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## A cladogram of the pleurodiran turtles

[With 1 text-fig.]

Kladogram żółwi *Pleurodira*

**Abstract.** A cladogram for eleven pleurodiran genera plus the family *Chelidae* is tested using shared derived characters of the skull and postcranium. The Triassic pleurodire *Prote-rochersis* is the sister group of all other pleurodires based on the presence in all other pleurodires of the following characters: absence of cleithra, three or less supramarginals, mesoplastra not meeting in midline. The Jurassic pleurodire *Platychelys* is the sister group of *Pelomedusidae* plus *Chelidae* based on equidimensional or absent mesoplastra and no supramarginal scutes. The monophyletic groups of pelomedusids are hypothesized: *Bothremys*, *Taphrosphys*, *Pelomedusa*, and *Pelusios* characterized by the occipital condyle formed only by the exoccipitals; and *Podocnemis*, *Peltocephalus*, *Erymnochelys*, *Shweboemys*, and *Stereogenys* characterized by the hypertrophied carotid canal.

Systematic study of the side-necked turtles has significantly lagged behind study of their more diverse sister taxon, the cryptodires. Biogeographic and adaptive scenarios (PRITCHARD and TREBBAU, 1984; WOOD, 1985) have been proposed for pleurodires and a number of alpha-level fossil taxa named, but detailed descriptions of good fossil material and well-tested phylogenetic hypotheses are rare. Despite claims to the contrary (WOOD, 1985), this situation is not the result of inadequate material, rather it is the result of a lack of interest in producing rigorous systematic studies with character analyses. Pleurodires are not intrinsically different from other turtles and they deserve more attention.

A cladogram for chelids is available (GAFFNEY, 1977a) but there are none for the pelomedusids. Most of the named, extinct taxa of pelomedusids (see list in PRITCHARD and TREBBAU, 1984) are barely diagnosable (some, e. g., "*Carteremys*" and "*Sokotochelys*" are apparently without specimens), let alone susceptible to detailed character analysis. However, this does not reflect the real situation. There are a number of fossil taxa known from good skull and

posterian material that, when described, will significantly add to our knowledge of pelomedusid diversity. The recent trend of naming taxa based on inadequate material will be an unfortunate legacy for future workers who try to identify good material with the fragmentary types.

The purpose of this paper is to present a cladogram (Fig. 1) for pleurodires known well enough at the present time to determine character distributions. The numbers for the groups in Fig. 1 are discussed in the text. This hypothesis of relationships must be considered preliminary because of the absence of some taxa that are present in collections but are not described in detail. The addition of such taxa may alter the character distributions enough to significantly change the cladogram. A thorough comparative study of pleurodiran morphology, particularly cranial, is needed to search for more characters and to produce a better tested hypothesis of pleurodiran relationships. Nearly all of the characters used here are described in the literature; figures of the skulls and references to systematic studies of pleurodires can be found in GAFFNEY (1979).

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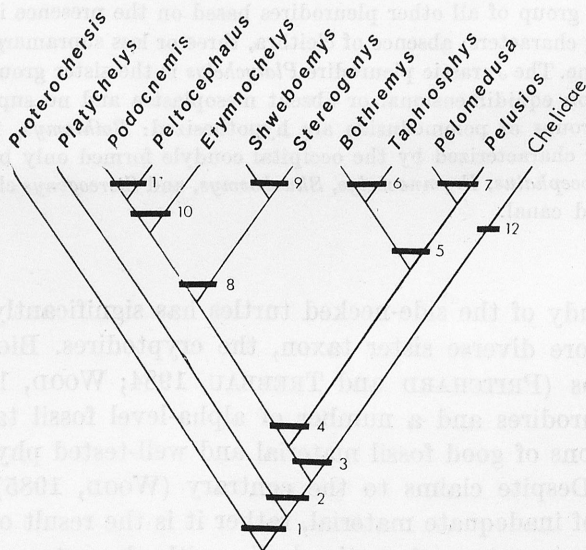


Fig. 1. A cladogram of recent and extinct pleurodiran turtles. The numbers refer to characters discussed in the text

1. *Pleurodira*. The derived cranial features of pleurodires are described in GAFFNEY (1975a), and the fused pelvis-shell of pleurodires was also hypothesized as a derived character in the postracnium. *Proterochersis* (FRAAS, 1913) and *Platycheilus* (RÜTIMEYER, 1873; BRÄM, 1965) have fused pelves in the pleurodiran manner and were identified as pleurodires by their original authors

and re-affirmed by GAFFNEY (1975a). *Proganochelys*, the sister taxon to all other turtles, has an unsutured pelvis and this may be hypothesized as the primitive chelonian condition.

*Proterochersis* and *Platycheilus* are known at present only from the shell (the vertebrae of *Platycheilus* await detailed description). *Proterochersis* has two pairs of mesoplastra meeting in the midline. *Proganochelys* has one pair meeting in the midline, and, in the absence of other considerations, this condition must be hypothesized as primitive for all turtles with two pairs of mesoplastra, in *Proterochersis*, being interpreted as autapomorphic. Nonetheless, medially meeting mesoplastra are primitive; all other pleurodires, including *Platycheilus*, have the mesoplastra separated, therefore, *Proterochersis* is hypothesized as the sister group to all other pleurodires.

2. Mesoplastra not meeting in the midline, absence of dorsal epiplastral processes, and three or less supramarginals, are the synapomorphies for the group containing *Platycheilus* and all other pleurodires.

*Proterochersis* has dorsal processes of the epiplastra articulating with the carapace. The dorsal epiplastral processes occur in *Proganochelys* and the cryptodire from the Early Jurassic Kayenta Formation. Both features are generalized amniote characters that are best interpreted as having been lost independently in cryptodires and pleurodires.

3. In terms of shell characters, *Platycheilus* is primitive compared with pelomedusids in having a nuchal scute and chelids in having mesoplastra. The mesoplastra in *Platycheilus* (BRÄM, 1965) are wider than long and extend closer to the midline than in pelomedusids. Equidimensional or absent mesoplastra and no supramarginal scutes may be used as synapomorphies at this level but hopefully cranial material will be found to aid in testing hypotheses of the pre-Cretaceous pleurodires in the future.

4. *Pelomedusidae*. This taxon is diagnosed and characters compared with chelids in GAFFNEY (1977a).

5. These four taxa, not otherwise similar in morphology, have the occipital condyle formed only by the exoccipital bones. This character does occur independently as a variation in *Carretochelys* (GAFFNEY, 1979).

6. *Bothremys* (GAFFNEY and ZANGERL, 1968; GAFFNEY, 1977b) and *Taphrosphys* (GAFFNEY, 1975b) are united by features of the quadrate. An extensive bony wall posterior to the stapes separates the stapes from the eustachian tube, and is unusual in pleurodires because in most pleurodires the stapes and eustachian tube are most commonly found together in the same bony opening. Both taxa also have the stapes enclosed by bone in an elongate canal and have a very small antrum postoticum in contrast to other pleurodires.

7. Although *Pelusios* and *Pelomedusa* are generally similar to each other, it is difficult to find synapomorphies unique to them, most of their shared characters seem to be primitive for pelomedusids. However, the wide distribution of a squamosal-parietal contact in chelids, other pelomedusids, and the sister group of *Pelusios* plus *Pelomedusa*, *Taphrosphys* (the roof is unknown in



*Bothremys*), argues that the temporal emargination of *Pelusios* and *Pelomedusa* is a synapomorphy. Both genera have the parietal and squamosal separated exposing the postorbital along the margin of the temporal excavation.

8. One of the best known of the cranial characters used to differentiate groups within pelomedusids, is the large carotid canal described by SIEBENROCK (1897), WILLIAMS (1954), and GAFFNEY (1979). This feature, found in *Podocnemis*, *Erymnochelys* and *Peltocephalus* among the living genera, is best described in GAFFNEY (1979) and SCHUMACHER (1973). A division of the pterygoideus musculature is attached within a large bony canal, also containing the carotid artery. The size and formation of the canal varies among taxa, but there is no reason to question its homology.

Some extinct taxa have this character and can be tentatively placed in this group but at the present time there are not enough characters known that are determinable in all these taxa to develop a complete cladogram.

9. *Stereogenys* (WOOD, 1970) and *Shweboemys* have secondary palates and may be hypothesized as a natural group based on this character.

10. *Erymnochelys*, *Peltocephalus*, and *Podocnemis* all have the quadrato-jugal separated from the ventral cheek margin by a contact of the quadrate and jugal, thereby reducing the degree of cheek emargination.

11. *Peltocephalus* and *Podocnemis* have well-developed saddle-shaped cervical articulations. This is a good character for the recent taxa but only a few fossil pelomedusids have cervicals and skulls described.

Although I am not diagnosing the terminal taxa in this cladogram, I would restrict *Podocnemis* to those taxa with an interorbital groove and a parietal-jugal contact on the skull roof.

12. *Chelidae*. This taxon is diagnosed in GAFFNEY (1977a).

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## STRESZCZENIE

Praca przedstawia kladogram jedenastu rodzajów żółwi *Pleurodira* z uwzględnieniem rodziny *Chelidae* w oparciu o wspólne wyspecjalizowane cechy czaszki i elementów pozaczaszkowych. Triasowy przedstawiciel *Pleurodira*, *Proterochersis*, tworzy grupę siostrzaną z wszystkimi pozostałymi *Pleurodira* w oparciu o następujące cechy: brak kości skoblowych, liczba supramarginaliów 3 lub mniej, mezoplastra nie schodzące się w osi ciała. Jurański przedstawiciel *Pleurodira*, *Platychelys*, tworzy grupę siostrzaną z rodzinami *Pelomedusidae* i *Chelidae* na podstawie jednakowych mezoplastrów lub ich braku oraz nieobecności tarczek supramarginalnych. Następujące grupy *Pelomedusidae* są uważane za monofiletyczne: *Bothremys*, *Taphrosphys*, *Pelomedusa* i *Pelusios* — charakteryzujące się kłykiem potylicznym utworzonym wyłącznie przez boczne kości potyliczne (exoccipitalia), oraz *Podocnemis*, *Peltocephalus*, *Erymnochelys*, *Shweboemys* i *Stereogenys* — charakteryzujące się przerośniętym kanałem tętnicy szyjnej.

