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The phylogenetic relationships among non-diplomystid catfishes as inferred from mitochondrial cytochrome *b* sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes)

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Abstract

The relationships among families of catfishes are poorly understood and have yet to be the subject of a comprehensive investigation with molecular data. Existing phylogenetic hypotheses are based on morphological data and incompletely resolved. This study analyzed complete sequences of mitochondrial gene cytochrome *b* for 170 species from 29 of 33 extant families, and focused on the relationships of Ictaluridae to other catfishes. In addition to previous phylogenetic studies, the fossil record, paleogeography, biogeography, and distribution of extant catfish families collectively suggest the location (if extant) of the ictalurid sister taxon to be Northern or Eastern Asia. Of the extant catfishes currently native to this area and included in this analysis, parsimony and Bayesian likelihood analyses recovered *Cranoglanis bouderius* as the most proximal sister taxon of Ictaluridae. Seemingly, ictalurids and cranoglanidids represent another biogeographic component linking freshwater fishes of North America and eastern Asia, e.g., catostomids and paddlefishes. The results coupled with present-day catfish distributions and inferences from the fossil record collectively suggest the ancestor of Ictaluridae to have invaded freshwaters of North America at the close of the Cretaceous through northeastern Asia and northwestern North America. Other superfamilial nodes supported the results of previous phylogenetic studies of narrower taxonomic scope. Several novel relationships were recovered (including a clade composed of Pimelodidae, Pseudopimelodidae, and Heptapteridae) and these along with sources of systematic error are discussed. A broad sampling of Bagridae permitted an examination of intergeneric relationships within this family and in light of recent morphological and molecular studies.
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Keywords: Siluriformes; Catfishes; Ictaluridae; Bagridae; Historical biogeography; Cranoglanis; Cytochrome *b*

1. Introduction

Approximately 1 in 20 vertebrate species is a catfish (Nelson, 1994). Catfishes constitute a monophyletic group (Arratia, 1987; De Pinna, 1993, 1998; Fink and Fink, 1981, 1996; Grande, 1987; Saitoh et al., 2003) and they, or their fossilized remains, can be found on every continent in freshwater, estuarine, and saltwater environments. Remarkable catfishes include wood-eating loricariids (Schaefer and Stewart, 1993), electric catfishes capable of generating charges of 400 V or more (Burgess, 1989), and parasitic catfishes that feed on the gills, scales, and blood of other fishes (Baskin, 1973; De Pinna, 1992). Clearly, catfishes have had a complex evolutionary history and offer an exciting opportunity to examine the evolution of a diverse and species-rich clade of vertebrates on a global scale. If this history is to be understood, the phylogenetic relationships among catfishes must be clarified. While a few superfamilial taxa appear to be well supported by independent data (De Pinna, 1993, 1998; Mo, 1991), the status and interrelationships of many of the catfish families remain unclear. Though several hypotheses based on morphological data exist,

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support for recovered nodes has yet to be discerned and analyses of nucleotide sequence data have so far been too incomplete or inconclusive.

1.1. Ictaluridae

This study addresses a particularly vexing problem in siluriform phylogeny concerning North American catfishes (Ictaluridae). Ictalurid catfishes are monophyletic (De Pinna, 1993, 1998; Hardman, 2002, 2004; Lundberg, 1970, 1992; Mo, 1991) and have been the only catfishes in North America for the last 30 Ma; prior to this time the now-extinct hypsidorids and other catfishes of uncertain phylogenetic affinity were also part of the freshwater ichthyofauna (Grande, 1987; Grande and De Pinna, 1998; Lundberg, 1975, 1992; Lundberg and Case, 1970). As far as can be discerned from the fossil record, the origin and diversification of Ictaluridae took place solely in North American freshwaters from at least as early as the Eocene (55 Ma) (Lundberg, 1975, 1992). While ictalurids are a well-diagnosed group (Lundberg, 1970, 1992) their phylogenetic relationships to other catfish families have remained among the most enigmatic. Ascertaining the sister taxon of Ictaluridae will shed light on the history of the North American freshwater ichthyofauna, itself an unsolved biogeographical problem in part due to a lack of explicit and phylogenetic hypotheses of its constituent groups and their sister taxa (Patterson, 1981).

1.2. Predictions from previous phylogenetic studies

Two hypotheses generated with contemporary phylogenetic methods are available concerning the majority of catfish lineages: Mo (1991) (Fig. 1 and Table 1) and De Pinna (1993) (Fig. 2, Table 1). Mo's (1991) study focused on the relationships among bagrid catfishes as inferred from 126 morphological characters drawn from 214 species in 30 families. Mo's study has been criticized as suffering from an arbitrary weighting scheme employed to enhance resolution, an unjustified reliance on the naturalness of nominal families included as terminals, and inconsistent reporting of relationships inferred from tree topologies (De Pinna and Ferraris, 1992; Ng, 2004). Nevertheless, this study will consider the result of Mo's unweighted analysis to be a testable hypothesis which predicts that the sister group of Ictaluridae will be recovered as any one or combination of the 10 other clades shown in Fig. 1.

In his unpublished thesis De Pinna (1993) analyzed 239 morphological characters from 400 catfish species representing 33 families but compressed his data set into 79 representative terminals based on hypotheses of monophyly provided by previous phylogenetic studies and his preliminary analysis. He thereby enforced their monophyly in subsequent analyses and described the

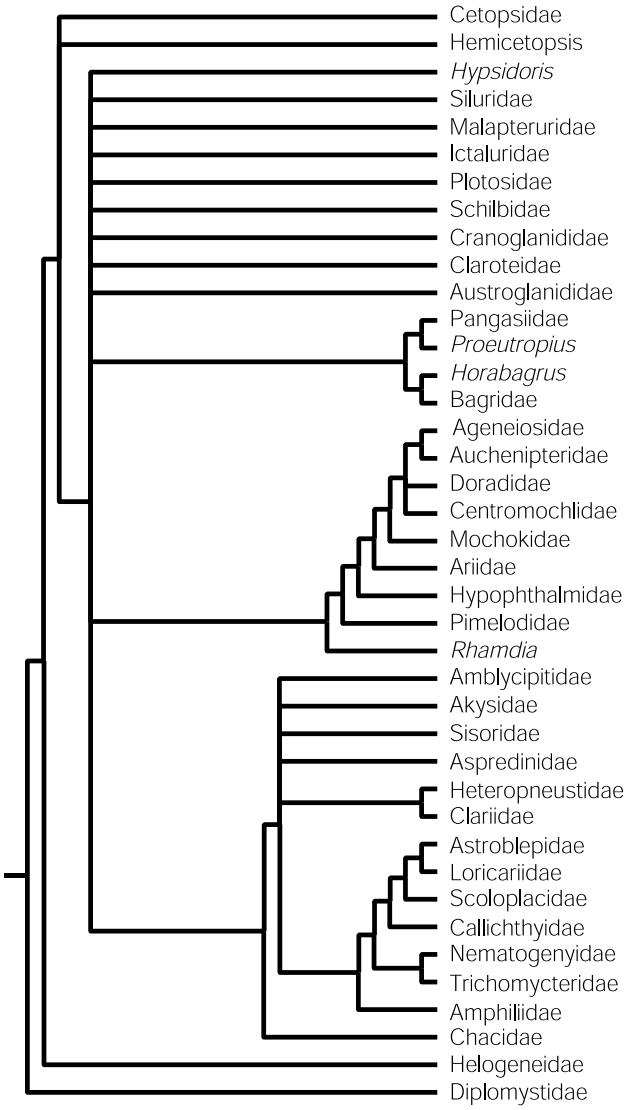

Fig. 1. Strict consensus of 327 equally parsimonious trees derived from the unweighted analysis of 126 morphological characters by Mo (1991).

measure as one that "fine-tuned" the parsimony analysis to recover relationships among rather than within families. Seemingly both Mo (1991) and De Pinna (1993) imposed monophyly on certain groups they deemed uncontroversial. The strict consensus of 360 equally short trees recovered by De Pinna is shown in Fig. 2. De Pinna's hypothesis predicts that ictalurids will be recovered as the sister group to any one or combination of the four other clades in his Eusiluroidei.

Additionally, Lundberg (1992) suggested that elements of the extant Asian Bagridae, specifically the Bagrichthyinae, represent the sister taxon of Ictaluridae while pointing out that morphological synapomorphies of such a clade were lacking, he also noted similarities among "general body form and habits" among ictalurids and pelteobagrins such as *Leiocassis*. Similarly, the opinions of earlier

Table 1
Sources of historical information considered in this study and hypotheses to be tested through phylogenetic analysis of the cyt *b* data

Hypothesis	Source	Assumptions and predictions
Phylogenetic	Mo (1991) (Fig. 1)	Ictaluridae will be recovered as the sister taxon to any one or combination of 10 other clades shown in Fig. 1
	De Pinna (1993) (Fig. 2)	Ictaluridae will be recovered as the sister taxon to any one or combination of four other clades shown in Fig. 2
Biogeographic	North American ichthyofauna (Patterson, 1981; Nelson, 1994)	If extant, the most-proximal ictalurid sister taxon will be found among fishes of the Northern Hemisphere, i.e., Europe, North or eastern Asia
Geologic	Plate tectonics (Barron et al., 1981) (Fig. 3)	Assumption: If the ancestral ictalurid was salt-intolerant, it most likely invaded North America from Africa approximately 180 Ma, or through Northeastern Asia approximately 60 Ma. Prediction: If extant, the most-proximal ictalurid sister taxon will be found in Africa or Northern or eastern Asia
Paleontologic	Fossil record (Fig. 3)	Assumption: Ictalurids were present in North America at least as early as the Eocene (55 Ma). Prediction: In light of the inferences made by the geologic record and if extant, the most-proximal ictalurid sister taxon will be found in Northern or eastern Asia

authors (Chardon, 1968; Günther, 1864; Regan, 1911) suggested ictalurid affinities for Asian "bagrids," though less explicitly and without providing evidence in support of these statements.

1.3. Predictions from biogeography

Biogeographical patterns and phylogenetic relationships provide predictions concerning the likely location(s) of unknown sister taxa (Humphries and Parenti, 1999; Nelson and Platnick, 1981). The majority of North American freshwater fishes belong to clades that are mostly restricted to the Northern Hemisphere, e.g., catostomids, cottids, esocids, osmerids, percids, and umbrids (Berra, 2001; Nelson, 1994; Patterson, 1981). These observations collectively imply historical connections between freshwater systems of eastern North America and Western Europe, and between western North America and Eastern Asia. In light of these inferences, the sister taxon of Ictaluridae should also be found in the Northern Hemisphere. However, this prediction is problematic to test because the vast majority of extant catfishes are found in South America, Africa, and Southern and Southeast Asia (Berra, 2001; Nelson, 1994).

1.4. Predictions from earth history and distribution of extant catfishes

Given that catfishes were widespread during the late Cretaceous, that catfishes today are found on every major landmass in non-monophyletic assemblages, and that catfishes are primary freshwater fishes unlikely to disperse through marine environments (Lundberg, 1993), the role that plate tectonics might have played in their diversification should be considered and included as a source of prediction. Given that ictalurids are only known from North America (since at least the Eocene), its geological history might offer some insights when coupled with the fossil record. North America separated from Africa approximately 180 Ma and was connected to Northeastern Asia approximately 60 Ma through the Bering Straits (Barron et al., 1981; Smith et al., 1981). The latter event has been implicated as the route through which Asian and American freshwater fishes were exchanged both recently and anciently (Bond, 1996; Cavender and Coburn, 1992; Grande and Bemis, 1991; Smith, 1992).

Catfish continental faunas are not monophyletic (De Pinna, 1993, 1998; Mo, 1991) but several recognized clades are endemic to a given continent or region (Berra, 2001; De Pinna, 1998). African amphiliids and mochokids have been suggested to represent the sister taxa of the South American superfamilies Loricarioidea and Doradoidea, respectively (De Pinna, 1993, 1998; Lundberg, 1993, 1998; Mo, 1991). These relationships and distributions have been offered as evidence (De Pinna, 1998; Lundberg, 1993, 1998) of the distribution and existence of ancestral lineages prior to the complete separation of these two continents approximately 90 Ma (Barron et al., 1981). Considering that these families and superfamilies are considered derived with respect to other catfishes (Diogo, 2004; De Pinna, 1993, 1998; Mo, 1991) any evolutionary scenario that replaces dispersal with a drift-vicariance model requires a considerable increase in the minimum age estimate for catfishes, which recent opinion places in the Mid-Late Cretaceous (De Pinna, 1998; Lundberg, 1992, 1993, 1998).

In addition to the implications of an ancient origin for catfishes from plate tectonic reconstructions, Saitoh et al. (2003) used calibrated nucleotide sequence divergences to date the split of cypriniforms from the ancestor of characiforms, gymnotiforms, and siluriforms (Characiphysi) approximately 250 Ma. Saitoh et al. (2003) reported some debatable results that suggested catfishes represent the sister clade of gymnoti-

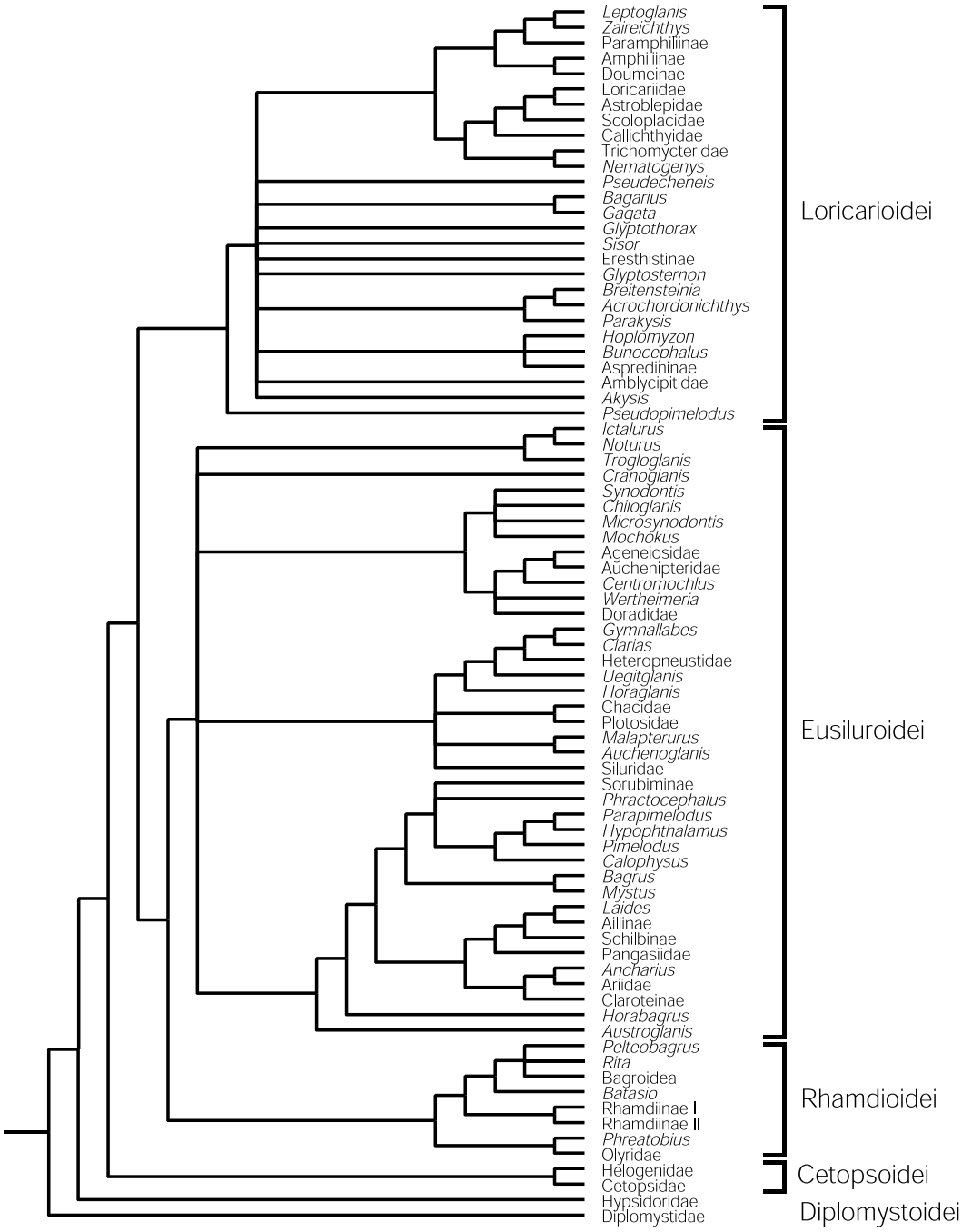

Fig. 2. Strict consensus of 360 equally parsimonious trees derived from the analysis of 239 morphological characters by De Pinna (1993). Suborder classification from De Pinna (1993).

forms and characiforms, and which they believed to have diverged shortly after the split of characiphysans from cypriniforms. Orti and Meyer (1997) utilized mitochondrial ribosome sequences to recover age estimates for the major characiform clades of approximately 100 Ma. This date is more similar to those proposed by morphologists and paleontologists (Arratia, 1997; Lundberg, 1998; Maisey, 1996). Still, the dramatic increase in age estimate for otophysan lineages provided by Kumazawa et al. (1999) and Saitoh et al. (2003) offers a more plausible window of time for an historical scenario to account for catfish diversification, dispersal, and vicariance through continental drift.

1.5. Predictions from the fossil record

The fossil literature provides several pieces of information concerning catfish paleobiogeography and evo-

lution (Fig. 3). At the close of the Cretaceous catfishes were widespread in freshwater and saltwater habitats (de la Peña and Soler-Gijón, 1996; de Muizon et al., 1983; Cione et al., 1985; Cione and Prasad, 2002; Frizzell, 1965; Gayet and Meunier, 1998, 2004). Phylogenetic diversification had taken place at least for the *Corydoras* lineage within Callichthyidae (Lundberg, 1998; Reis, 1998), doradoids in South America (Gayet and Meunier, 1998), the extinct lineages represented by *Andinichthys*, *Hoffstetterichthys*, and *Incaichthys* (Gayet, 1988, 1990, 1991; Gayet and Meunier, 1998, 2004), the derived "Family Indet 1 nov. gen." (Gayet and Meunier, 1998, 2004; Lundberg, 1998) and possibly the lineage leading to Diplomystidae in present-day Bolivia (Gayet and Meunier, 1998, 2004). Shortly after the end of the Cretaceous, many modern families appear in freshwater and marine deposits worldwide and phylogenetic diversification had taken place at least for the lineages leading to Ariidae, Bagridae, and Clariidae (Gayet and Rage, 1987), Hypsidoridae (Grande, 1987; Grande and De Pinna, 1998; Lundberg and Case, 1970), Ictaluridae and "titanoglanis" (Lundberg, 1993), and an uncertain family found in Antarctica (Grande and Eastman, 1986). At least as late as the Miocene many modern genera and species had already emerged as part of the Neotropical freshwater ichthyofauna (Lundberg, 1997, 1998; Lundberg et al., 1988). These same fossils imply that the majority of siluriform diversification took place prior to the Neogene (23 Ma) and that since then relatively little macroevolution of catfishes has taken place in the Neotropics (Lundberg, 1998).

The fossil record does not provide evidence for historical distributions of extant catfish families beyond their present-day limits although the historical diversity of North American catfishes was considerably greater in the past. Fossilized fragments from Mongolia and Bolivia that have been likened to Ictaluridae (Gayet, 1991; Stucky, 1982) have been doubted as such by Lundberg (1992). Several lineages are known only from their fossilized remains in North America (*Hypsidoris*, *Rhineastes*, *Astephus*, "titanoglanis" and the "Big Sheep Creek Catfish") and South America (*Andinichthys*, *Hoffstetterichthys*, and *Incaichthys*), generalized fragments have been found in Eocene deposits of Antarctica (Grande and Eastman, 1986) and many Chinese fossils representing previously unrecognized lineages are reportedly awaiting description (Grande, pers. commun.) so the fossil record is far from well known.

With respect to ictalurid fossils, late Paleocene deposits in Wyoming have yielded a fossilized partial skull which provides a minimum age estimate for the family of approximately 55 Ma (Lundberg, 1970, 1992). The fossil is believed to have once belonged to an indeterminate species of the extinct genus *Astephus* referred to as the "Polecat Bench catfish" (Lundberg, 1970, 1975, 1992). This information coupled with the inferences made by Earth history predicts that the ictalurid sister taxon will be found in Northern or Eastern Asia and the reconstructed age of cladogenesis will be approximately 60 million years (Table 1).

2. Materials and methods

2.1. Source of phylogenetic information

Mitochondrial gene cytochrome *b* (cyt *b*) has been used widely to infer phylogenetic relationships within and among taxonomic categories of fishes ranging from populations to Classes (Akihito et al., 2000; Briolay et al., 1998; Derome et al., 2002; Farias et al., 2001; Lavoué et al., 2000; Lovejoy and de Araújo, 2000; Lydeard and Roe, 1997; Murphy and Collier, 1996; Orrell et al., 2002; Reed et al., 2002; Waters et al., 2000), and is one for which comparative and biochemical information is available (Esposti et al., 1993; Lydeard and Roe, 1997). Given its common use, limitations of cyt *b* have been recognized in the form of base compositional bias, substitutional saturation at the 3rd codon positions, rate heterogeneity among lineages, and conservation of amino acid residues (Graybeal, 1993; López et al., 2000; Lovejoy and Collette, 2001; Meyer, 1994; Naylor et al., 1995). Attempts to minimize the suspected systematic error have evaluated transversion weighting schemes (Broughton et al., 2000; Farias et al., 2001; Griffiths, 1997), excluded certain substitution-codon categories (Lydeard and Roe, 1997) and developed more specific methods and models (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1981; Nei and Kumar, 2000; Swofford et al., 1996). However, methods designed to massage signal from noisy data often merely demonstrate an absence of signal rather than successfully revealing its encryption (but see Naylor et al., 1995 and Griffiths, 1997).

The gene is generally considered to be informative over recent time scales, e.g., the past 10–15 million years (Graybeal, 1993; Griffiths, 1997; Meyer, 1994). Despite these findings, several studies using cyt *b* have resolved relationships among taxa much older than this. Broughton et al. (2000) found that as a product of their abundance more phylogenetically consistent transitions were present in a data set than any other substitution class and that transversion weighting schemes had the undesirable effect of emphasizing homoplastic transversions at the expense of consistent transitions. Given the conflicting evidence and incomplete understanding of the causes of error in molecular phylogenetic data sets it seems premature to discount the information cyt *b* is able to provide for a given phylogenetic problem.

Additional pitfalls with cyt *b* concern the amplification of pseudogenes. Nonfunctional copies of cyt *b* have been identified in the nuclear genome of crayfishes (Nguyen et al., 2002), rodents (Smith et al., 1992), primates

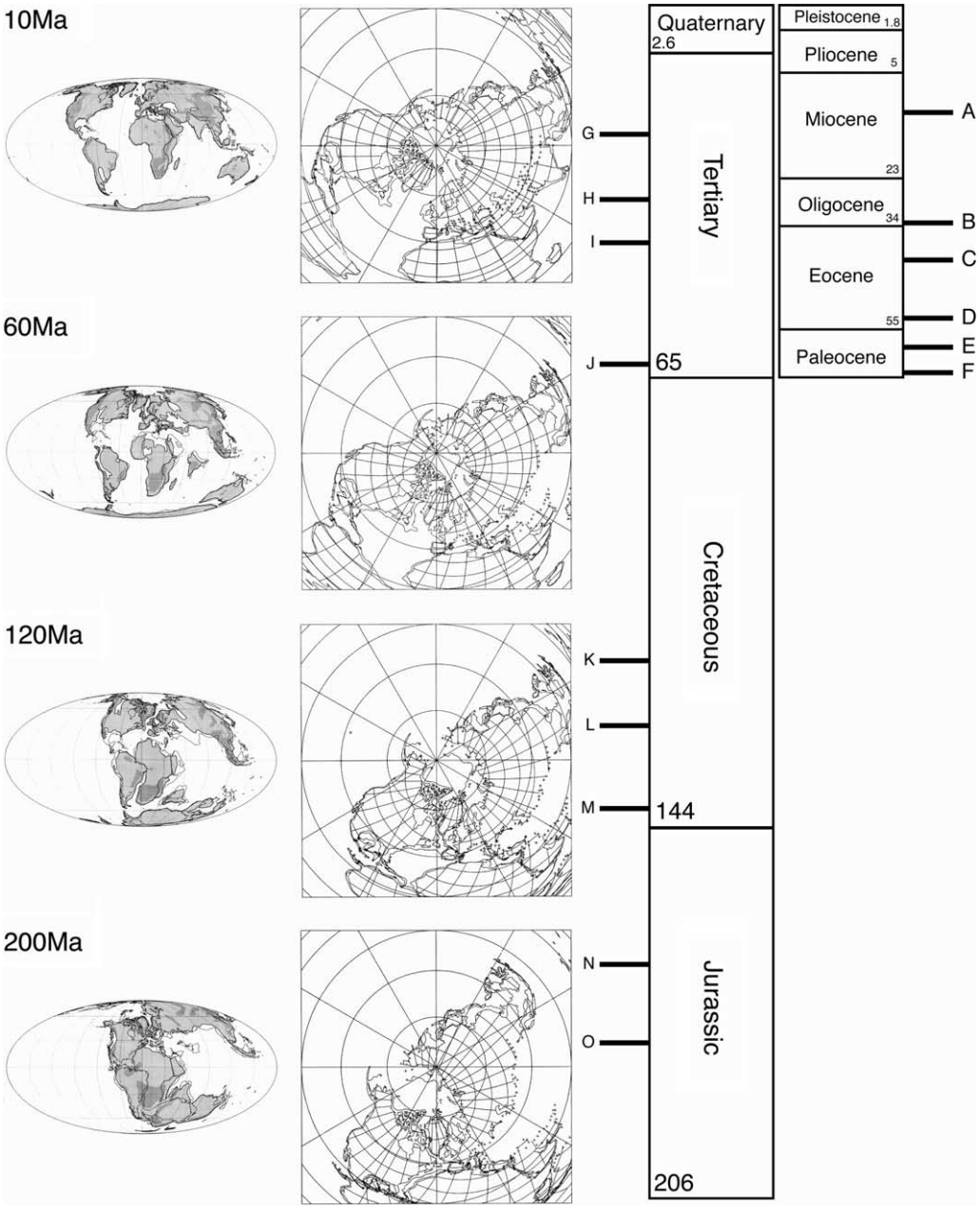

Fig. 3. Summarized fossil record (A–F) and paleogeography (G–O) (Barron et al., 1981; Smith et al., 1981) pertaining to catfishes: (A) Fossilized remains of Callichthyidae, Loricariidae, Ariidae (Monsch, 1998) and Doradidae (Aguilera, 1994) in northwestern South America and *Nematogenys cuivi*† in Chile (de las Mercedes Azpelicueta and Rubilar, 1998); (B) *Rhineastes*†, *Astephus*†, *Hypsidoris*†, ictalurids, and fossils of an uncertain family in western North America (Lundberg, 1970, 1975, 1992; Grande and Lundberg, 1988; Gayet and Meunier, 1998); (C) Siluriform fossils in Mongolia (Stucky, 1982), Bagridae, Clariidae, and Ariidae in Pakistan (Gayet and Rage, 1987), an uncertain family in Antarctica (Grande and Eastman, 1986), *Hypsidoris*† in Oregon and Wyoming (Lundberg and Case, 1970; Grande, 1987; Grande and De Pinna, 1998) and "Titanoglanis†" in Arkansas (Lundberg, 1993); (D) *Astephus*† (Ictaluridae) in North America (Lundberg, 1975; Grande and Lundberg, 1988); (E) *Corydoras revelatus*† (Callichthyidae) in Argentina (Lundberg, 1998; Reis, 1998); (F) Generalized fragments in Spain (de la Peña and Soler-Gijón, 1996), India (Cione and Prasad, 2002), Bolivia (de Muizon et al., 1983), Argentina (Cione et al., 1985), South Dakota (Frizzell, 1965), *Andinichthys*, *Hoffstetterichthys*, and *Incaichthys* in Bolivia (Gayet, 1988, 1990, 1991), diplomystids and doradoids in Bolivia (Gayet and Meunier, 1998); (G) Continental landmasses assumed their modern positions, inland seas reached their minimum; (H) Japan separated from Asian landmass; (I) Australia rifted from Antarctica, India collided with Asia, and South America separated from Antarctica; (J) Asia and Alaska converged with the opening of the North Atlantic, the Seychelles became fixed with respect to Africa, and India continued to rift towards Asia; (K) Epicontinental seas reached their maximum, Madagascar became fixed with respect to Africa, and the Anatolia-Apulia block collided with Europe; (L) A shallow sea covered Australia, proto-Indian Ocean begins to form, much of Asian inland sea reduced in Area, the Kolyma block collided with Asia; (M) Southern landmass separates into Australia-Antarctica, South America-Africa and Madagascar-India; (N) Epicontinental seas increase and begin to form Atlantic and Arctic Oceans; (O) Single landmass from Pole to Pole, coastal areas under marine influence, North America and Africa begin to separate. Paleomap illustrations modified from Smith, Hurley, and Briden *Phanerozoic paleocontinental world maps* (1981), and Smith, Smith and Funnell *An atlas of Mesozoic and Cenozoic coastlines* (1994), © Cambridge University Press.

(Mundy et al., 2000), and birds (Kornegay et al., 1993). To detect pseudogene copies of cyt *b* all composite files were translated to their amino acid residues, checked for stop codons and compared to a reference sequence (*Eigenmannia* sp. GenBank Accession: AB054131; Saitoh et al., 2003).

2.2. Taxonomic sampling

Siluriformes contains more than 30 extant families, and approximately 2700 species in 430 genera are distributed unequally among them (De Pinna, 1998; Nelson, 1994; Teugels, 2004). This study concerns the higher phylogenetic relationships among non-diplomystid catfishes, i.e., interfamilial. The fossil record provides evidence of extinction for certain lineages but the mostly fragmentary and generalized nature of available fossils does not permit an examination of the phylogenetic distribution of extinction. Thus, the comparison of past and present phylogenetic diversity among catfishes is a difficult one to make but given the distribution and wide range of morphologies shown by extant catfishes the group probably contains extant representatives of most lineages produced by cladogenetic events distributed throughout catfish evolutionary history. Taxonomic sampling was dependent on suitably preserved tissues but whenever possible morphologically distinct taxa were included to maximize the phylogenetic diversity represented in the data set. Sampling was responsive to the recovery of long branches and an effort was made to include closely related taxa of the long branch to minimize its effect on character optimization during subsequent parsimony analyses (Hendy and Penny, 1989). In contrast to uncertain phylogenetic relationships among the majority of catfish families, considerable morphological evidence has been presented supporting the sister group relationship of diplomystids and all other catfishes (Arratia, 1987; De Pinna, 1993, 1998; Grande, 1987; Grande and De Pinna, 1998; Mo, 1991). In light of these convincing results, *Diplomystes mesembrinus* (Diplomystidae) were used as outgroup in all phylogenetic analyses.

2.3. Phylogenetic analysis

PAUP* (version 4.0b8, Swofford, 2001) was used to evaluate alternative topologies, generate pairwise genetic distances, base frequencies, ensemble consistency (CI) and retention (RI) indices, conduct the Shimodaira–Hasegawa (Shimodaira and Hasegawa, 1999) test of tree score differences, likelihood ratio tests (Felsenstein, 1988; Goldman, 1993; Muse and Weir, 1992; Sanderson, 1998) and zero branch length test of Slowinski (2001). Multiple optimal topologies were summarized through consensus methods.

The hypotheses of Mo (1991) and De Pinna (1993), as they applied to the taxonomic sample of this study, were tested by constraining the analysis of the cyt *b* data to recover the optimal tree(s) compatible with each. Lineages not available for inclusion in this study were pruned from the trees of Mo (1991) and De Pinna (1993) prior to their use as constraints as in Hardman (2004). The scores of the constrained tree(s) were compared to those of the optimal tree(s) derived from the unconstrained analysis of the same data through the S–H test using 1000 replicates of RELL bootstrap and parameters estimated by Modeltest 3.06 (Posada and Crandall, 1998).

With respect to the parsimony criterion the cyt *b* data were analyzed with the Tree–Bisection–Reconnection (TBR) search algorithm with 1000 replicates in which taxa were added randomly to the starting tree. All characters were treated as unordered and transformations were assigned equal weight. Nodal support was evaluated with 1000 nonparametric bootstrap pseudoreplicates (Felsenstein, 1985) using the TBR search algorithm on a starting tree to which taxa were added randomly. Nodes recovered in more than 90% of pseudoreplicates were considered strongly supported, i.e., accurately represented in the optimal tree(s).

The Bayesian-likelihood method of phylogenetic analysis (Huelsenbeck et al., 2001) was used to evaluate alternative tree topologies through the estimation of posterior probabilities using MrBayes v.3.0 (Ronquist and Huelsenbeck, 2003). Parameters were estimated for each of six substitution categories over each of three codon positions using the UNLINK command. The model corresponded to the generalized time reversible (GTR) model of sequence evolution (Lanave et al., 1984; Rodríguez et al., 1990; Tavaré, 1986). In addition to substitution probabilities the proportion of invariant sites and among-site rate heterogeneity were modeled over each codon position. The MrBayes analysis ran four chains simultaneously each for 1.5×10^6 generations. Every 100th generation was sampled and the asymptote of likelihood score was detected with the SUMP command. All sampled topologies beneath the asymptote were discarded from the population of trees considered in the subsequent majority-rule consensus. The frequency with which a particular clade appeared in the population of retained topologies was interpreted as its posterior probability. Posterior probabilities were interpreted as a measure of how likely the clade appears in the optimal topology rather than accuracy of the node with respect to species relationships or clade stability.

2.4. Molecular polytomies

Many phylogenetic studies recover optimal topologies that display short internal branches with low support val-

ues. Results of this kind are often identified as periods in the history of the group in which cladogenesis occurred at a rate faster than synapomorphies could accumulate to track the branching order (Kraus and Miyamoto, 1991; Lessa and Cook, 1998); so-called adaptive radiations or hard polytomies. However, this interpretation has come under criticism as one that is often made prematurely (Jackman et al., 1999; Slowinski, 2001).

Slowinski (2001) drew a distinction between a species polytomy and a molecular polytomy in that a species polytomy refers to the simultaneous (or near simultaneous) cladogenesis of three or more species in a species phylogeny whereas a molecular polytomy is found in a gene tree and of which there are two kinds; true and false. True molecular polytomies reflect species polytomies as they are a product of them. False molecular polytomies result from a lack of the substitutions required to resolve the branches involved in the gene tree polytomy. Slowinski (2001) also demonstrated how parsimony methods can falsely resolve true molecular polytomies and described how the likelihood ratio test with critical values provided by Goldman and Whelan (2000) can be used to test the null hypothesis of zero branch length pertaining to a given node. Slowinski (2001) stressed that to distinguish between true and apparent molecular polytomies (and therefore to detect a species polytomy) data from several independent loci must be analyzed in this way. Slowinski's method was used here and nodes that failed to reject the null hypothesis of zero length were interpreted as false molecular polytomies, i.e., too few characters to provide resolution. The use of a single locus prohibits the detection of species polytomies.

2.5. Specimen and data collection

Specimens were collected using a variety of methods including seines, baited traps, and electrofishing equipment but were also obtained from markets and the aquarium industry. Muscle and liver tissue was dissected from the anesthetized catfishes according to a protocol (No. 00303) approved by the University of Illinois' Laboratory Animal Care Advisory Committee and frozen immediately in liquid nitrogen or preserved in 100% ethyl alcohol. Along with syntopic material, specimens from which tissue was removed were fixed in 10% formaldehyde solution and later transferred to 70% ethyl alcohol. Specimens and carcasses were deposited in the permanent collections of the Illinois Natural History (INHS), Auburn University Museum (AUM), and The JLB Smith Institute of Ichthyology (RUSI). Several taxa were unavailable as samples but fortunately available for inclusion in this study as files deposited with GenBank thanks to the efforts of staff at the Department of Ichthyology, Institute of Hydrobiology, Chinese Academy of Sciences, Luojiashan, Wuhan, Hubei Province 430072, PR China. See Appendix A for institutional catalog numbers and GenBank accession numbers for samples included in this study. Institutional abbreviations are as listed in Leviton et al. (1985).

Nucleic acids were isolated using either a standard protein digest and phenol–chloroform procedure followed by ethanol precipitation or with the Qiagen DNEasy Tissue Kit according to the manufacturer's protocol. Approximately 300 ng of the nucleic acid extract were used as template in the polymerase chain reaction (PCR) amplification of the target region using the primers listed in Hardman and Page (2003), Hardman (2004) and Table 2. PCR was performed using a PTC-100 Programmable Thermal Controller (MJ Research) in 25 or 50 μL reactions consisting of 0.4 mM of dNTP, 1.25 mM magnesium chloride, 0.25 μM of each primer, and 1.24 U of *Taq* polymerase in a reaction buffer containing 50 mM potassium chloride, 10 mM Tris–hydrochloric acid (pH 9.0), and 0.1% Triton X-100. Thermal cycling conditions consisted of an initial denaturation step of 94 °C for 3 min followed by 25 cycles of a denaturation step of 94 °C for 30 s, a variable annealing step of between 40 and 62 °C for 30 s, and an extension step of 72 °C for 90 s. A final incubation of 72 °C for 5 min was added to ensure complete extension of amplified products. Amplified DNA was purified using the Qiagen QIAquick PCR Purification Kit and

Table 2
Primer sequences and approximate annealing locations used in PCR and sequencing of cyt *b* in addition to those reported in Hardman and Page (2003) and Hardman (2004)

Primer	Sequence	Annealing location[a]
OsCytb-F1	5′-CAC CCA TAC TTC TCM TAy AAA GA-3′	15876–15898: 657 bp downstream of cyt *b* start codon
OsCytb-R1	5′-TCT TTr TAk GAG AAG TAT GGG TG-3′	15898–15876: 679 bp downstream of cyt *b* start codon
SCytb-F1	5′-AAA ATT GCT AAC GAC GCA CTA AT-3′	15249–15271: 30 bp downstream of cyt *b* start codon
SCytb-R1	5′-TCT TTT CTG GCG CTA GGG AGG-3′	16437–16417: 61 bp downstream of cyt *b* stop codon, within threonine tRNA
ACytb-F1	5′-GAT CyT mCC yGC CCC mTC yAA yAT yTC T-3′	15273–15299: 54 bp downstream of cyt *b* start codon
ACytb-R1	5′-TCC GGA TTA CAA GAC CGG yGC TTT-3′	16399–16376: 20 bp downstream of cyt *b* stop codon, within threonine tRNA
L14673	5′-TAA TGG CGT GAA AAA CCA CCG TTG T-3′	15176–15200: 43 bp upstream of cyt *b* start codon, within glutamine tRNA

[a] Primer annealing locations determined through comparison with *Ictalurus punctatus* mitochondrial genome (GenBank: NC 003489).

sequenced with the Perkin-Elmer BigDye DNA Sequencing Kit according to the manufacturer's protocol with primers used in PCR and those designed to anneal at various downstream locations within the amplified region to provide complete, double-stranded sequence (Table 2). Sequenced product was purified by passing the reaction through 700 μL Sephadex columns (2.0 g Sephadex G-100: 32.0 mL water) and dried prior to visualization with an ABI Prism 377 automated DNA sequencer (PE Applied Biosystems).

The cyt *b* gene region was sequenced for 144 catfish species from 28 of 33 families. Twenty-six species representing eight families were added to the data set from sequences published on GenBank (Appendix A). Sequence chromatograms were edited with Sequencher 4.1 (GeneCodes) and corresponding forward and reverse sequences were aligned to produce a composite file of the amplified product for each individual. The alignment of composite files for both protein-coding loci was trivial and the character matrix analyzed by PAUP* was generated by Sequencher 4.1.

3. Results

3.1. Preliminary data analysis

An alignment of 1170 contiguous nucleotides of cyt *b* and partial sequence of the downstream threonine tRNA was assembled for 170 catfish species representing 29 of 33 extant families and is available from the author upon request. Not all terminals have complete sequence and the mean ± standard deviation sequence length was 1125.3 ± 87.6 nucleotides. The character matrix contained 650 parsimony-informative characters among the ingroup. Cyt *b* nucleotide composition was found to be typical for protein-coding mitochondrial genes among vertebrates (Lydeard and Roe, 1997) and common to all taxa.

3.2. Parsimony analysis

The TBR search algorithm identified three most parsimonious topologies each of 17,595 steps (CI 0.085, RI 0.387) and their summarized strict consensus is shown in Fig. 4. Additional details of the phylogenetic results can be found in the figure legend. With respect to the identity of the sister taxon of Ictaluridae maximum parsimony recovered *Cranoglanis bouderius* (Cranoglanididae) as the sister group from among those sampled.

With respect to data-decisiveness (Kitching et al., 1998) a score of 0.289 was recovered (1.0 = no conflict, 0 = wholly undecisive) suggesting considerable character conflict. Non-parametric bootstrap proportions of nodes subtending clades of multiple families did not provide evidence of convincing resolution for deeper nodes in the optima. While many familial and subfamilial clades were recovered in a high proportion of boostrap pseudoreplicates the lack of support suggests weak signal overall and probable inaccuracy among deeper nodes recovered by the analysis of these data.

3.3. Bayesian likelihood analysis

When the likelihood scores of the 1.5×10^6 generations were plotted an asymptote was observed at approximately the 220,000th generation. In light of this samples of the first 250,000 generations were discarded as burn-in and the remaining 12,500 trees (representing 1.25×10^6 generations) were summarized as a 50% majority-rule consensus (Fig. 5). Branch lengths are means estimated by MrBayes and displayed in PAUP* as user-supplied values. Parameter estimates (mean ± variance) for each of the codon-based models are shown in Table 3.

The Bayesian consensus was fully resolved (Fig. 5), and several superfamilial nodes were associated with posterior probabilities (pp) greater than 90, including an exclusive clade of Ictaluridae and *C. bouderius* (pp = 100). While considerable taxonomic congruence was noted with respect to the results of the parsimony analysis, several cases of conflict were detected as well as several nodes subtending clades of distantly related and obviously non-monophyletic groups of catfishes. Demonstrably monophyletic clades such as Callichthyidae, Siluridae, and Akysidae were not recovered in the Bayesian analysis probably due to problems associated with rate heterogeneity and a relatively spartan sample of these problematic clades. Particularly problematic clades were identified through the unorthodox inclusion of members that clearly belong to other clades and were characterized by long terminal branches with short nodes subtending them (noted in Fig. 5).

Modeltest suggested the use of GTR + I + Γ for these data. Estimated base frequencies over all codons were: adenine (A) 0.3576, cytosine (C) 0.4099, guanine (G) 0.0436, and thymine (T) 0.1889. The substitution model applied the following estimated rates for each of the six substitution categories to all codons simultaneously: A ↔ C 0.1295, A ↔ G 4.1827, A ↔ T 0.2800, C ↔ G 0.3584, C ↔ T 3.3910, and G ↔ T 1.000. With respect to among-site rate variation, the proportion of invariant sites was 0.3135 and the gamma distribution shape parameter was 0.4127 implying both fast and slow rates of change among sites (Yang, 1996). The zero length branch test was conducted with the model described above and nodes that were statistically indistinguishable from zero are shown in Figs. 4–6.

3.4. Shimodaira–Hasegawa test results

The optimal topologies compatible with each of the phylogenetic hypotheses provided by Mo (1991) and De Pinna (1993) were all significantly less likely

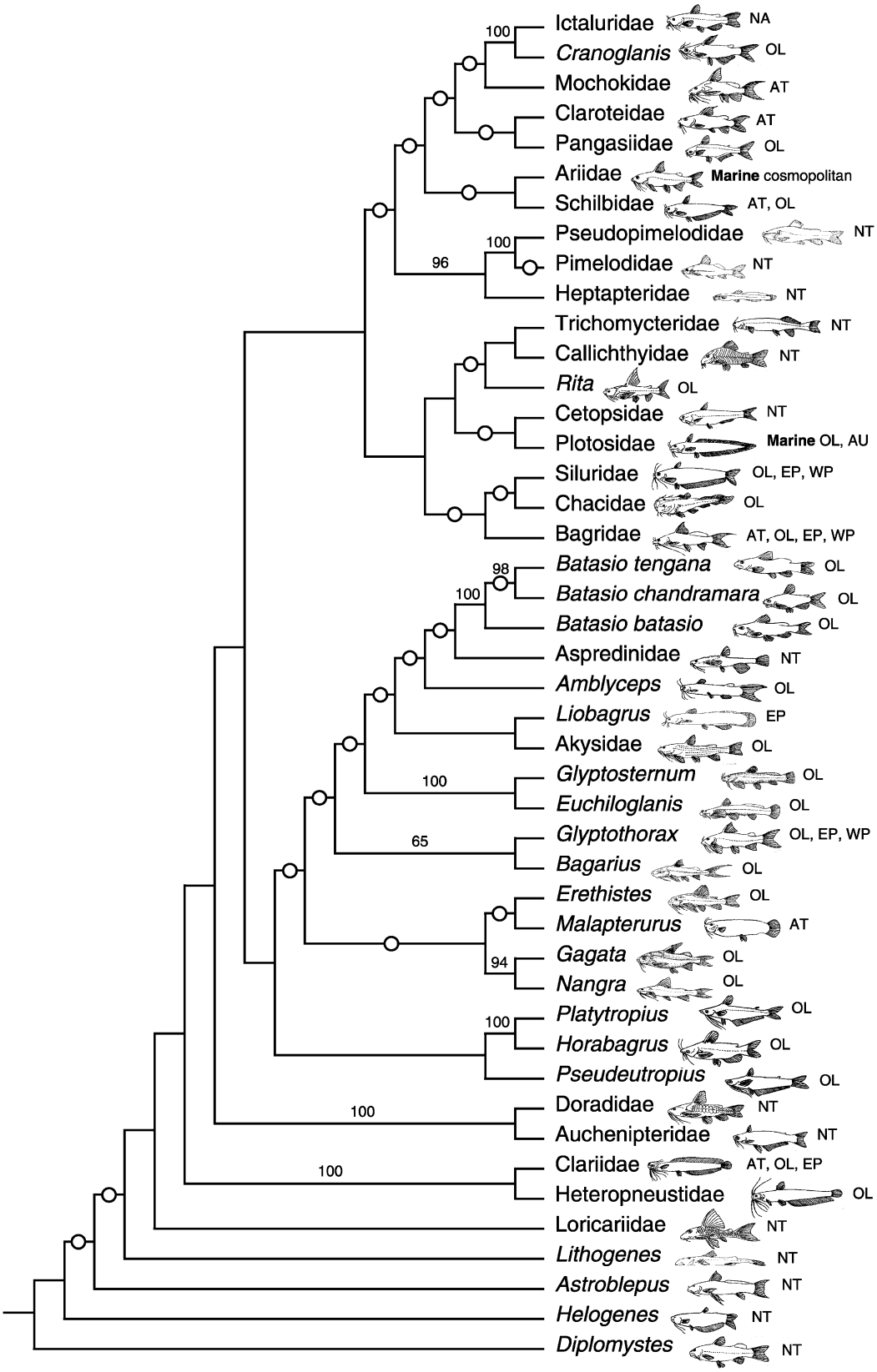

Fig. 4. Summarized consensus of three most parsimonious topologies each of 17,595 steps (CI 0.085, RI 0.387). Clades containing multiple samples of a family that were recovered monophyletic are shown as a single terminal with the appropriate higher taxon name applied. Numbers above nodes are posterior probabilities recovered by the Bayesian analysis for those clades common to both parsimony and likelihood topologies. Nodes with ○ failed to reject the null hypothesis of zero length, and are considered falsely resolved. Illustrations modified from Eigenmann (1912), Burgess (1989), and Nelson (1994).

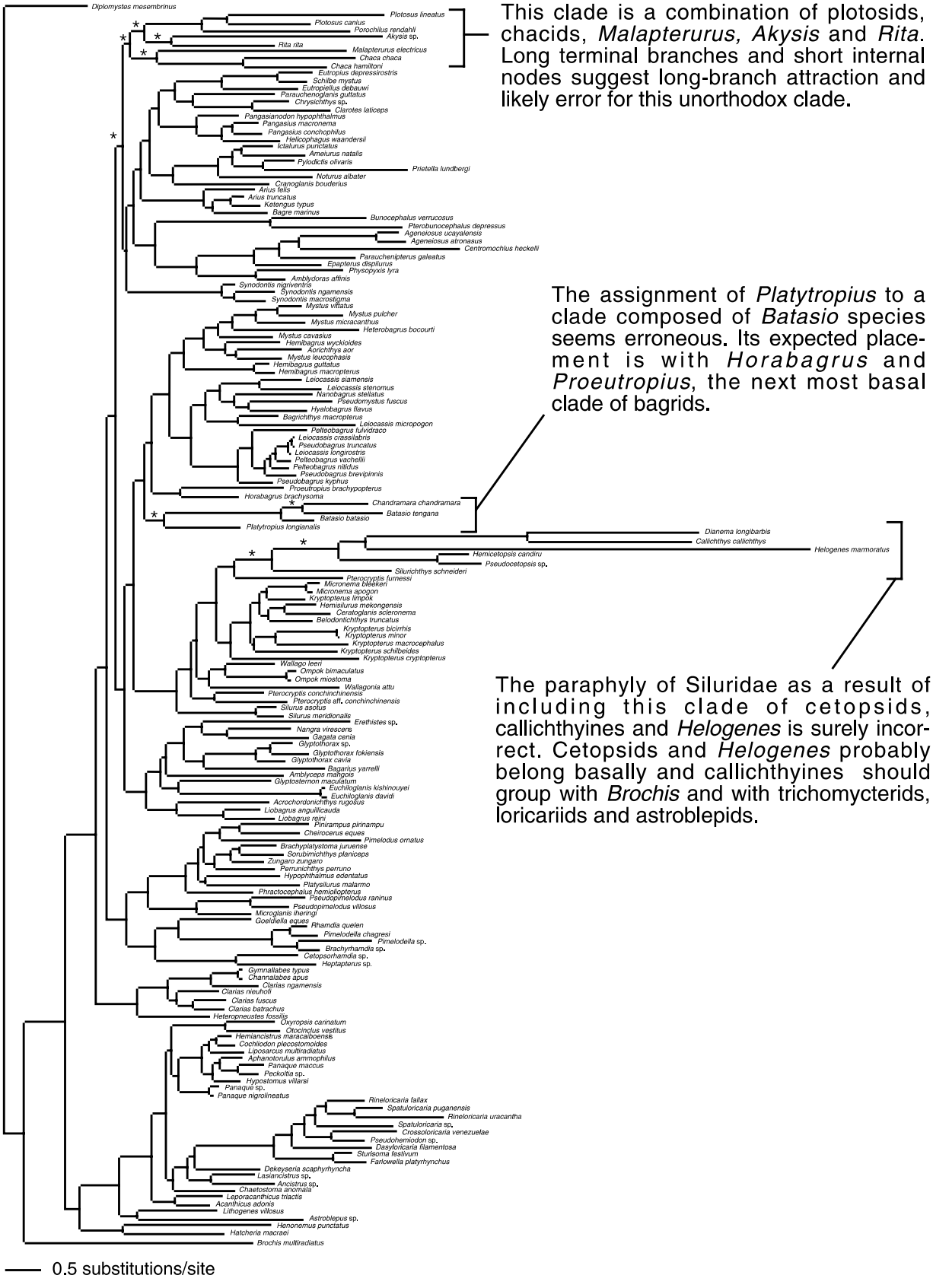

Fig. 5. Majority-rule consensus of sampled trees from 1.25×10^6 post burn-in generations of the Bayesian likelihood analysis. Branch lengths are means estimated by MrBayes, and displayed in PAUP* as user-supplied values. Unorthodox nodes are marked with *, and are believed to be incorrectly resolved. Parameter estimates are provided in Table 3.

Table 3
Model parameters (mean ± variance) estimated by MrBayes during likelihood analysis of 1.25×10^6 post burn-in generations

Codon position	1	2	3
P[Adenine]	0.3309 ± 0.0001	0.1690 ± 0.0001	0.4114 ± 0.0002
P[Cytosine]	0.3350 ± 0.0001	0.3256 ± 0.0002	0.3758 ± 0.0001
P[Guanine]	0.2022 ± 0.0001	0.1067 ± 0.0001	0.0385 ± 0.0000
P[Thymine]	0.1319 ± 0.0000	0.3986 ± 0.0003	0.1743 ± 0.0000
G ↔ T	1.0 ± 0.0	1.0 ± 0.0	1.0 ± 0.0
C ↔ T	33.7213 ± 27.8050	3.8864 ± 0.7106	11.4150 ± 7.4020
C ↔ G	0.1300 ± 0.0019	1.2726 ± 0.1534	1.1436 ± 0.1326
A ↔ T	1.8585 ± 0.0876	0.8491 ± 0.0506	0.4774 ± 0.01567
A ↔ G	3.6628 ± 0.2712	6.4358 ± 3.0175	13.3108 ± 8.4582
A ↔ C	0.4728 ± 0.0086	0.9877 ± 0.0774	0.1546 ± 0.0018
α	0.2848 ± 0.0001	0.2499 ± 0.0001	0.5784 ± 0.0047
p-inv	0.2497 ± 0.0047	0.3957 ± 0.0006	0.0098 ± 0.0000

The GTR + I + Γ model was estimated for each of the three codon positions independently.

($P < 0.0001$) than the optima of unconstrained analyses. As such, previous phylogenetic hypotheses as they apply to these data, analyses and taxonomic sample (several lineages were unavailable for inclusion) were rejected in their explicit form. The extent to which subclades of the hypotheses provided by Mo (1991) and De Pinna (1993) were tolerated by the cyt *b* data were not explored and such an approach may yield elements of these hypotheses that are not significantly less likely than unconstrained optima.

4. Discussion

This study consistently identified *Cranoglanis* as the extant sister taxon of Ictaluridae from among those sampled, it should be stressed that the taxonomic sample of this study was not exhaustive. Of the families recognized by Ferraris and De Pinna (1999) this study did not include representatives of Scoloplacidae, Amphiliidae, Nematogenyidae, and Austroglanididae as well as taxa presently placed incorrectly within non-monophyletic families, e.g., *Olyra* and *Phreatobius*. Of the named absentees perhaps the African Austroglanididae poses the greatest concern as a potentially close relative of Ictaluridae. In Mo's Cladogram II (1991) resulting from his weighted analysis austroglanidids and Cranoglanididae were recovered as sister taxa. The other missing families are understood to be parts (Scoloplacidae and Nematogenyidae) or a close relative (Amphiliidae) of the well-diagnosed Loricarioidea (Baskin, 1973; De Pinna, 1992, 1993, 1998; Lundberg and Baskin, 1969; Mo, 1991; Schaefer, 1990; Schaefer and Lauder, 1986). The newly-discovered "Chiapas" catfish (Rodiles et al., 2000) does not exhibit any of the ictalurid synapomorphies and does not appear to be a close relative (J.G. Lundberg, pers. commun.). While most of the missing taxa are of minor concern, the phylogenetic relationships between ictalurids, cranoglanidids, and austroglanidids should be ascertained before firm conclusions are drawn with respect to historical reconstructions of ictalurid origins and diversification.

The result of a proximal relationship between cranoglanidids and ictalurids is consistent with predictions drawn from phylogenetic, biogeographic, paleontologic, and geologic information pertinent to ictalurid evolutionary history (Figs. 3–5 and Table 1). If the result is accurate it seems that the ictalurid ancestor speciated from the ancestor of Cranoglanididae some time before a northern route became available through northeastern Asia and northwestern North America in the late Cretaceous. Between this time and approximately 55 Ma, the ictalurid ancestor had undergone diversification at least for the now-extinct *Astephus* in Wyoming and Oregon. Present-day ictalurids are distributed east of the North American continental divide (Lee et al., 1980; Page and Burr, 1991) so it seems that an eastern expansion in their range took place along with a retreat from their western limits most likely as a result of climate change during the Oligocene (Retallack, 2004; Retallack et al., 2004; Smith et al., 1998). Evidence from the fossil record (see Section 1), suggests that non-ictalurid catfishes present in western North America (along with the ictalurid genus *Astephus*) did not successfully escape to the east, e.g., *Hypsidoris* and *Rhineastes*. In addition to moving eastwards, ictalurid diversification had taken place for at least the lineages leading to *Ictalurus* and *Ameiurus* by (at the latest) the end of the Eocene and for *Pylodictis* by at least the early Miocene (Lundberg, 1975, 1992).

With respect to interrelationships among catfish families in general, the results of this study were unconvincing in that few nodes subtending multiple families were insensitive to method of analysis, supported by non-parametric bootstrap proportions and statistically distinguishable from zero length. The ensemble consistency and retention indices suggested high homoplasy, moderate synapomorphy, and the data were only somewhat decisive. However, given the results of the S–H test the data contain sufficient signal to reject alternative topologies suggesting that considerable covariation exists and that signal is incongruent with the morphological covariation scored so far. Also, the majority of species were recovered in their assigned families as expected of data containing phylogenetic information, and several multifamilial clades were recovered which have also been demonstrated by morphologists. In light of these observations, it would be premature to propose changes to the existing classification or discuss the evolutionary history of Siluriformes as a whole but a discussion of some clades and their consistency with the results of phylogenetic studies focused on them is warranted.

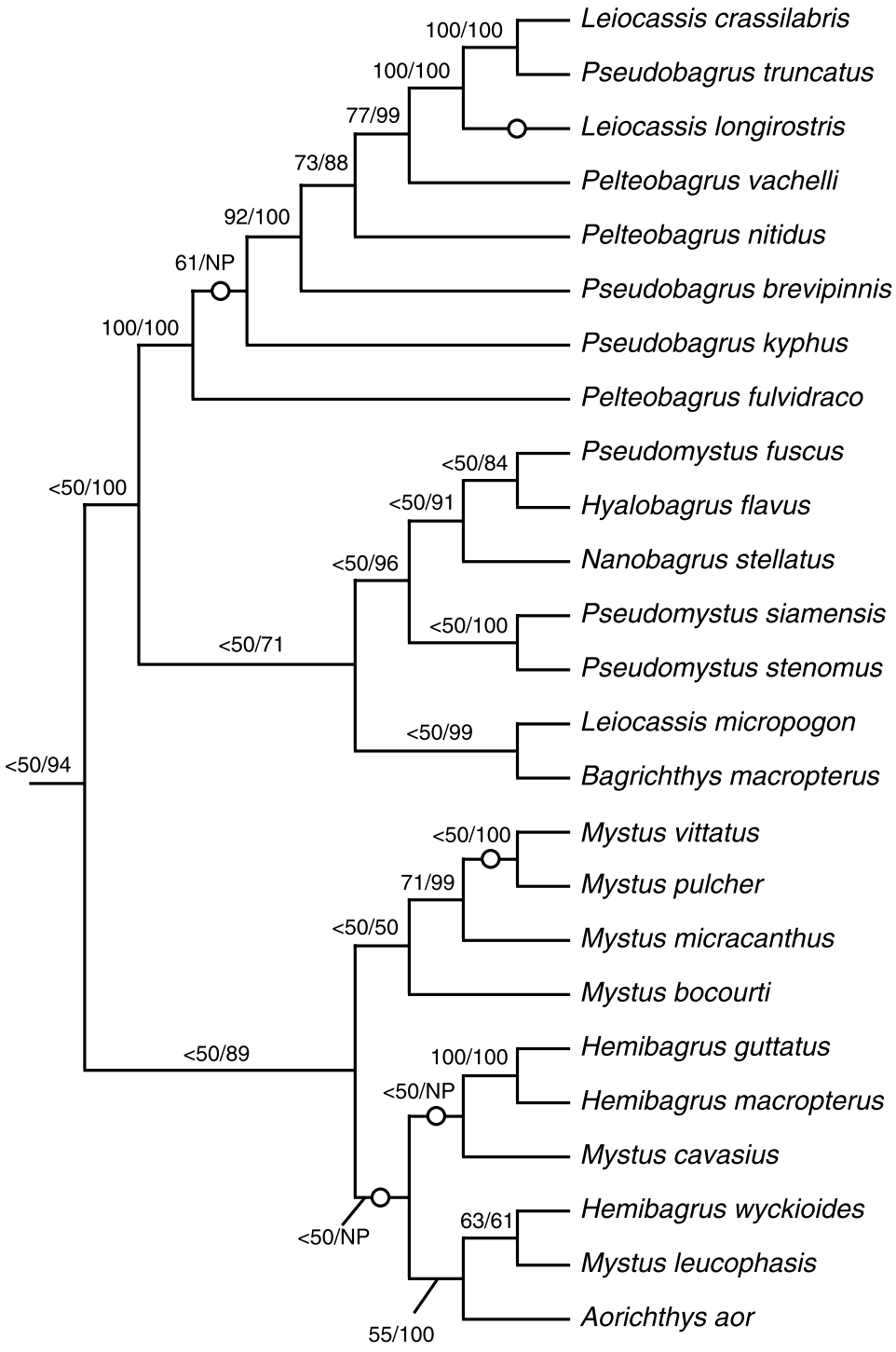

Fig. 6. Relationships among bagrids recovered by parsimony analysis of entire data set. Numbers above nodes are percentage of non-parametric bootstrap pseudoreplicates and posterior probabilities. NP, node not present in majority-rule consensus of Bayesian samples. Nodes with ○ failed to reject the null hypothesis of zero length, and are considered falsely resolved.

4.1. Results of the parsimony analysis

With respect to the parsimony analysis, several expected clades were not recovered monophyletic despite the fact that compelling morphological synapomorphies have been identified. Most notable among these is the inferred non-monophyly of the Loricarioidea. Also troubling is the recovered paraphyly of loricariids, *Lithogenes* and *Astroblepus* with respect to all other non-diplomystid, non-helogeneid catfishes; a clade for

which abundant morphological synapomorphies exist (Armbruster, 2004; De Pinna, 1993, 1998; Schaefer, 1986, 1987). The placement of *Malapterurus* as sister to *Erethistes* is probably an artefact due to long-branch attraction (Felsenstein, 1978; Huelsenbeck, 1998). Lastly, the superfamily Sisoroidea (Sisoridae, Akysidae, Amblycipitidae, Aspredinidae, and Erethistidae) was recovered non-monophyletic with respect to the nesting of *Malapterurus* and a clade composed of *Batasio* species. Nodes subtending these contentious clades all failed to reject the null hypothesis of zero length and were interpreted as falsely resolved (Slowinski, 2001). The removal of *Malapterurus* and the *Batasio* clade makes the Sisoroidea monophyletic and this is likely to be the case. In spite of likely errors in the recovered topologies several clades were recovered which morphologists have long suspected but for which synapomorphies have not yet been observed. Most notable among these are the "pimelodoids": Pimelodidae, Pseudopimelodidae, and Heptapteridae.

Other novel results worthy of consideration include the non-monophyly of Amblycipitidae with *Liobagrus* consistently being recovered as more closely related to akysids than *Amblyceps*. This is an unexpected result and an unorthodox clade. Chen (1994) and De Pinna (1996) recovered *Liobagrus*, *Amblyceps*, and *Xiurenbagrus* monophyletic and recognized synapomorphies in the suspensorium and branchial skeleton. In this analysis *Liobagrus* and *Amblyceps* were not recovered monophyletic in either the Bayesian or parsimony analyses (Figs. 4 and 5). These two genera have non-overlapping ranges; *Amblyceps* is found in hillside streams of Pakistan, northern India, and the Malay Peninsula, and *Liobagrus* in similar habitats of Korea, Japan, and central China (Berra, 2001).

4.2. Results of the Bayesian analysis

Methods of phylogenetic inference are constantly scrutinized and a recent simulation study by Kolaczkowski and Thornton (2004) showed that likelihood methods (including Bayesian Markov Chain Monte Carlo) performed worse than parsimony when molecular evolution across lineages takes place at different rates and internal nodes are short. Clearly, the estimated branch lengths shown in Fig. 5 (as well as the results of Modeltest) describe mtDNA evolution as one with a wide range of rates among lineages, and consequently the Bayesian results could be influenced by this source of error more so than those of the parsimony analysis (Kolaczkowski and Thornton, 2004), although unorthodox resolution discussed above and below suggests similarly biased results for parsimony.

Several nodes in the Bayesian consensus suggest rate heterogeneity to have misled the analysis and yielded erroneous resolution (Fig. 5). These nodes include the inferred non-monophyly of Callichthyidae, Siluridae, Sisoridae, Akysidae, and Loricaridoidea. Additionally, a long branch subtending a clade composed of *Batasio* species is probably interfering with the clustering of *Horabagrus*, *Platytropius*, and *Pseudeutropius*. Curiously, when the zero branch length test was carried out on the parsimony trees, the dubious nodes were indistinguishable from zero length whereas in the Bayesian analysis similarly contentious nodes were not, implying a less conservative test even though an identical model was used. Presumably, this is due to the misrepresentation of homoplasy as incorrectly resolved synapomorphy in the Bayesian consensus. However, much of the resolution provided by the Bayesian analysis is satisfying and appears to have avoided the problems evident in the parsimony results. Given that both methods have problems, a simple choice between the Bayesian and parsimony results would be difficult to defend.

4.3. Bagridae

The composition and relationships among members of Bagridae have been the focus of cladistic analyses of morphological (De Pinna, 1993; Mo, 1991; Ng, 2004) and biochemical data (Okazaki et al., 1999; Peng et al., 2002; Watanabe and Nishida, 2003). However, the taxonomic sampling of these studies has been influenced by the historical treatment of this non-monophyletic group of catfishes and this makes their results difficult to interpret. Typically, catfishes such as *Rita*, *Austroglanis*, auchenoglanidids, claroteids, *Horabagrus*, *Batasio* and the more familiar bagrines and bagrichthyines are included and their interrelationships discussed. Studies that do not include representatives of other catfish lineages risk imposing monophyly on a non-monophyletic group, particularly when terminals are chimeric representatives of multiple taxa (e.g., De Pinna, 1993; Mo, 1991; Ng, 2004). This study maintained terminals as individual entries representing species. In this way, generic monophyly could be tested and the constituents of Bagridae better understood by revealing those members that were more closely related to other catfish lineages.

This study included many of the lineages discussed in the context of Bagridae but data from *Austroglanis* were not available. Mo's (1991) bagrid study remains the most taxonomically complete and his inclusion of non-bagrids emphasized the non-monophyly of Bagridae *sensu lato*. Mo erected the Austroglanididae to accommodate *Austroglanis* catfishes as he found them to be a distinct lineage and quite distantly related to bagrids, and he noted a similar distinction for African claroteids. In doing so, he restricted the Bagridae to two subfamilies: Bagrinae and Ritinae. The former roughly corresponds to the clade shown in Fig. 6, while a sister group relationship between bagrines and the

latter was not recovered in this study. *Rita* was a particularly labile taxon during preliminary analyses and its placement here should be received very cautiously. Its reported sister taxon, *Nanobagrus* (De Pinna, 1993; Mo, 1991; Ng, 2004), is sister to a clade composed of *Pseudomystus fuscus* and *Hyalobagrus* nesting well within Bagrinae (Fig. 6).

While the parsimony results did not identify a clade composed of catfishes considered by Mo (1991) to comprise Bagridae *sensu stricto* (bagrines inclusing *Batasio* and ritines), the Bayesian results included a clade of bagrids sister to *Horabagrus* and *Pseudeutropius* (although its branch length was not distinguishable from zero), and a clade of *Batasio* and *Platytropius* sister to these (Fig. 5). *Rita* was not found in this clade, and claroteids were recovered as closely related to schilbids and pangasiids similar to De Pinna (1993).

In line with the results of Mo (1991) and De Pinna (1993), *Horabagrus* was found to be distinct from bagrines and (echoing the findings of Mo) a member of a clade composed of the Asian schilbids *Platytropius* and *Pseudeutropius*. Mo (1991) transferred *Horabagrus* to Schilbidae based on a close relationship to *Platytropius* and *Pseudeutropius* and recognition of its distinction from bagrids. However, Mo also pointed out that the Schilbidae is a non-monophyletic assemblage composed of at least three lineages; African schilbids, *Ailia,* and Asian schilbids. De Pinna (1993) found *Horabagrus* to be distinct and distantly related to both bagrids and schilbids. This study demonstrated non-monophyly of Schilbidae, with African members *Schilbe*, *Eutropius*, and *Eutropiellus* forming a clade closely related to claroteids and pangasiids, and the Asian *Horabagrus*, *Platytropius*, and *Pseudeutropius* as a separate and distantly related clade. Given the problems with Mo's recognition of a non-monophyletic Schilbidae and De Pinna's recognition of Horabagridae, results presented here suggest the transfer of *Platytropius* and *Pseudeutropius* from Schilbidae to Horabagridae. Other Asian schilbids should be examined to define the limits of a family that may actually be restricted to Africa.

Mo (1991) emphasized the distinction of *Batasio* with respect to other bagrids. The phylogenetic relationships of this clade to other catfishes are not obvious, with parsimony nesting the clade apically within a mixed clade of sisoroids and *Malapterurus* whereas the Bayesian analysis recovered a sister group relationship between it and a clade of bagrids and horabagrids. Mo (1991) and De Pinna (1993) recovered similarly basal resolution of the *Batasio* clade, although neither thought horabagrids to be close relatives of bagrids. Fig. 5 shows a long branch subtending the *Batasio* clade and this is likely interfering with the parsimony analysis and placement of the clade.

With respect to the results of the parsimony and Bayesian analyses, many of the recovered clades were common although non-parametric bootstrap support was not evident for many of them and several could not be distinguished from zero length (Fig. 6). As mentioned by Mo (1991, p. 135), the genera *Pelteobagrus* and *Pseudobagrus* are closely related but probably not reciprocally monophyletic. A clade composed of species assigned to these two genera along with Chinese species of *Leiocassis*, also believed by Mo (1991) to belong to *Pseudobagrus* or *Pelteobagrus*, was recovered by both analyses and in all bootstrap pseudoreplicates. These results encourage the synonymization of *Pelteobagrus* Bleeker 1864 with *Pseudobagrus* Bleeker 1860 and the transfer of *Leiocassis crassilabris* and *L. longirostris* to *Pseudobagrus*.

Pseudobagrus catfishes were recovered as sister to a clade composed of *Pseudomystus*, *Hyalobagrus*, *Nanobagrus*, *Leiocassis*, and *Bagrichthys*, although without strong bootstrap support. *Leiocassis* was recovered as most closely related to *Bagrichthys* in agreement with Mo (1991). In contrast to the suggestion made by Ng and Kottelat (1998) that *Hyalobagrus* is more closely related to schilbids than bagrids, the genus nested well within the bagrines and sister to *Pseudomystus fuscus*. Two other species of *Pseudomystus* were included (*P. siamensis* and *P. stenomus*) and these were recovered as sister species forming a clade sister to *P. fuscus*, *Hyalobagrus*, and *Nanobagrus*. Seemingly, the non-monophyly of *Pseudomystus* could be removed by synonymizing these genera.

There are several common clades between this study and those recovered by Mo (1991). *Pseudobagrus* catfishes have already been discussed, and an exclusive clade of *Mystus*, *Hemibagrus*, and *Aorichthys* is another common result. Within this clade, more congruence exists in the form of a close relationship between *Hemibagrus* and *Aorichthys*, although in this study the non-monophyly of *Mystus* is obvious. *Mystus* is poorly defined (Mo, 1991; Ng, 2004) so this result is not controversial. Mo (1991) recognized two clades within *Mystus* and a clade approximately corresponding to one of them was demonstrated here of *M. pulcher*, *M. vittatus*, and *M. micracanthus*, although *M. bocourti* was thought by Mo to be more closely related to another clade of *Mystus* catfishes which were nested within *Hemibagrus* in this study. The synonymization proposed by Mo (1991) of *Heterobagrus* with *Mystus* is supported. *Hemibagrus* is not diagnosed by any unique synapomorphies but was considered a natural group by Mo (1991) because of overlapping morphology and distribution. *Hemibagrus* was recovered polyphyletic here because of two species of *Mystus* and a closer relationship between *H. wyckioides* and *Aorichthys aor* than to other *Hemibagrus* species.

5. Conclusions

This study analyzed cyt *b* sequences from 170 species of catfishes from 29 of 33 families, and found a sister group relationship between North American ictalurids and Southeast Asian *Cranoglanis*. This result is consistent with other cases of North American freshwater fishes that have their sister taxa in eastern or southeastern Asia, e.g., catostomids, paddlefishes, and cyprinids, as well as the fossil record, paleogeographic reconstructions and existing phylogenetic hypotheses. The evolutionary scenario inferred from this study and extant distributions of ictalurids and *Cranoglanis* is of an invasion of North America from Asia through a freshwater route during the late Cretaceous or early Tertiary with a subsequent dispersal to eastern and southern freshwaters and a retreat from western limits of the lineage represented today by Ictaluridae. A southern retreat is also implied for the lineage represented today by *Cranoglanis*.

Several multifamilial clades were recovered that are consistent with the results of recent morphological studies (Sisoroidea, Doradoidea) as well as ones that are novel and warrant further investigation (Pimelodoidea, Bagridae, Horabagridae, Schilbidae, and Amblycipitidae). While the results of this study contain error due to rate heterogeneity and weak signal in certain substitution categories, consistently recovered nodes and test results imply moderate phylogenetic structure in the character covariation. Parsimony and Bayesian methods of phylogenetic analysis each suffered from different technical problems, and their estimates contained obvious errors in resolution of relationships. Additional data could help alleviate these problems. The results of preliminary analyses of a less taxonomically complete data set suggested that taxonomic sample plays a critical role in the inferred topologies, i.e., as taxa were added to the matrix (particularly to clades subtended by long branches), resolution of expected relationships and familial monophyly increased. The mitochondrial data on which this study is based are undoubtedly suffering from the effects of multiple substitution and while subfamilial resolution was satisfying in places, the addition of genes with a slower rate of evolution would likely improve the accuracy of the phylogenetic estimate. However, the analysis of a less-taxonomically complete data set (Hardman, 2002) composed of nuclear recombination activating gene 2 (RAG2) identified other problems in the form of an absence of signal for mid-depth nodes. Hardman (2002) suspected an accelerated rate of diversification during this phase of siluriform evolution, and suggested the trunk of the catfish tree to be a hard polytomy. Additional data sets are now being compiled to test this hypothesis.

Acknowledgments

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Appendix A. GenBank and depository information for species included in this study

AKYSIDAE: *Acrochordonichthys rugosus* INHS93578 DQ119410. *Akysis* sp. INHS93604 DQ119404. **AMBLYCIPITIDAE**: *Amblyceps* sp. INHS93530 DQ119364. *Liobagrus reini* DQ119478. *Liobagrus anguillicauda* AF416888. **ARIIDAE**: *Arius felis* AUM5233-02 (#5342) DQ119355. *Arius truncatus* INHS93580 DQ119391. *Bagre marinus* AUM5234-003 (#5342) DQ119472. *Ketengus typus* INHS93581 DQ119485. **ASTROBLEPIDAE:** *Astroblepus* sp. INHS55444 DQ119407. **AUCHENIPTERIDAE**: *Ageneiosus atronasus* INHS54689 DQ119403. *Ageneiosus ucayalensis* INHS52920 DQ119396. *Centromochlus heckelii* INHS52712 DQ119426. *Epapterus dispilurus* INHS54692 DQ119401. *Parauchenipterus galeatus* INHS49034 DQ119398. **ASPREDINIDAE**: *Bunocephalus verrucosus* INHS49301 DQ119352. *Pterobunocephalus depressus* INHS54703 DQ119353. **BAGRIDAE**: *Aorichthys aor* INHS93870 DQ119373. *Bagrichthys macropterus* DQ119455. *Batasio batasio* DQ119436. *Batasio chandramara* DQ119413. *Batasio tengana* INHS93643 DQ119422. *Hemibagrus guttatus* AF475154. *Hemibagrus macropterus* AF416890. *Hemibagrus wyckioides* DQ119372. *Hyalobagrus flavus* DQ119475. *Leiocassis crassilabris* AF416882. *Leiocassis longirostris* AF416889. *Leiocassis micropogon* DQ119476. *Mystus*

bocourti INHS93586 DQ119357. *Mystus cavasius* DQ119437. *Mystus leucophasis* DQ119423. *Mystus micracanthus* DQ119365. *Mystus pulcher* DQ119441. *Mystus vittatus GenBank@proof. Pelteobagrus fulvidraco* AY744502. *Pelteobagrus nitidus* AF416893. *Pelteobagrus vachelli* AF416896. *Pseudobagrus brevicorpus* AB015990. *Pseudobagrus kyphus* AB085622. *Pseudobagrus truncatus* AF416895. *Pseudomystus fuscus* DQ119452. *Pseudomystus siamensis* INHS93920 DQ119366. *Pseudomystus stenomus* INHS 93600 DQ119440. *Nanobagrus stellatus* DQ119446. *Rita rita* DQ119457. **CALLICHTHYIDAE**: *Brochis multiradiatus* INHS53234 DQ119381. *Callichthys callichthys* INHS49302 DQ119448. *Dianema longibarbis* INHS93876 DQ119359. **CETOPSIDAE**: *Helogenes marmoratus* INHS49125 DQ119419. *Hemicetopsis candiru* INHS52924 DQ119402. *Pseudocetopsis* sp. INHS56143 DQ119412. **CHACIDAE**: *Chaca chaca* INHS93595 DQ119374. *Chaca hamiltoni* INHS93864 DQ119461. **CLARIIDAE**: *Channalabes apus* AF126820. *Gymnallabes typus* INHS93588 DQ119368. *Clarias batrachus* INHS93494 DQ119368. *Clarias fuscus* AF416885. *Clarias ngamensis* RUSI63391 DQ119399. *Clarias nieuhoefi* INHS93510 DQ119377. **CLAROTEIDAE**: *Chrysichthys* sp. INHS93871 AY327266. *Parauchenoglanis guttatus* INHS93869 DQ119360. *Clarotes laticeps* AF126821. **CRANOGLANIDIDAE**: *Cranoglanis bouderius* AF416879. **DIPLOMYSTIDAE**: *Diplomystes mesembrinus* DQ119350. **DORADIDAE**: *Amblydoras affinis* INHS49305 DQ119411. *Physopyxis lyra* INHS53725 DQ119408. **ERETHISTIDAE**: *Erethistes* sp. INHS94106 DQ119358. **HEPTAPTERIDAE**: *Brachyrhamdia* sp. INHS56216 DQ119489. *Cetopsorhamdia* sp. INHS56139 DQ119442. *Goeldiella eques* INHS49299 DQ119386. *Heptapterus* sp. INHS89831 DQ119451. *Pimelodella chagresi* DQ119466. Pimelodella sp. DQ119432. Rhamdia quelen INHS49300 DQ119395. **HETEROPNEUSTIDAE**: *Heteropneustes fossilis* INHS93590 DQ119383. **HORABAGRIDAE**: *Horabagrus brachysoma* INHS93585 DQ119454. **ICTALURIDAE**: *Ameiurus natalis* INHS47265 AY184265. *Ictalurus punctatus* INHS47559 AY184254. *Noturus albater* INHS38562 AY327270. *Pylodictis olivaris* INHS46529 DQ119439. *Prietella lundbergi* AY458865. **LORICARIIDAE**: *Acanthicus adonis* DQ119450. *Ancistrus* sp. DQ119447. *Aphanotorulus ammophilus* DQ119415. *Chaetostoma anomala* DQ119479. *Cochliodon plecostomoides* INHS54578 DQ119418. *Crossoloricaria venezuelae* DQ119458. *Dasyloricaria filamentosa* DQ119400. *Dekeyseria scaphyrhyncha* INHS55362 DQ119470. *Farlowella platyrhynchus* DQ119488. *Hemiancistrus maracaiboensis* DQ119380. *Hypostomus villarsi* DQ119474. *Lasiancistrus* sp. INHS54582 DQ119397. *Leporacanthicus triactis* DQ119367. *Lithogenes villosus* INHS49570 DQ119405.*Liposarcus multiradiatus* INHS54585 DQ119420. *Otocinclus vestitus* DQ119487. *Oxyropsis carinatum* DQ119354. *Peckoltia* sp. DQ119484. *Panaque maccus* DQ119463. *Panaque nigrolineatus* DQ119465. *Panaque* sp. DQ119421. *Pseudohemiodon* sp. DQ119469. *Rineloricaria fallax* INHS49306 DQ119389. *Rineloricaria uracantha* DQ119462. *Spatuloricaria puganensis* DQ119416. *Spatuloricaria* sp. DQ119444. *Sturisoma festivum* DQ119467. **MALAPTERURIDAE**: *Malapterurus electricus* INHS 93868 DQ119362. **MOCHOKIDAE**: *Synodontis nigriventris* DQ119417. *Synodontis ngamensis* DQ119427. *Synodontis macrostigma* DQ119477. **PANGASIIDAE**: *Helicophagus waandersii* INHS93678 DQ119468. *Pangasianodon hypophthalmus* INHS96664 DQ119393. *Pangasius conchophilus* INHS93705 DQ119453. *Pangasius macronema* INHS93471 DQ119443. **PIMELODIDAE**: *Brachyplatystoma juruense* INHS54694 DQ119363. *Cheiroceros eques* INHS52717 DQ119473. *Hypophthalmus edentatus* INHS52182 DQ119438. *Perrunichthys perruno* INHS54805 DQ119394. *Phractocephalus hemioliopterus* INHS54697 DQ119390. *Pimelodus ornatus* INHS49102 DQ119378. *Pinirampus pirinampu* INHS52921 DQ119361. *Platysilurus malarmo* AUM22654 DQ119490. *Sorubimichthys planiceps* INHS54701 DQ119385. *Zungaro zungaro* INHS43365 DQ119459. **PLOTOSIDAE**: *Plotosus canius* INHS93591 DQ119445. *Plotosus lineatus* DQ119351. *Porochilus rendahli* INHS93922 DQ119425. **PSEUDOPIMELODIDAE**: *Microglanis iheringi* INHS54568 DQ119464. *Pseudopimelodus raninus* INHS52482 DQ119384. *Pseudopimelodus villosus* INHS55359 DQ119471. **SCHILBIDAE**: *Eutropius depressirostris* Y15697. *Eutropiellus debauwi* DQ119424. *Platytropius longianalis* AF416894. *Proeutropius brachypopterus* DQ119388. *Schilbe mystus* INHS93872 DQ119449. **SILURIDAE**: *Belodontichthys truncatus* INHS93576 DQ119456. *Ceratoglanis scleronema* INHS93462 DQ119460. *Hemisilurus mekongensis* INHS93677 DQ119392. *Kryptopterus bicirrhis* INHS93776 DQ119480. *Kryptopterus cryptopterus* INHS 93923 DQ119434. *Kryptopterus limpok* DQ119431. *Kryptopterus macrocephalus* INHS93777 DQ119483. *Kryptopterus minor* DQ119481. *Kryptopterus schilbeides* DQ119482. *Micronema apogon* INHS93706 DQ119409. *Micronema bleekeri* INHS93727 DQ119369. *Ompok bimaculatus* INHS93924 DQ119433. *Ompok miostoma* DQ119435. *Pterocryptis furnessi* DQ119428. *Pterocryptis conchinchinensis* INHS93511 DQ119371. *Pterocryptis* aff. *conchinchinensis* DQ119429. *Silurichthys schneideri* INHS93512 DQ119430. *Silurus asotus* DQ119376. *Silurus meridionalis* AF416892. *Wallago leeri* INHS93598 DQ119387. Wallagonia attu AF508083. **SISORIDAE**: *Bagarius yarrelli* INHS93673 DQ119406. *Euchiloglanis davidi* AY416883. *Euchiloglanis kishinouyei* AY207478. *Gagata cenia* AF499599. *Glyptosternum maculatum* AF416891. *Glyptothorax cavia* AF477830. *Glyptothorax fukiensis* AF416884. *Glyptothorax* sp. INHS93660 DQ119379. *Nangra virescens* DQ119375. **TRICHOMYCTERIDAE**: *Hatcheria macraei* DQ119414. *Henonemus punctatus* INHS53842 DQ119382.

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