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# A NEGLECTED LINEAGE OF NORTH AMERICAN TURTLES FILLS A MAJOR GAP IN THE FOSSIL RECORD

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**Abstract:** The fossil record of the two primary subclades of softshell turtles (Trionychidae) is exceedingly asymmetric, as a result of a ghost range of total clade Cyclanorbinae that is estimated at 80 Ma. Herein, we present the first phylogenetic analysis of Trionychidae that includes a representative of the poorly studied taxon Plastomenidae, which is known from the Campanian to Eocene of North America. The analysis reveals that plastomenids are stem cyclanorbines, thus significantly reducing the apparent ghost range of total group Cyclanorbinae to approximately 30 Ma. Plastomenids are either an early branching clade of stem Cyclanorbinae, or they represent a paraphyletic grade that gave rise to modern cyclanorbines. Although abundant, the fossil record is still too poorly understood to distinguish between these two primary hypotheses. The previously persistent extremely long ghost range of total clade Cyclanorbinae appears to have been the result of a research bias.

**Key words:** Trionychidae, Plastomenidae, Cyclanorbinae, ghost range, fossils.

EXTANT members of the clade Trionychidae (softshell turtles) are among the most enigmatic group of turtles because of their reduced shell, loss of nearly all scales and scutes and the development of an elongate proboscis (Ernst and Barbour 1989). Phylogenetically, this clade is currently placed as sister to the equally enigmatic pig-nosed turtle *Carettochelys insculpta* at the base of crown group Cryptodira (Shaffer *et al.* 1997; Krenz *et al.* 2005). Because of the unique surface sculpturing and subsurface structure (Scheyer *et al.* 2007) of their shells, even the smallest fossil fragment can be recognized in the fossil record (e.g. Holroyd and Hutchison 2002). The general pattern of the origin and distribution of the group is consequently well understood. In particular, Trionychidae originated in Asia in the late Early Cretaceous, spread to North America in the Late Cretaceous, and then at least temporarily occupied all other continents with exception of Antarctica during the Tertiary (Wood and Patterson 1973; Gaffney and Bartholomai 1979; Hirayama *et al.* 2000; Lapparent de Broin 2000). Currently, trionychids inhabit North America, Eurasia, Africa and New Guinea (Ernst and Barbour 1989).

Over the course of the last century, a strong consensus emerged using both morphological (Lydekker 1889; Hummel 1929; Meylan 1987) and molecular data (Engstrom *et al.* 2004) that Trionychidae consists of two primary subclades: Cyclanorbinae (flapshell softshell turtles) and Trionychinae (common softshell turtles). In general, cyclanorbines are diagnosed by the presence of skin flaps that cover the limb openings of the shell when their head and limbs are retracted (Ernst and Barbour 1989). Their shells are also more extensively ossified than trionychines, a set of traits that is generally considered to be primitive (Meylan 1987). In cyclanorbines a greater percentage of the carapace is ossified, the relative size of the eighth costals is greater, and the epiplastral, entoplastral and xiphiplastral callosities are more extensive (Text-fig. 1A). In contrast, trionychines exhibit a number of traits that are typically interpreted as derived, including a reduction in the ossified carapacial disk to the point that the pelvis is not covered by bone, the resulting development of an extensive leathery carapacial perimeter with the formation of extensive free rib ends, and the reduction in the plastral callosities, particularly those of the entoplastron and epiplastra (Text-fig. 1B).

Even though the fossil record of Trionychidae as a whole is excellent, the fossil record of the two primary subclades is exceedingly asymmetric. On the one hand, fossils attributable to total clade Trionychinae based on the reduced plastron and carapace have been reported from the upper part of the Alamyshik Formation of Kyrgyzstan (Nessov 1995) and thus tentatively date back to


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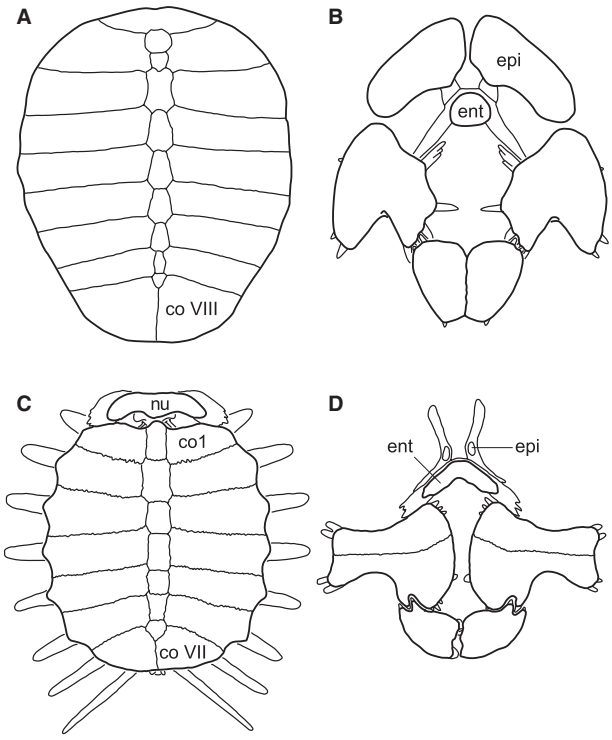



**TEXT-FIG. 1.** A–D, the carapace and plastron of extant Trionychidae. A, the carapace of the cyclanorbine *Cycloderma frenatum*, after AMNH 110180. B, the plastron of the cyclanorbine *Lissemys punctata*, redrawn from Meylan (1987). C, the carapace of *Apalone ferox*, redrawn from Meylan (1987). D, the plastron of *Pelodiscus sinensis*, redrawn from Meylan (1987).

the Albian (*c.* 100 Ma; dated by Verzilin *et al.* 1970 as Albian using faunal comparisons with other Central Asian localities). In contrast, the oldest known cyclanorbines, or stem cyclanorbines, are known from a series of African and Arabian localities that date to as far back as the early Miocene (*c.* 20 Ma; see Lapparent de Broin 2000 for summary of localities and their placement in the European MN faunal chronology) implying a cyclanorbine ghost range of approximately 80 million years. No other major clade of extant turtles has such an extensive ghost range.

Three primary hypotheses exist that could explain this conundrum: (1) pre-Miocene cyclanorbines have not yet been discovered; (2) basic assumptions regarding the character evolution are incorrect, and the split between the two trionychid crown groups is significantly younger than currently hypothesized; or (3) stem cyclanorbines have already been discovered, but have not yet been recognized as such. Unfortunately, although fossil trionychids are rather common in the fossil record (e.g. Hay 1908; Hummel 1932), only few have been phylogenetically analysed (e.g. Gardner *et al.* 1995). We therefore conclude that it is not possible to distinguish rigorously between these three hypotheses until further fossil material has been studied in an explicit phylogenetic context.

Plastomenidae is a poorly studied group of fossil trionychids that is primarily documented from the Campanian to Eocene of North American (e.g. Hay 1908; Holroyd and Hutchison 2002). The group is based on the genus *Plastomenus*, which originally served as one of E. D. Cope's wastebasket taxa for new trionychids that he named from the emerging fossil fields of the American West (see Hay 1908 for review). Nevertheless, by the time Hay (1908) performed his comprehensive review of the fossil record of North American turtles, *Plastomenus* and Plastomenidae had emerged as a group of turtles diagnosed by a greater degree of ossification to the shell than was apparent from other North American fossil trionychids. In particular, plastomenids appear to lack an extensive leathery carapacial perimeter, as is evidenced by the lack of elongate free rib ends, the ossified portion of the carapace covers the pelvis, and all plastral callosities are well developed. Interestingly, even though these characters are otherwise found in cyclanorbines, plastomenids have never been allied with cyclanorbines. Although most plastomenids are known from partial shells only, at least one complete shell (AMNH 6018) and skull (AMNH 6015) are known from the Eocene Bridger Formation of Wyoming that show nearly all characters that are currently considered to be phylogenetically informative (Meylan 1987). Given that the alpha taxonomy of plastomenids is currently unresolved (see below), we refer this material herein to *Plastomenus* aff. *thomasii* Cope, 1871.

The purpose of this contribution is to cladistically assess, for the first time, the phylogenetic position of any plastomenid, in this case of *Plastomenus* aff. *thomasii*. The outcome of this analysis is expected to help inform the debate regarding the asymmetric fossil record outlined above, as the inclusion of plastomenids in a phylogenetic analysis of Trionychidae may fill the apparent cyclanorbine ghost range, result in a topological shift or simply corroborate the currently existing conundrum. The outcome may further inform current molecular calibration studies (e.g. Near *et al.* 2005), as an Early Cretaceous versus Neogene divergence of crown Trionychidae implies vastly different morphological and molecular divergence rates.

## TAXONOMIC COMMENTS REGARDING *PLASTOMENUS THOMASII*

J. Leidy and E. D. Cope were notorious for naming fossil turtles based on highly fragmentary remains (see Hay 1908 for summary of names). Yet, even though much of this taxonomic confusion could have been resolved with the comprehensive summary of the fossil turtles of North America provided by Hay (1908), he abstained from declaring taxa undiagnostic or from synonymising names.

Instead, Hay (1908) often assigned diagnostic material to poorly typified taxa.

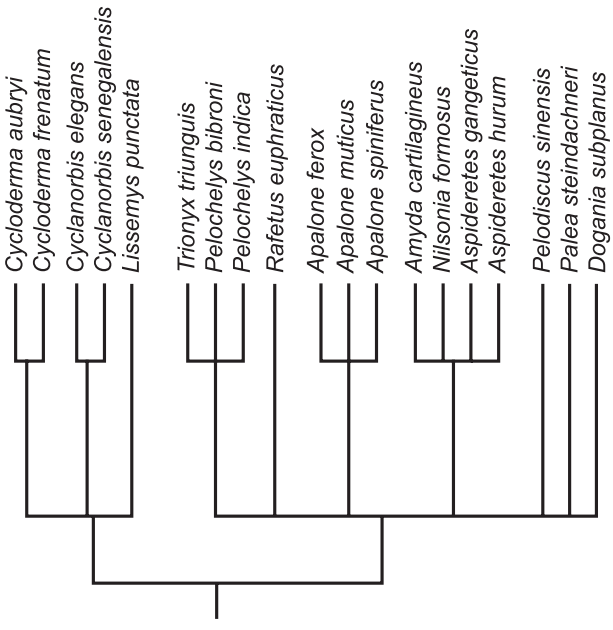
*Plastomenus thomasii* is a prime example. In the type publication, Cope (1871) did not explicitly refer any material to this taxon, which was typical for the time. However, in later publications, Cope contradicted himself as to whether the type material consisted of plastral or carapacial elements, he contradicted himself as to which portions of the original type material belong to *Plastomenus thomasii* versus *Plastomenus multifoveatus,* he contradicted himself as to whether *P. thomasii* or *P. multifoveatus* is the type species of *Plastomenus*, he contradicted himself whether *P. thomasii* belongs to *Plastomenus* or '*Trionyx*,' and, finally, he used an earlier description of *P. thomasii* later verbatim for the description of *P. multifoveatus* (see Hay 1908 for summary). At present, specimens are catalogued as part of the type series of *P. thomasii* at the USNM (USNM 4092, 4093, 5838) and at the AMNH (AMNH 3948), yet ironically, those fragments that can be recognized from illustrations (Cope 1884), were figured under the name *P. multifoveatus*. In a rare move, Hay (1908) decided to synonymise both taxa under the name *P. thomasii* and to retain *P. thomasii* as the type species of *Plastomenus*. The legality of the entire situation under the current rules of the IZCN is unclear to us; however, we conclude that the type material is not diagnostic at the species level and that *P. thomasii* should be considered a *nomen dubium*.

In addition to synonymising *P. multifoveatus* with *P. thomasii*, Hay (1908) also assigned to *P. thomasii* more complete material, in particular a rather complete shell that only lacks the entoplastron and the epiplastra (AMNH 6018) and a beautifully preserved skull, mandible and some shell remains of another individual (AMNH 6015). The shell was figured in Hay (1908, figs 631, 632), and the skull was figured in Hay (1908, figs 633–635) and again in Gaffney (1979, fig. 183). Although we are uncertain whether this material can truly been assigned to *P. thomasii*, it is apparent that researchers have treated this material as *de facto* being *P. thomasii* (e.g. Hummel 1929; Młynarski 1976; Gaffney 1979). Given that a main goal of the ICZN is stability, it therefore appears prudent to designate AMNH 6018 as the neotype of this taxon. We are currently preparing the necessary appeal to the ICZN. Until a decision is available from the ICZN, we feel it prudent to assign the two specimens used in this study (i.e. AMNH 6015, 6018) to *Plastomenus* aff. *thomasii*.

## MATERIALS AND METHODS

The cladistic analysis of Meylan (1987) remains the only comprehensive morphological analysis of extant Trionychidae to date. In our experience, this analysis is nearly exhaustive in regard to characters that can be observed from the osteology of living trionychids, and this analysis therefore serves as our basis. Meylan's (1987) analysis consists of 113 characters, of which 66 pertain to variation found within Trionychidae (including autapomorphies), whereas the rest help resolve the placement of Trionychidae within Cryptodira. We did not undertake any revision of Meylan's (1987) character list and scored *Plastomenus* aff. *thomasii* for the 66 informative characters as originally defined. For simplicity, we retain the numbering of characters used by Meylan (1987). Our scoring of the postcranial characters is based on AMNH 6018 (see Hay 1908, figs 631, 632) and those of the cranium and mandible based on AMNH 6015 (see Hay 1908, figs 633–635; Gaffney 1979, fig. 183). The list of characters used and our scorings for *Plastomenus* aff. *thomasii* are provided in the Appendix.

As an alternative to combining the morphological data set of Meylan (1987) with the newly compiled molecular data of Engstrom *et al.* (2004), we use the approach of Danilov and Parham (2006, 2008) of running the morphological data under parsimony with a conservative molecular backbone topology (Text-fig. 2). This topological backbone only forces a small number of clades that were retrieved from separately run ND4, cytochrome b and nuclear intron data sets of Engstrom *et al.* (2004). Our maximum parsimony analysis was run using PAUP 4.0b10 (Swofford 2002). All characters were left unordered and unweighted. The tree bisection and reconnec-




**TEXT-FIG. 2.** The conservative molecular constraint tree used herein as the backbone for the parsimony analysis. The topology is a strict consensus topology of the separately run ND4, cytochrome b, and nuclear intron data sets of Engstrom *et al.* (2004).

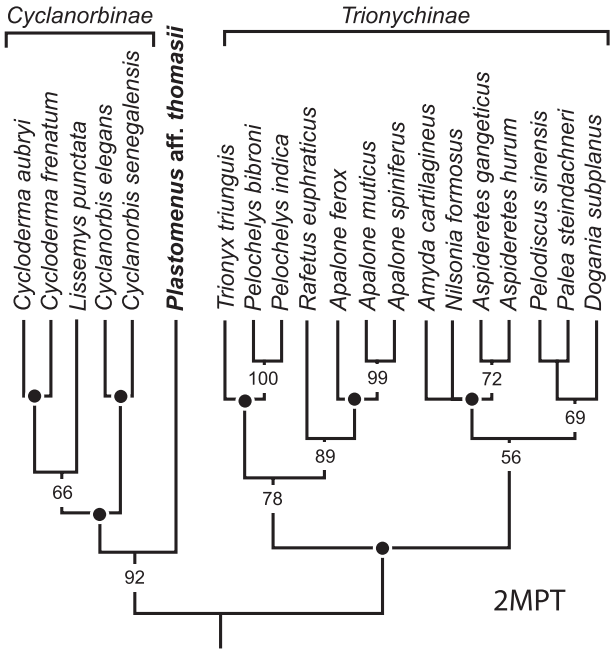
tion (TBR) heuristic algorithm was used for all analyses, and each analysis was run for 100 000 replicates. Minimum branch lengths were set to collapse. Support for each node was measured by calculating bootstrap frequencies (Felsenstein 1985) with 1000 bootstrap replicates and 100 random sequence addition replicates. Bootstrap frequencies >70% is considered strong support (Hillis and Bull 1993). Unfortunately, we were not able to produce Bremer support values, because the available software programs cannot run a decay analysis with a backbone constraint.

*Institutional abbreviations and nomenclature.* AMNH, American Museum of Natural History, New York; USNM, United States National Museum, Washington DC. We herein explicitly follow Joyce *et al.* (2004) and Engstrom *et al.* (2004) by referring the most commonly used traditional taxon names to the equivalent crown clades.

## RESULTS

Our phylogenetic analysis results in two most parsimonious trees, the strict consensus of which is presented in Text-figure 3. Given that a molecular backbone constraint was used, many clades retrieved from the parsimony analysis are not a result, but rather part of the primary set of assumptions. Within Trionychinae, our analysis confirms the results of Meylan (1987) and Engstrom *et al.* (2004) by placing the middle-eastern trionychine *Rafetus euphraticus* as sister to the North American clade *Apalone* and by confirming the monophyly of *Pelochelys.* Our results confirm the monophyly of Meylan's (1987) clade Pelodiscini and of Meylan's (1987) unnamed clade consisting of Pelodiscini and Apalonini. Engstrom *et al.* (2004), in contrast, interpret these two groupings as paraphyletic, which indicates conflict between the molecular and morphological data. On the cyclanorbine side, our results contradict both Meylan (1987) and Engstrom *et al.* (2004) in that the African cyclanorbines are paraphyletic relative to the Indian *Lissemys*.

Within the context of this analysis, the most important result is that *Plastomenus* aff. *thomasii* is firmly identified as a stem cyclanorbine. Four characters support this placement: the lateral placement of the hypoplastron relative to the xiphiplastron, the division of the maxillae by the vomer (only in ACCTRAN), the formation of the foramen palatinum posterius by the palatine only and the exclusion of the foramen jugulare posterius from the fenestra postotica (Meylan 1987, characters 13, 48, 54, 58). A series of conspicuous similarities between the shells of *Plastomenus* aff. *thomasii* and cyclanorbines are here interpreted as symplesiomorphies, in particular the presence of a preneural, the presence of seven callosities,




**TEXT-FIG. 3.** A strict consensus phylogeny of 2MPTs of Trionychidae, which indicates the placement of *Plastomenus* aff. *thomasii* along the phylogenetic stem of Cyclanorbinae. Clades highlighted with a black dot are not an insight from the analysis, but rather result from the backbone constraint (see Text-fig. 2). Numbers below clades indicate bootstrap values.

fusion of the hyo/hypoplastron, absence of suprascapular fontanelles and the presence of a depression for contact with the ilium (Meylan 1987, characters 4, 9, 10, 18, 21). The alternative interpretation of *Plastomenus* aff. *thomasii* as a stem trionychid (Meylan 1990) is at least four steps longer.

## DISCUSSION

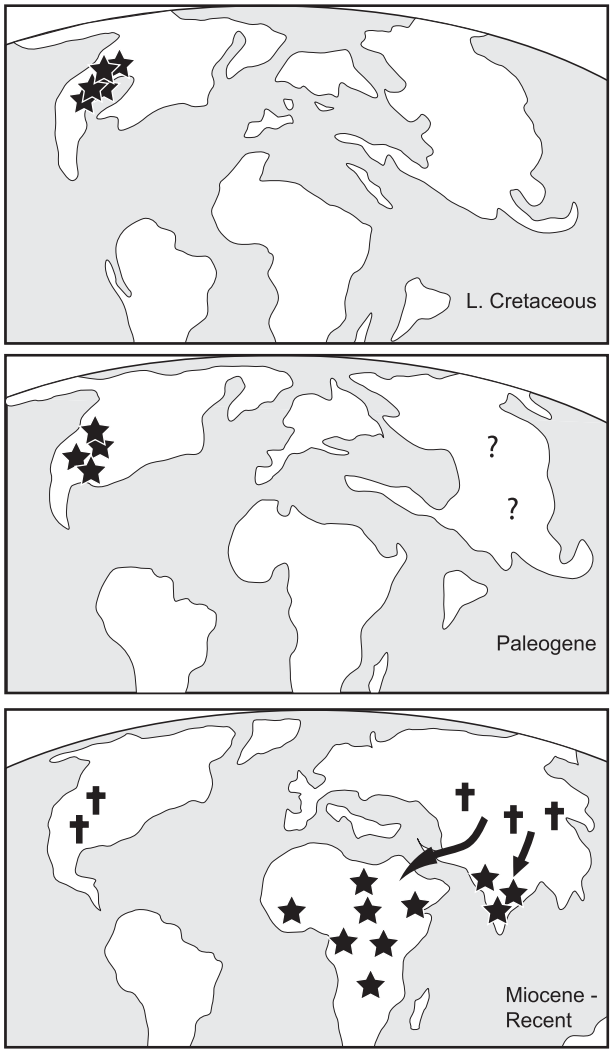
Our analysis firmly interprets *Plastomenus* aff. *thomasii* as a stem cyclanorbine (92% bootstrap frequency; Text-fig. 3). The previously oldest recognized total group cyclanorbines were reported from the early to late Miocene of a number of African and Arabian localities (see Lapparent de Broin 2000 for summary), which imply an 80 Ma ghost range for total group Cyclanorbinae.

The materials referred herein to *Plastomenus* aff. *thomasii* (AMNH 6015, 6018) are both from the Grizzly Buttes Locality in Uinta County, Utah and thus can be referred biostratigraphically to the Bridgerian North American Land Mammal Age, level 2B. Within this level, two magnetic reversals take place, C22n to C21r, dated at 49.04 Ma, and C21r to C21n, dated at 47.91 Ma, and an ash layer dated at 47.96 ± 0.13 Ma. The next available dates are the C22r to C22n reversal within Bridgerian

level 1 (49.71 Ma) and an ash layer within the Bridgerian level 3 (46.92 ± 0.17 Ma; see Robinson *et al.* 2004 for summary and sources of these dates). The Bridgerian level 2 can thus be conservatively dated as being between 49.71 and 46.75 Ma, which results in a reduction in the cyclanorbine ghost range by approximately 25 Ma. However, considering that plastomenids have been described from the Campanian and Maastrichtian as well (e.g. Hay 1908; Holroyd and Hutchison 2002; Brinkman 2005), the available fossil evidence appears to support a much greater age of the cyclanorbine lineage and a total reduction in the ghost range from approximately 80 to 30 Ma. Future research will need to investigate whether the assemblage of turtles traditionally referred to as 'plastomenids' or 'plastomenines' (e.g. Hay 1908; Holroyd and Hutchison 2002) is an early branching clade of stem cyclanorbines, or a paraphyletic assemblage ancestral to Cyclanorbinae. These hypotheses imply vastly different palaeobiogeographic scenarios (see below).

Although numerous authors previously hinted at similarities between plastomenids and cyclanorbines (e.g. Hay 1908; Hummel 1929), we suspect that biogeographical considerations hindered them from proposing a stronger link. In particular, cyclanorbines are currently limited to the Gondwana continents Africa and India (Hummel 1929), whereas plastomenids are historically only known from North America (Text-fig. 4). Plastomenids have occasionally been reported from Asia in the past (e.g. Chkhikvadze 1970), but more recent reviews of the group question these identifications (e.g. Kordikova 1994). Hummel (1929) dismissed the possibility that cyclanorbines originated in Gondwana because of the complete lack of any type of pre-Miocene trionychid fragment from India or Africa/Arabia (Lapparent de Broin 2000), which indicates their absence prior to the collision of the continents with Asia. Trionychids appear in the fossil record of Europe during the Palaeogene and remain an extremely common faunal element until the Plio/Pleistocene (Lapparent de Broin 2001; Danilov 2005). However, cyclanorbines, diagnosable by a positive shell pattern consisting of fine knobs, are notably lacking from that region as well. Although there is no positive evidence for cyclanorbines from Asia, the group must have occurred on that continent at least for some time, and we suspect that the group inhabited the poorly sampled south-western region of the continent prior to the collision, thus allowing easy dispersal to nearby Africa and India.

The earlier history of the cyclanorbine stem lineage remains more speculative until more fossils are analysed. In general, trionychids are thought to have originated in Asia, because the oldest definite trionychid material is from that continent (Hirayama *et al.* 2000). However, although the oldest trionychids are typically diagnosed as being trionychines, these forms have not yet been analysed in a rigorous cladistic context and it is reasonable to speculate that these earliest forms may represent stem trionychids instead. Two possibilities generally exist regarding the early evolution of Trionychidae. Either the basal trionychid split occurred in Asia, or the split is the result of vicariance arising from the early invasion of a side lineage to North America. A monophyletic Plastomenidae is more consistent with an Asiatic origin of the cyclanorbine lineage, because it only requires a single incursion into North America with its subsequent extinction. In contrast, a paraphyletic 'Plastomenidae' is more consistent with an early invasion of North America with a secondary return of the lineage to Asia at a later date. Once again, more fossils will need to be analysed in a rigorous system-




**TEXT-FIG. 4.** A palaeobiogeographic overview for the distribution of the stem and crown lineage of Cyclanorbinae from the Late Cretaceous to Present. Stars denote known occurrences, question marks indicate speculated occurrences, and crosses indicated inferred regional extinctions.

atic context to test these hypotheses, and the analysis presented herein is just the first step in that direction.

The reality and quality of ghost ranges (sensu Benton and Storrs 1996) have received much attention during the last two decades (e.g. Norell 1992; Benton and Storrs 1996; Wagner 1998; Paul 2003). At the species level, it is apparent that many ghost ranges are an artefact created by the incorrect interpretation of cladistic 'trees' as phylograms, a situation that can be avoided somewhat by considering metaspecies (Archibald 1993; see Lyson and Joyce in press, for an example of application to the turtle fossil record). Paul (2003) noted that the speed at which new range extensions are found for higher taxa appears to be slowing down for most fossil groups, thus supporting the notion that the fossil record is generally well understood and that ghost ranges may not only be a cladistic artefact at the species level, but for higher taxa as well. Nevertheless, given that higher taxa originate from single species, not other higher taxa, cladistically predicted ghost ranges should only be dismissed *a posteriori* if higher taxa were used as terminal taxa but not if single species were used in the analysis. Instead, taphonomic biases, included errors in the analysis, appear to be a better explanation for persistent ghost ranges. It is apparent from this analysis that the predominating reason why total group Cyclanorbinae used to exhibit an 80 Ma ghost range was a taphonomic bias as well. However, this bias was not the result of a lower fossilization potential or lower collecting rate of stem cyclanorbines relative to stem trionychines, but rather a simple research bias, as this was the first analysis to ever investigate the phylogenetic placement of a plastomenid. Given that the vast majority of fossil vertebrates have yet to be included in a phylogenetic analysis, we speculate that many more similar discoveries are to be made in the future and urge the integration of fossil taxa into explicit phylogenetic analyses.

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## APPENDIX

*Character list and scoring for* Plastomenus aff. thomasii

For simplicity, we retain the character numbering of Meylan (1987). Character definitions and formulations of character states follow Meylan (1987) verbatim. For detailed descriptions and figures of characters, please refer to that publication as well.

Meylan 1987, Character 1, width/length of nuchal bone: 4 (>4).
Meylan 1987, Character 2, anterior and posterior costiform processes of nuchal bone united: 2 (yes).
Meylan 1987, Character 3, position of anterior edge of first body vertebra relative to nuchal bone: ? (cannot be determined).
Meylan 1987, Character 4, first and second neurals fused: 1 (no).
Meylan 1987, Character 5, total number of peripherals: 4 (zero).
Meylan 1987, Character 7, prenuchal bone: 1 (absent).
Meylan 1987, Character 8, size of eighth pleurals [i.e. costals]: 1 (large).
Meylan 1987, Character 9, number of plastral callosities: 1 (seven).
Meylan 1987, Character 10, hyoplastra and hypoplastra fuse just after hatching: 1 (no).
Meylan 1987, Character 12, fusion of xiphiplastra: 2 (present).
Meylan 1987, Character 13, hypo-xiphiplastral union: 2 (hypoplastra lateral to xiphiplastra).
Meylan 1987, Character 14, number of neurals (fused 1 and 2 counted as 2): 4 (seven or eight).
Meylan 1987, Character 15, variability in position of neural reversal: ? (cannot be determined).

Meylan 1987, Character 16, pleurals [i.e. costals] which meet at midline: 3 (sixth, seventh, and eighth or seventh and eighth).
Meylan 1987, Character 17, point of reversal of orientation of neurals: ? (cannot be determined).
Meylan 1987, Character 18, suprascapular fontanelles: 1 (closed at hatching).
Meylan 1987, Character 19, epiplastron shape: ? (cannot be determined).
Meylan 1987, Character 20, length epiplastra anterior to entoplastron contact: ? (cannot be determined).
Meylan 1987, Character 21, depressions on eighth pleurals [i.e. costals] for contact of ilia: 1 (present).
Meylan 1987, Character 23, bridge length: 1 (long).
Meylan 1987, Character 24, largest adult size 200 mm or less (disc length): 1 (no).
Meylan 1987, Character 25, carapace margin straight to concave posteriolaterally: 1 (no).
Meylan 1987, Character 29, sexual dimorphism in disc length: ? (cannot be determined).
Meylan 1987, Character 32, jugal contacts squamosal: 1 (no).
Meylan 1987, Character 34, jugal contacts parietal on skull surface: 1 (no).
Meylan 1987, Character 36, vomer contacts prefrontal: ? (cannot be determined).
Meylan 1987, Character 41, dorsal edge of apertura narium externum laterally emarginate: ? (cannot be determined).
Meylan 1987, Character 42, dorsal edge of apertura narium externum medially emarginate: ? (cannot be determined).
Meylan 1987, Character 46, basisphenoid contacts palatines: 1 (no).
Meylan 1987, Character 48, vomer divides maxillae: 2 (no).
Meylan 1987, Character 49, vomer reaches intermaxillary foramen: ? (cannot be determined).
Meylan 1987, Character 51, vomer contacts basisphenoid: 1 (no).
Meylan 1987, Character 53, size of foramen palatinum posterius: 2 (small).
Meylan 1987, Character 54, foramen palatinum posterius forms in: 2 (palatine only).
Meylan 1987, Character 58, foramen jugulare posterius excluded from fenestra postotica by pterygoid arching to contact opisthotic: 2 (yes).
Meylan 1987, Character 59, foramen jugulare posterius excluded from fenestra postotica by descending process of opisthotic which reaches pterygoid: 2 (yes).
Meylan 1987, Character 60, foramen posterius canalis carotici interni relative to lateral crest of basioccipital tubercle: 3 (below).
Meylan 1987, Character 62, maxilla contacts frontal in front of orbit: 2 (yes).
Meylan 1987, Character 63, exoccipital contacts pterygoid: 1 (no).
Meylan 1987, Character 64, basisphenoid shape: 1 (not medially constricted).
Meylan 1987, Character 65, premaxilla absent: 1 (no).
Meylan 1987, Character 66, vomer lost: 1 (no).
Meylan 1987, Character 67, jugal contacts orbit: 1 (yes).
Meylan 1987, Character 68, epipterygoid, if present, contacts the palatine: ? (cannot be determined).
Meylan 1987, Character 69. contact between pterygoid and foramen nervi trigemini occurs when epipterygoid is present: ? (cannot be determined).
Meylan 1987, Character 70, when epipterygoid is present pterygoid contacts foramen nervi trigemini: ? (cannot be determined).
Meylan 1987, Character 71, epipterygoid contacts prootic anterior to foramen nervi trigemini: ? (cannot be determined).
Meylan 1987, Character 72, epipterygoid contacts prootic posterior to foramen nervi trigemini: ? (cannot be determined).
Meylan 1987, Character 73, epipterygoid fuses to pterygoid: ? (cannot be determined).
Meylan 1987, Character 74, average ratio of intermaxillary foramen length to length primary palate: ? (cannot be determined).
Meylan 1987, Character 75, postorbital bar relative to orbit: 2 (<1/5 of orbit).
Meylan 1987, Character 76, quadratojugal participates in processus trochlearis oticum: 1 (no).
Meylan 1987, Character 78, proportion of processus trochlearis oticum made up by parietal: 1 (15.6% or less).
Meylan 1987, Character 87, ventral keel on 8th cervical present and limited to posterior end: ? (cannot be determined).
Meylan 1987, Character 88, strong dorsal processes on cervicals: ? (cannot be determined).
Meylan 1987, Character 90, number of ossifications in corpus hyoidis: ? (cannot be determined).
Meylan 1987, Character 91, number of ossifications in comu branchiale II: ? (cannot be determined).
Meylan 1987, Character 92, ossifications of comu branchiale II broad and strongly sutured: ? (cannot be determined).
Meylan 1987, Character 93, basihyals in close contact and projecting anteriorly: ? (cannot be determined).
Meylan 1987, Character 95, symphyseal ridge strong and present in a depression: 1 (no).
Meylan 1987, Character 98, foramen intermandibularis caudalis enclosed by prearticular: ? (cannot be determined).
Meylan 1987, Character 100, ilia curve medially: ? (cannot be determined).
Meylan 1987, Character 107, ischia extend into thyroid fenestra: ? (cannot be determined).
Meylan 1987, Character 109, metischial processes present and distinct: ? (cannot be determined).
Meylan 1987, Character 112, angle of acromion process to scapula approaches that of coracoid to acromion: ? (cannot be determined).
Meylan 1987, Character 113, coracoid longest of three pectoral processes: ? (cannot be determined).