotheses. Although there are efforts to quantify such assessments, in general, homology hypotheses are subjectively judged by such criteria as morphologic topology, complexity of structures, developmental constraints and congruence with other characters. The characters used here are, by vertebrate standards, relatively well tested, perhaps unusually well tested, homology hypotheses, but there are only 39 that we have decided to use in the analysis. We have effectively "weighted" by deleting possible characters that failed our tests of homology, (i.e. the tail club of *Proganochelys* and *Meiolania*). We are aware that some systematists (Kluge, 1989)

argue that "all relevant evidence" should be used. We consider characters relevant only if the homology hypothesis cannot be refuted.

The emphasis on proliferation of computer generated cladograms at the apparent expense of character analysis, is an unfortunate trend in cladistics. Most of the effort in morphology-based systematics should go into the formulation and testing of homology hypotheses of characters. Our "data" sets are not really data in the same sense as the relatively raw measurements and experimental results that are analysed in other fields. It is certainly true that all observations are hypothesis-biased but our character matrices should be summaries of extensive analyses of homology hypotheses. The ability provided by computers to manipulate large quantities of "data", regardless of the degree to which homology hypotheses have been (or can be) tested, can favour the production of weak phylogenetic hypotheses. Ideally, large numbers of well-analysed homology hypotheses should be used, but, as Platnick (1988: 312) has said: ". . . our analytical toolbox . . . already outweighs the supply of data worth analyzing".

(1) LACRIMAL BONE AND DUCT (PRESENT = 0, ABSENT = 1)

The generalized amniote condition of a lacrimal bone and lacrimal duct is present in *Proganochelys* (Gaffney, 1990), but absent in all other turtles (Gaffney, 1979).

(2) BASIPTERYGOID ARTICULATION (OPEN = 0, FUSED = 1)

The generalized amniote condition of a moveable articulation between the neurocranium and the palatoquadrate elements (Romer, 1956) is retained in *Proganochelys* but these units are fused in all other turtles (Gaffney, 1979). This is a complex morphologic feature and may be divided into different conditions. But the simple condition, of sutural fusion between basisphenoid, prootic and basisphenoid, seen in *Kayentachelys* (Gaffney et al., 1987), is here interpreted as primitive for casichelydians (turtles minus *Proganochelys*). All turtles, except *Proganochelys*, have at least this degree of fusion and contacts.

(3) VOMER (PAIRED = 0, SINGLE = 1)

More than one vomer (usually a pair) seems to be primitive for all amniotes (Romer, 1956). *Proganochelys* (Gaffney, 1990) has two, while all other turtles have one, which is interpreted as the advanced condition.

(4) LATERAL WALL TO MIDDLE EAR REGION (LATERAL WALL ABSENT = 0, LATERAL WALL PRESENT = 1)

Generalized amniotes, such as captorhinids (Heaton, 1979; Gaffney, 1990), have a middle ear region that is open at least laterally and ventrally. *Proganochelys* also has an open ear region but in all other turtles there is a variably developed flange of the quadrate that forms at least a partial lateral wall to the middle ear region.

(5) PROCESSUS PAROCCIPITALIS OF THE OPISTHOTIC (LOOSELY ARTICULATED, IF AT ALL, TO SQUAMOSAL AND QUADRATE = 0, TIGHTLY SUTURED TO SQUAMOSAL AND QUADRATE = 1)

Proganochelys agrees with the primitive amniote condition in having an opisthotic paroccipital process that is only loosely sutured to the more anterior elements (Gaffney, 1990). In the advanced condition, found in all other turtles, this process is tightly fused along its anterior margin to the quadrate and squamosal (Gaffney, 1979, 1990).

(6) Processus Trochlearis Octicum Formed by Prootic and Quadrate (Absent = 0, Present = 1)

The living cryptodires have the main adductor tendon or bodenaponeurosis directed over a process on the otic chamber (Schumacher, 1973; Gaffney, 1975, 1979). Although the tendon itself is never fossilized, the thickened bone on the anterodorsal surface of the prootic, the quadrate, and sometimes the parietal, is preserved in fossil skulls. *Proganochelys* lacks an otic process and this thickening is absent in all other amniotes (Gaffney, 1990). This is interpreted as the primitive chelonian condition. Pleurodires have no indication of thickening or of an otic trochlea, rather they have the condition seen in *Proganochelys* (Gaffney, 1990).

Although thickened bone in the prootic and quadrate *per se* is a relatively simple feature, the entire system of redirected bodenaponeurosis, cartilaginous covering of the process, and a true synovial capsule making up the articular region (all described in Gaffney, 1975, 1979) make this a complex character that could be divided into more than one character. There are no morphologic reasons to doubt the homology of this character and we interpret it as a well-established synapomorphy.

It has been suggested (Dryden, pers. commun., Gauthier et al., 1989) that this character and 20, the pterygoid trochlea, are homologous and should be analysed as two unordered states of the same character. The two trochlear conditions do have some common features. Both involve a redirection of the bodenaponeurosis of the main adductor musculature and both have a sesamoid cartilage at the trochlea. However, the morphologic structure of the two trochleas is completely different and involve no common skeletal elements.

Gaffney summarized the features arguing for non-homology in an earlier (1975) cladistic analysis of the Cryptodira and Pleurodira:

1. Bony elements of the trochlea are not homologous.
2. Morphology of the trochlear articulation surfaces is non-homologous (see characters 25 and 26).
3. Position of the trochlea within the M. adductor mandibulae internus is different in cryptodires and in pleurodires.

The redirection of the tendon appears to be related to common constraints imposed by the turtle skull and tendons commonly develop sesamoids when they cross a bone or joint (Haines, 1969). We see no evidence that the two trochlea are homologous and instead consider them well tested synapomorphies for their respective groups.

(7) Vertical Flange on the Processus Pterygoideus Externus (Absent = 0, Present = 1)

In captorhinids and most generalized amniotes the pterygoid flange ends laterally in a rugose, swollen area that bears a cartilage and lies medial to the mundplatte (Romer, 1956; Frazetta, 1962). *Proganochelys* has a smaller pterygoid flange (in turtles termed the

processus pterygoideus externus) that has a rolled edge rather than a swollen one (Gaffney, 1990). Cryptodires have a vertical plate, oriented anteroposteriorly that bears the cartilage and mundplatte laterally. No other turtles or generalized amniotes have this vertical plate on the processus pterygoideus externus, which we, therefore, interpret as a cryptodire synapomorphy. In pleurodires, the processus pterygoideus externus is laterally directed and is covered by a curved anterolateral facing plate (see character 20).

(8) PREFRONTAL–VOMER CONTACT (ABSENT = 0, PRESENT = 1)

Although *Captorhinus* has a descending process of the prefrontal that partially defines the foramen orbitonasale (Heaton, 1979), the prefrontal does not extend ventrally to reach the vomer. A similar condition exists in *Proganochelys* in which the prefrontal ventral process is more extensive but still does not reach the vomer (earlier statements in Gaffney et al., 1987, about the uncertainty of this contact have been clarified by further preparation of *Proganochelys* skulls, see Gaffney, 1990). In pleurodires, the prefrontal also does not reach the vomer but in all cryptodires it does. We interpret this feature as a cryptodire synapomorphy.

(9) MIDDLE EAR WITH OSSIFIED FLOOR FORMED BY A POSTEROMEDIAL PROCESS OF THE PTERYGOID, PREVENTING VENTRAL EXPOSURE OF THE PROOTIC (ABSENT = 0, PRESENT = 1)

Within the cryptodires only *Kayentachelys* lacks this process of the pterygoid. Before the discovery of *Kayentachelys* (Gaffney et al., 1987), Gaffney (1975) considered this feature a cryptodiran synapomorphy. Now it is interpreted as a synapomorphy of the Selmacryptodira (Gaffney and Meylan, 1988), the group consisting of all cryptodires except *Kayentachelys*. This feature does not occur outside turtles. In pleurodires the prootic is ventrally exposed.

(10) PALATAL TEETH (PRESENT = 0, TEETH ABSENT = 1)

Among amniotes, the presence of palatal teeth is widespread in forms thought to be primitive sister taxa of the Synapsida and Diapsida (Gauthier et al., 1988a,b). Captorhinids and *Proganochelys* also have palatal teeth and this is interpreted as the primitive condition. All pleurodires lack palatal teeth and all cryptodires, except *Kayentachelys*, also lack them. This is a character that is consistent with a paraphyletic Cryptodira in which *Kayentachelys* would be the sister group of pleurodires plus remaining cryptodires. However, we think that a "loss" character of this sort, in which the actual synapomorphy is "smooth palate", is difficult to homologize morphologically. Many amniote groups have independently lost the palatal teeth and evolved a smooth palate (fide Gauthier et al., 1988a,b) and the resultant bone surface appears nearly the same in all. Although we feel that this character is less reliable in terms of evidence for homology, than a complex character such as the otic trochlear system, there is no strictly morphologic evidence for homoplasy. The smooth palate of cryptodires is virtually identical to the smooth palate of pleurodires, and this character is included, unweighted, in the analyses.

(11) INTERPTERYGOID VACUITY (OPEN = 0, CLOSED = 1)

The primitive amniote condition of the palate is the presence of a space along the median line so that the pterygoids are separated. *Captorhinus* and other generalized amniotes show this condition. *Proganochelys* (Gaffney, 1990) has an interpterygoid vacuity—which has a small midline contact of the pterygoids anteriorly but is nonetheless distinct and well developed. In *Kayentachelys* there is also an interpterygoid vacuity, but it is more restricted than in *Proganochelys*. In the advanced condition the pterygoids meet for most of their length on the midline, although the basisphenoid may separate them to a variable extent. In any case, a space open to the cavum cranii is no longer present. All pleurodires have a closed palate and all cryptodires, except *Kayentachelys*, also have a closed palate. Although our shortest cladogram requires the independent acquisition of this character or a reversal in *Kayentachelys*, there is no morphologic evidence for homoplasy of this character in turtles. However, in other tetrapods the loss of kinesis and fusion of the basipterygoid articulation is almost always followed by the closure of the interpterygoid vacuity. This appears to have occurred independently at least in temnospondyls, synapsids and crocodilians.

(12) CANALIS CAROTICUS INTERNUS AT LEAST PARTIALLY FORMED BY PTERYGOID (NOT FORMED BY PTERYGOID TO ANY EXTENT = 0, PARTIALLY OR ENTIRELY FORMED BY PTERYGOID = 1)

In captorhinids and other generalized amniotes, the foramen by which the internal carotid artery enters the skull is formed entirely within the basisphenoid. This is also the case in *Proganochelys* and *Kayentachelys* (for pleurodire condition see below) and is interpreted as the primitive condition for turtles (Gaffney, 1990). Within all other cryptodires, an extension of the pterygoid posteriorly and medially forms at least the lateral wall. In pleurosternids and baenids, both the pterygoid and basisphenoid form the actual entry foramen of the carotid (foramen posterior canalis carotici interni), while in other cryptodires the canals is buried within the pterygoid (Gaffney, 1979; Gaffney and Meylan, 1988).

(13) CANALIS CAROTICUS INTERNUS FORMED ENTIRELY BY PTERYGOID POSTERIORLY (NOT FORMED ENTIRELY BY PTERYGOID = 0, FORMED ENTIRELY BY PTERYGOID TO DISTAL LENGTH = 1)

In this character the entrance foramen of the carotid (foramen posterior canalis carotici interni) is entirely formed by the pterygoid and the posterior portion of the canalis caroticus internus is also formed by the pterygoid (Gaffney, 1979). It is likely that character 12 is the primitive condition for this character, and that 12 and 13 could be coded as a morphocline. We have preferred to treat them as separate characters (we did run them both ways and the shortest tree was the same).

(14) CANALIS CAROTICUS INTERNUS FORMED ENTIRELY BY PROOTIC (ABSENT = 0, PRESENT = 1)

The primitive condition for this character is the generalized amniote one where the carotid enters via the basisphenoid, also seen in *Proganochelys* (Gaffney, 1990). In all

pleurodires, the carotid entrance is formed by the prootic (or in some advanced forms the pterygoid covers the entrance) and this is interpreted as the derived condition (Gaffney, 1979; Gaffney and Meylan, 1988). As developed in pleurodires, this character does not occur outside turtles.

(15) PARIETAL–SQUAMOSAL CONTACT (PRESENT = 0, ABSENT = 1)

This character reflects the degree of temporal emargination of the skull roof. Captorhinids and other generalized tetrapods have solid skull roofs with a broad parietal–squamosal contact. Turtles (with some exceptions) show a general trend toward temporal emargination, but this is a variable character with a simple morphology, often difficult to homologize. *Proganochelys* has a well-developed parietal–squamosal contact and is interpreted as primitive within turtles (Gaffney, 1990). Pleurodires have two distinct patterns; absence of contact in most pelomedusids and presence in most chelids. On the basis of outgroup comparison and an assumed phylogeny of pleurodires (Gaffney, 1988; Gaffney and Meylan, 1988), a well-developed parietal–squamosal contact is interpreted as primitive for pleurodires and the pelomedusid condition is interpreted as derived independently within the Pleurodira.

Cryptodires, such as *Kayentachelys* and pleurosternids, have a well-developed parietal–squamosal contact similar to the primitive chelonian condition and to the proposed primitive pleurodire condition, and this is interpreted as primitive within Cryptodira. Most remaining cryptodires have *a posterior* temporal emargination that separates or nearly separates the parietal and squamosal, and Gaffney (1984) has proposed that this character is a synapomorphy for the Daiocryptodira (consisting of baenids, plesiochelyids, meiolaniids, chelydrids, chelonioids, trionychoids and testudinoids). There are, however, inconsistencies with this character because a broad squamosal–parietal contact does occur within the Daiocryptodira. This contact occurs in some baenids, but not primitively for the group, if one uses Gaffney (1972) and Gaffney and Meylan (1988) as an assumed phylogeny. Some cheloniids also have a broad contact, but again using lower level cladograms of Gaffney and Meylan (1988) it is not primitive for the Chelonioidea. Meiolaniids have an unusually extensive contact, greater than in *Proganochelys*. The unusual shape of the parietal, squamosal and related skull roofing elements has been interpreted as unique to this family (Gaffney, 1983) and the small size of the parietal in *Meiolania* has been interpreted (ibid.) as morphologically more consistent with the derived emarginate condition than with the primitive chelonian condition. There is, therefore, good evidence that homoplasy of this character has occurred in baenids, meiolaniids, pleurodires and chelonioids.

(16) THICKNESS OF PTERYGOID FLOOR OF CANALIS CAROTICUS INTERNUS (THIN OR ABSENT = 0, THICK = 1)

Within the turtles that have a pterygoid-formed canalis caroticus internus, the plesiochelyids have a thin floor, here interpreted as the primitive condition. In some specimens of *Plesiochelys* (Gaffney, 1976), the seam or suture closing the canalis is still present. The thick condition lacks indication of a suture and is seen in all other eucryptodires. Presumably the thick, seamless condition is more advanced because during development the canalis floor is thin at first and shows the enclosing of the carotid (Kunkel, 1912).

(17) EPIPTERYGOID (PRESENT = 0, ABSENT = 1)

As ossified epipterygoid bone is a primitive amniote feature (Romer, 1956) and its absence is derived. All known cryptodires have an epipterygoid bone or cartilage precursor, but a separate epipterygoid is lacking in pleurodires. In *Dermochelys*, a chelonioid, the epipterygoid does not ossify, but the epipterygoid cartilage (the processuss ascendans of the palatoquadrate cartilage) is present. Ossified epipterygoids are present throughout the remaining Chelonioidea, and dermochelyids have extensive retention of cartilage in the adult.

In most baenids, the epipterygoid is fused to the parietal but juvenile specimens from the Cretaceous of Alberta, being studied by D. Brinkman, show its presence as in all other cryptodires.

Pleurodires have no indication of an epipterygoid and do not as far as is known, retain a cartilage remnant in the adult (Gaffney, 1975). As yet unpublished developmental data from pleurodires (Esswein, pers. comm.) suggests that the cartilage precursor of the epipterygoid does not form in pleurodires.

(18) NASAL (PRESENT = 0, ABSENT = 1)

Paired nasal bones are the primitive amniote and chelonian condition, being present widely in amniotes and in *Proganochelys*. With pleurodires nasals are present in chelids, but absent in pelomedusids. Within cryptodires, nasals are lost (or fused) in the baenid *Baena* (Gaffney, 1972) and *Palatobaena* (Archibald and Hutchison, 1979), and we interpret this as an independent acquisition of this character. Chelydrids, trionychoids and testudinoids all lack nasals, but the primitive condition of chelonioids appears to be the presence of nasals. Living chelonioids have no nasals.

The absence of nasals is generally accompanied by the relatively large size of the prefrontals, although this is not always the case. The distribution of this character shows evidence of homoplasy within families.

(19) PREFRONTALS (NOT MEETING IN MIDLINE = 0, MEETING IN MIDLINE = 1)

Captorhinids and other generalized amniotes, as well as *Proganochelys*, have the dorsal lappets of the prefrontals separated from each other by contact of the nasals and frontals. In pelomedusids and living cryptodires, the prefrontal lappets are large and meet in the midline. Within pleurodires, the chelids have what is interpreted as the primitive pleurodiran condition, the prefrontals being separated. Pelomedusids, having prefrontals meeting, are interpreted as derived within Pleurodira.

In the cryptodires, prefrontals are separated in *Kayentachelys*, pleurosternids, baenids and meiolaniids, but they meet in plesiochelyids and the remaining Eucryptodira. There is some morphologic evidence of homoplasy in meiolaniids (Gaffney, 1983) because the unusual skull roof of *Meiolania* has uniquely large nasal bones, containing part of a system of sinuses not found in other turtles.

(20) PROCESSUS TROCHLEARIS PTERYGOIDEI (ABSENT = 0, PRESENT = 1)

All pleurodires for which the skull is known, have the main adductor tendon (or bodenaponeurosis) redirected over a trochlea formed by a lateral process of the

pterygoid, the processus trochlearis pterygoidei (Schumacher, 1973; Gaffney, 1975). This trochlea is functionally analogous but not homologous to the trochlea in cryptodires. The elements that form it are quite different (see character 6 above and Gaffney, 1975, 1979). In pleurodires, the processus trochlearis pterygoidei is formed by a process of the pterygoid that has a cartilage-covered anterolateral surface in contact with oral mucosa. The process appears to be homologous with the mundplatte of other amniotes, which cryptodires retain in its generalized amniote condition. A true synovial capsule as seen in the otic trochlea of cryptodires is absent. The primitive condition would be a main adductor tendon without any trochlear articulation extending from the adductor musculature directly to the lower jaw, as appears to be the case in *Proganochelys* (Gaffney, 1990).

(21) QUADRATE WITH VENTRAL PROCESS EXTENDING MEDIALLY TO BRAINCASE BELOW CRANIOQUADRATE SPACE (ABSENT = 0, PRESENT = 1)

A separate canal for the hyomandibular branch of the facial nerve, absent in other amniotes, is present in all known pleurodire skulls and absent in other turtles and amniotes. The primitive condition would be that seen in captorhinids, *Proganochelys* and *Kayentachelys* (Gaffney, 1979; Gaffney and Meylan, 1988).

(22) HYOMANDIBULAR BRANCH OF FACIAL NERVE (NERVE LIES WITHIN CANALIS CAVERNOUS = 0, LIES IN ITS OWN CANAL = 1)

This character, absent in other amniotes, is found in all known pleurodire skulls (Gaffney, 1975), and has also been reported in *Meiolania* (Gaffney, 1983). There is some evidence of homoplasy regarding *Meiolania* because the basicranium is unusually thick and well ossified, but this also occurs in many testudinids and there is no separation of the hyomandibular nerve. Also, as meiolaniids are extinct there is no certainty that this canal contained the hyomandibular nerve, but scoring it as present is conservative relative to the purpose of this paper.

(23) FORAMEN PALATINUM POSTERIUS (IN FLOOR OF ORBIT = 0, BEHIND ORBIT = 1)

The primitive condition is seen in generalized amniotes, *Captorhinus, Proganochelys* and all cryptodires. The advanced condition is found in all pleurodires (Gaffney, 1975, 1979).

(24) SUPRATEMPORAL (PRESENT = 0, ABSENT = 1)

The supratemporal bone is present in the primitive tetrapod and primitive amniote conditions (Romer, 1956), and is also present in *Captorhinus* and *Proganochelys* (Gaffney, 1990). The advanced condition is the absence of the bone and it is absent in all turtles except *Proganochelys*.

(25) SYNOVIAL CAPSULE ON OTIC CHAMBER (ABSENT = 0, PRESENT = 1)

A true, enclosed synovial capsule with cartilaginous surfaces forming the articulation between the adductor cartilage and the processus trochlearis oticum occurs in all living cryptodires as part of the jaw mechanism. The structure of this capsule is described in

Schumacher (1956) and Gaffney (1975, 1979). Clearly, this character is a functional element of the trochlear mechanism in cryptodires and its presence is correlated with the otic process formed by the quadrote and prootic. In purely morphologic terms, however, there are no developmental or other constraints that require complete dependence. We have chosen to use this character and the next one (ductus angularis oralis) to reflect the importance that the jaw mechanism holds in our analysis of chelonian phylogeny. The respective trochlear mechanism characteristic of living cryptodires and pleurodires are complex features that widely affect the cranial architecture. We could reflect this by combining the otic trochlea and synovial capsule characters and then weighting them. However, we think that a better argument can be made for taking a somewhat conservative approach by using two characters to describe this complex. Three or even more characters could be used (e.g. position of the sesamoid within the adductor muscle, histological nature of the trochlear surface, positions of pinnae in M. adductor mandibularis internus), if we choose to "atomize" it. There is no completely satisfactory method to reflect quantitatively the higher confidence we have in homology hypotheses of the respective jaw mechanisms and associated basicranial features of cryptodires and pleurodires. We feel using at least two characters in this analysis is justifiable. The presence of a synovial capsule cannot be definitely determined for fossil taxa (although nutrient rich rugosities could be used as an indication) and our data matrix reflects this with a question mark for all extinct cryptodires.

(26) DUCTUS ANGULARIS ORALIS (ABSENT = 0, PRESENT = 1)

In all living pleurodires, the mundplatte is highly modified to function as an articulation surface for the trochlear mechanism in the jaw. The primitive condition of the mundplatte is a pocket or fold of the soft tissues of the mouth at the lateral corners of the oral cavity where the coronoid or other part of the lower jaw passes lateral to the pterygoid process of the palate. Two bony surfaces could contact each other here every time the mouth is closed and the mundplatte provides mucous-secreting tissue to lubricate this contact so that damage and abrasion are avoided. Living lizards have essentially the primitive condition (Frazetta, 1962) and cryptodires are only slightly different.

The living pleurodires, however, have a unique and unusual structure, the ductus angularis oralis, that appears to be the homologue of the mundplatte (Gaffney, 1975, 1979). This structure, described by Schwarz (1934), Schumacher (1973) and Gaffney (1975, 1979) is a fluid-filled sac that lies between the main adductor sesamoid (cartilago transiliens) and the processus pterygoideus trochlearis, providing a lubricated surface for the tendon. The ductus angularis oralis communicates with the oral cavity by means of a narrow duct and is made up of the same type of mucous-secreting tissue as the rest of the mouth. It seems to perform the same function as the synovial capsule of cryptodires, i.e. lubrication for the sesamoid in the main adductor tendon.

As with character 25, the synovial capsule of cryptodires, this character is closely correlated with the trochlear mechanism and might be considered as correlated with character 20, the processus trochlearis pterygoidei.

(27) POSTORBITAL–SQUAMOSAL CONTACT (PRESENT = 0, ABSENT = 1)

Temporal emargination of the dermal skull roof has developed in turtles perhaps as a

functional analogue to the fenestration of diapsids and synapsids. The type of emargination seen in turtles is unique to this group and does not occur in other amniotes.

The degree of temporal emargination in turtles is correlated with the size and contacts of the skull roof bones. A relatively extreme degree of emargination separates the post-orbital and squamosal bones and is characteristic of the Trionychoidea and Testudinoidea (Gaffney, 1979; Gaffney and Meylan, 1988). This character has no serious contradictions as presented in this analysis but in qualitative evaluation of homology hypotheses it is relatively poor. The temporal roof of turtles has apparently repeatedly evolved emarginate and well-roofed conditions (Gaffney, 1979; Gaffney and Meylan, 1988) and the simple morphology of the region makes it difficult to develop morphologic arguments of any complexity. Nonetheless, this character as used here is relatively consistent.

(28) PERIPHERAL BONES (MORE THAN 11 PAIRS = 0, 11 PAIRS OR FEWER = 1)

The primitive condition is found in *Proganochelys*, which has 17 pairs of peripheral bones (Gaffney, 1990). All other turtles have 11 pairs, as found in *Kayentachelys*, pleurosternids and pleurodires. Baenids have 11 pairs with a divided pygal (as interpreted by H. Hutchison, pers. comm.), while many trionychoids have fewer than 11 pairs. The absence of a shelled outgroup for turtles makes shell characters less reliable in some cases, but the acceptance of *Proganochelys* as the sister group to all other turtles (a relatively well-tested hypothesis) allows resolution of many shell characters.

(29) SUPRAMARGINAL SCALES (PRESENT = 0, ABSENT = 1)

Proganochelys and the pre-Cretaceous pleurodires *Proterochersis* and *Platychelys* have supramarginal scales on the carapace, and this is interpreted as the primitive condition (Gaffney, 1990). Cryptodires (except *Macroclemys*) and the extant pleurodires lack supramarginals, the derived condition. Scale variations, however, are common in turtles (Zangerl, 1969) and all turtles show a general tendency toward bone and scale reduction in the shell. All other amniotes lack a shell of the sort seen in turtles.

(30) MESOPLASTRA NOT MEETING IN MIDLINE (MESOPLASTRA PRESENT AND MEET IN MIDLINE = 0, MESOPLASTRA DO NOT MEET ON MIDLINE = 1)

Extension of the mesoplastra across the plastron to meet in the midline is interpreted as the primitive condition because this occurs in *Proganochelys* (Gaffney, 1990). This is another shell character that is morphologically simple and homology of the advanced conditions of separated or absent mesoplastra is difficult to test using morphology. All other amniotes lack mesoplastra.

(31) MESOPLASTRA ABSENT (MESOPLASTRA PRESENT = 0, MESOPLASTRA ABSENT = 1)

The complete absence of mesoplastra characterizes the pleurodiran family Chelidae and the eucryptodires (meiolaniids, plesiochelyids, chelydrids, chelonioids, trionychoids and testudinoids). The presence of mesoplastra in *Proganochelys* is interpreted as the primitive condition and their absence is derived. This character and character 30 could

be placed in the matrix as one character, with the absence of mesoplastra 31 coded as more derived than mesoplastra not meeting in midline 30. In our shortest tree, we required mesoplastra to be lost twice, once in chelids and once within cryptodires. There is no morphologic evidence to support this.

(32) Pelvis–Shell Attachment (Pelvis Attached to Shell by Ligaments = 0, All Three Bones of Pelvis Tightly Sutured to Shell = 1)

The classic shell character of pleurodires is the suturing of the pelvis to the shell. The adoption of *Proganochelys* as the sister group to all other turtles allows the interpretation of this character as derived. *Proganochelys* (Gaffney, 1990) has a free pelvis which is therefore the primitive condition. Cryptodires retain this condition. In all known pleurodires, all three pelvic elements are sutured to the shell, ilum to the carapace, pubis and ischium to the plastron. There is no evidence that this character exhibits any degree of homoplasy.

(33) Central Articulations of Cervical Vertebrae (Platycoelous or Amphicoelous = 0, Concavo-convex = 1)

The primitive condition for amniotes is amphicoelous vertebrae, as seen in *Captorhinus*. *Proganochelys* has amphicoelous centra and this is interpreted as the primitive chelonian condition (Gaffney, 1990). If the baenid cladogram of Gaffney (1972) and Gaffney and Meylan (1988) is accepted, then the primitive baenids are amphicoelous and advanced ones have formed centra. We have therefore coded Baenidae as zero for this character. Formed centra appear independently within a number of other amniote groups and the widely divergent central articulation pattern in turtle necks (Williams, 1950) is also evidence of probable homoplasy.

(34) Anterior Articulation of First Thoracic Vertebral Centrum (Faces Anteriorly = 0, Faces Anteroventrally = 1)

In the absence of a shelled outgroup the primitive condition is based on *Proganochelys* (Gadfney, 1990). The derived condition (Meylan and Gaffney, 1989) is found only in the living cryptodires (Chelydridae, Trionychoidea, Chelonioidea and Testudinoidea). The posterior central articulation of the eighth cervical is formed to fit closely the ventrally facing first thoracic. This character is the principal morphologic indication of a well-developed vertical neck withdrawal mechanism. There is no evidence of homoplasy.

(35) First Thoracic Rib (Extends to Peripherals or Nearly So and Lies Behind the Tip of the Auxillary Buttress = 0, Extends Less than Halfway Across First Costal = 1)

In the absence of a shelled outgroup, *Proganochelys* is interpreted as having the primitive condition (Gaffney, 1990). The primitive condition also occurs in *Kayentachelys* and the other extinct cryptodires, and in *Proterochersis* and *Platychelys*, the two pre-Cretaceous pleurodires. The advanced condition (Meylan and Gaffney, 1989), in which the rib is much smaller and not near the edge of the costal, appears to have evolved

independently within pleurodires and within cryptodires (in our favoured cladogram), but there is no morphologic evidence for homoplasy.

(36) CHEVRONS (WELL DEVELOPED AND PRESENT ON NEARLY ALL CAUDALS = 0, SMALL TO ABSENT; IF PRESENT, ONLY ON A FEW POSTERIOR CAUDALS = 1)

The presence of chevrons is a widespread amniote feature, occurring in *Captorhinus* and *Proganochelys* (Gaffney, 1990). They are small or absent in the advanced condition. As a "loss" character, the relatively simple morphology of the advanced condition makes rigorous homology assessments difficult. In our preferred cladogram, we require independent loss of chevrons within the Cryptodira (absent in Chelonioidea, Trionychoidea and Testudnoidea) and in all pleurodires.

(37) CAUDALS (AMPHICOELOUS OR OPISTHOCOELOUS = 0, PROCOELOUS = 1)

Amphicoelous caudals are widespread in the primitive amniote condition and in *Captorhinus* and *Proganochelys* (Gaffney, 1990). We are here including opisthocoelous caudals and amphicoelous together because the distinction is often gradual. Baenids, meiolaniids and chelydrids (except at the base of the tail) have distinctly opisthocoelous caudals and we conclude that this is primitive with respect to completely procoelous caudals. There is no morphologic evidence for homoplasy but in our preferred cladogram the appearance of procoelous caudals must occur independently within Cryptodira and Pleurodira.

(38) CERVICAL RIBS (PRESENT = 0, ABSENT = 1)

Cervical ribs are a primitive amniote feature and occur in *Proganochelys* (Gaffney, 1990). Gaffney (1985) has argued that cervical ribs also occur in pleurosternids and *Kayentachelys*, on the basis of articulation facets, although the ribs themselves are as yet unknown. *Meiolania* has cervical ribs, but their shape is different from *Proganochelys* and the expected primitive chelonian pattern and their presence is probably homoplastic. They are nonetheless coded as present.

(39) TENTH THORACIC VERTEBRA (NOT INCORPORARED IN SACRUM = 0, INCORPORATED IN SACRUM = 1)

One of the few shell characters beside the pelvis that appears to be a pleurodire synaponorphy is this character (Fraas, 1913). It is also one of the few characters in our analysis determinable in the pre-Cretaceous pleurodires. It relies on the acceptance of *Proganochelys* (Gaffney, 1990) as having the primitive condition. *Captorhinus* and other primitive amniotes also lack this character. There is no evidence of homoplasy.

Results

The Branch and Bound algorithm of PAUP found a single most parsimonious cladogram to explain the distribution of the 39 characters for 14 higher taxa of turtles shown in Table 1. The cladogram (Fig. 1) has a length of 55 steps and a consistency
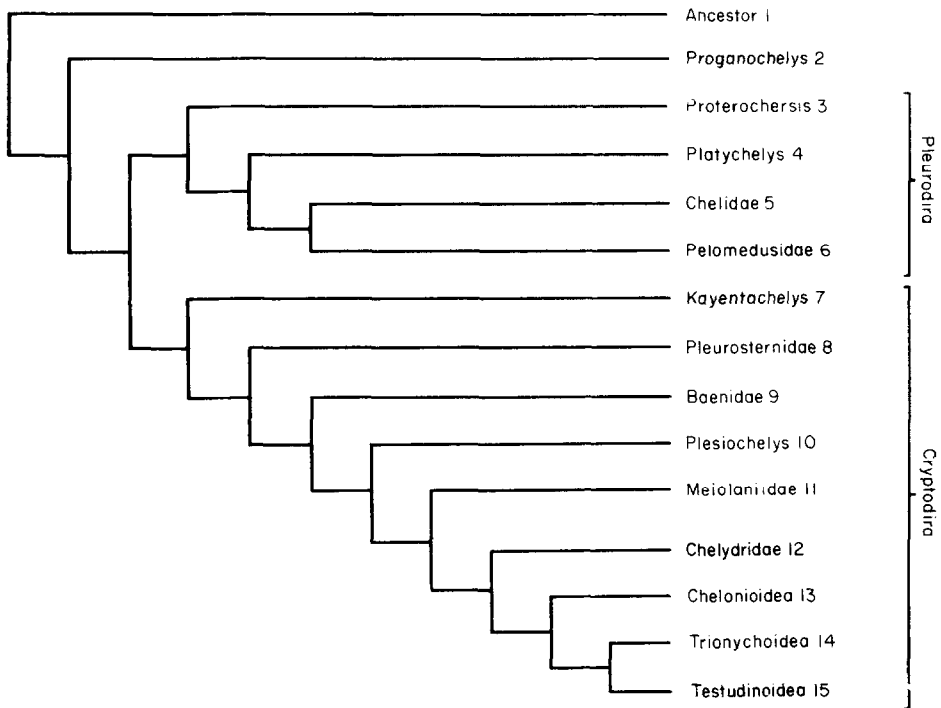
Fig. 1. Shortest tree for higher relationships of turtles based on 39 characters (Table 1). Total length is 55 steps, CI = 0.709, RC = 0.601.

index of 0.709, a retention index of 0.848 and a rescaled consistency index of 0.601. The topology is identical to that summarizing higher turtle relationships in Gaffney and Meylan (1988). The Pleurodira and Cryptodira are each shown to be monophyletic and the arrangements within these taxa are as proposed in that paper.

Optimization for 14 of the 39 characters on our solution cladogram is ambiguous, largely as a result of missing values for the two first clades within the Pleurodira, *Proterochersis* and *Platychelys*. However, all of the higher taxa are unambiguously supported. Seven characters unambiguously support the Casichelydia, four support the Cryptodira and two the Pleurodira (inclusive of the two shell taxa). Eleven terminal taxa do not enjoy unambiguous support but this is not surprising since we did not include autapomorphies for terminal taxa.

Discussion

We consider the hypothesis for higher relationships among turtles proposed in Gaffney and Meylan (1988) to be corroborated by the current study. However, there are alternative hypotheses worthy of discussion. Gauthier et al. (1989) rely on Dryden (1988) to suggest that the Cryptodira is not monophyletic. We have attempted to judge the strength of this alternative by examining the additional tree length required and the corroboration of homology hypotheses for characters that are critical to these two alternatives.
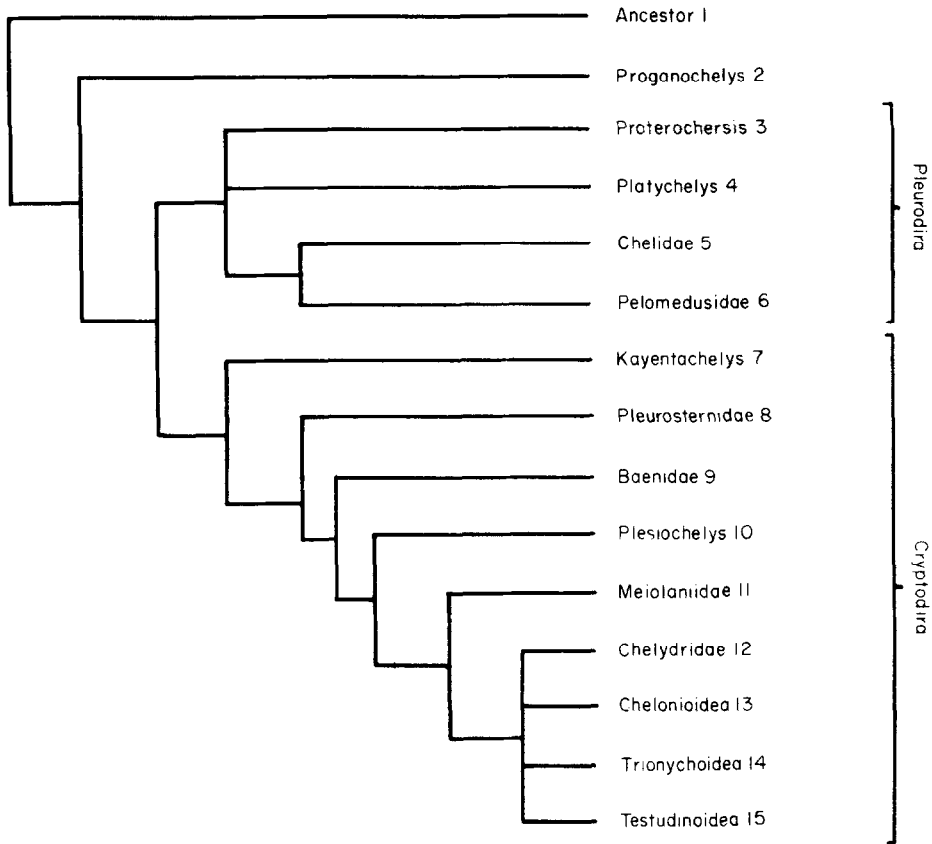
Fig. 2. Strict consensus tree of all solutions 56 or fewer steps in length.

The shortest tree we obtained was 55 steps. At 56 steps, PAUP yields seven trees, all of which retain a monophyletic Pleurodira and Cryptodira. A strict consensus tree of these seven (Fig. 2) has multichotomies in those regions of higher turtle phylogeny with which we have not been fully satisfied. Although monophyly of the Pleurodira is supported, the relationships between the Mesozoic genera *Proterochersis* and *Platychelys* and the Eupleurodira (Chelidae plus Pelomedusidae) are weak because the mesozoic genera lack skulls. Similarly, the monophyly of the Cryptodira is indicated, but the relationship of two families, Pleurosternidae and Baenidae, to the Eucryptodira may best be considered incompletely resolved. One alternative suggests the resurrection of Gaffney's (1975) Paracryptodira uniting these families. Also within the Cryptodira, resolution of the relationships among the living families (the Polycryptodira) is less than completely satisfactory, based on the characters used here. However, the relationships within the Polycryptodira are not the focus of this paper and we have intentionally deleted characters that might more adequately resolve the relationships within this group (i.e. plastral buttresses, bridge sutures) because we are unsure of character distributions in some taxa currently under study.

At 57 steps, two steps beyond our shortest tree, there are 38 equally parsimonious trees. A majority-rule concensus tree of these 38 trees (Fig. 3) shows that nearly all of these trees support a monophyletic Pleurodira and Cryptodira. The Pleurodira is
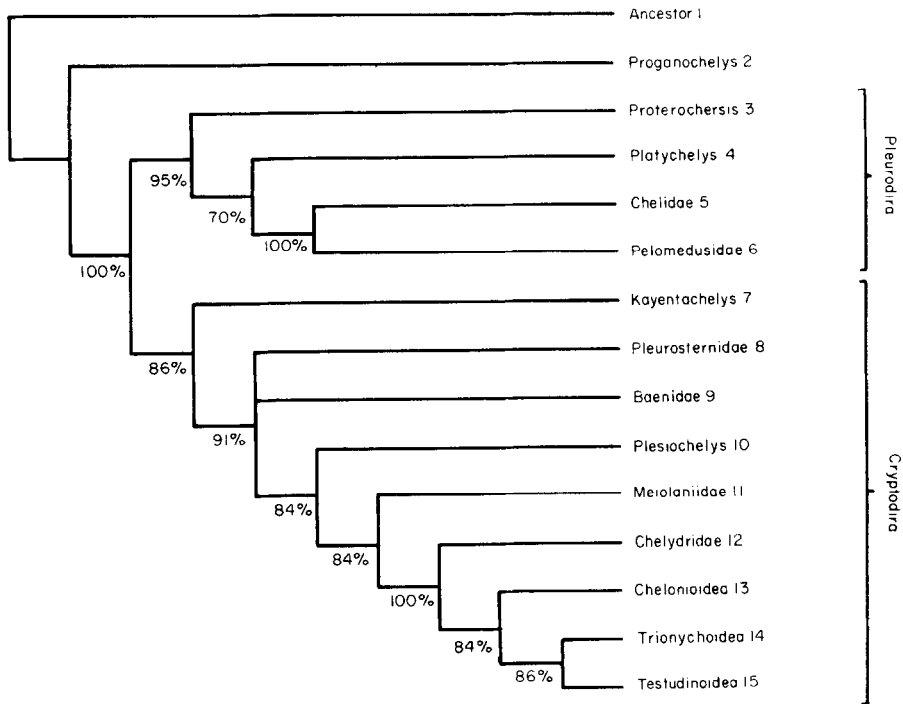
Fig. 3. Majority rule consensus tree of all solutions 57 or fewer steps in length.

monophyletic in 36 (95%) of them and the Cryptodira is monophyletic in 31 (82%) of them.

The alternative to a monophyletic Cryptodira used in seven of the 38 trees places *Kayentachelys* as the sister group to the Pleurodira plus the remainder of the Cryptodira. This is the solution advocated by Gauthier et al. (1989). Although the possibility of a paraphyletic Cryptodira is not remote if one considers only the number of steps involved, an examination of the homology hypotheses for the critical characters at this level reveals that the argument for a monophyletic Cryptodira is supported by characters for which more defendable homology hypotheses can be proposed. Characters supporting the monophyly of the Pleurodira plus the Cryptodira exclusive of *Kayentachelys*, are characters for which the morphological support for homology is weak or absent.

Only six characters differ in their consistency between arrangements with a monophyletic versus paraphyletic Cryptodira. In the shortest solution (55 steps) with a monophyletic Cryptodira the otic trochlea (character 6), the vertical flange of the pterygoid (character 7), and prefrontal-vomer contact (character 8) appear once, while the loss of palatal teeth (character 10) and the closure of the interpterygoid vacuity (character 11) occur twice. In the 57 step solution with a paraphyletic Cryptodira, the otic trochlea, pterygoid flange and prefrontal-vomer contact appear twice while palatal tooth loss and interpterygoid vacuity loss occur only once. In addition, the condition of the mesoplastra is slighty more consistent with the former solution (CI = 0.67) than with the latter (CI = 0.50).

The features that support monophyly of the Cryptodira, the pterygoid flange, prefrontal–vomer contact, and particularly, the otic trochlea, involve novel structures or

novel contacts not repeated in groups outside of turtles. For these characters, there is strong morphological evidence for homology. The two characters supporting the solution with the paraphyletic Cryptodira are loss characters. The conditions that result when palatal teeth and interpterygoid vacuities are lost offer fewer possibilities for morphological support of homology.

The higher consistency of characters supporting the monophyly of the Cryptodira is also reflected in the results from recursive weighting of characters based on the results at 57 steps. The solution tree that results after all characters are weighted on the basis of their average consistency in all trees of 57 steps or fewer, is identical to our most parsimonious solution (Fig. 1; characters were weighted on a linear scale such that any character having an average CI of 1.0 had a weight 10-times greater than a character having an average CI of 0.0). This result is not surprising in light of the majority-rule consensus tree in which monophyly of the Cryptodira (and thus high consistency of its defining features) is abundant and paraphyly of the Cryptodira is relatively rare.

Our conclusions differ from those of Dryden (1988, as reported by Gauthier et al., 1989) for three reasons. We treat otic and pterygoid trochlea as independently derived phenomena (see discussion of characters 6, 20, 25 and 26). We have evidence for the monophyly of the Pleurodira that is used here for the first time (character 39); and we have data for two taxa that were apparently unavailable to Dryden (*Proterochersis* and *Platychelys*).

If these two earliest pleurodires are deleted from our analysis, the result is two equally parsimonious cladograms of 54 steps. One has the topology shown in Fig. 1. In the other, the Cryptodira is broadly paraphyletic with respect to the Pleurodira: the Pleurodira is the sister group to the Polycryptodira. If only living pleurodires are included in the study, monophyly of the pleurodira is still strongly supported, but characters, which our results suggest occur in parallel, conflict with characters supporting monophyly of the Cryptodira. It is only when primitive pleurodires are included and the monophyly of that group upheld, that it becomes clear that loss characters of the shell (i.e. loss of supramarginal scales, and inframarginal scales, and the reduction of mesoplastra), occur independently in pleurodires and cryptodires. It should be emphasized that these two early pleurodires are known only from shells and the discovery of very early pleurodire skulls will provide a further test of our hypothesis that loss characters of the skull, like those of the shell, arose independently in the two major groups of living turtles.

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