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Discovery of African roots for the Mesoamerican Chiapas catfish, *Lacantunia enigmatica*, requires an ancient intercontinental passage

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ABSTRACT.— Mesoamerica is famous for its complex biota assembled from diverse sources. The recent discovery of a highly distinct freshwater catfish, *Lacantunia enigmatica* (Lacantuniidae), in Chiapas, México, added an unresolved taxon to this biogeographic puzzle. Morphology has not resolved the relationships of *Lacantunia* among the >3000 species of Siluriformes. We added *Lacantunia* to an expanding phylogenetic study of family-level taxa of living catfishes using >3.6 kilobases of nuclear DNA. We find that *Lacantunia* is derived from within a multi–family clade of African freshwater catfishes. Without living or fossil intermediates marking a wider lacantuniid distribution, this is an extraordinary case of biogeographic disjunction. Continental clades distributed in the New and Old World tropics are often explained by vicariance of Gondwanan ancestors of deep Mesozoic age. However, our fossil-calibrated, relaxed-clock molecular analyses estimate lacantuniid divergence between 75 to 94 mya, after separation of Africa and South America. During Late Cretaceous and early Tertiary, warm conditions and North Atlantic and Beringian land bridges provided migration routes for numerous warm-adapted taxa between the Old World and North America. In mid-Eocene, freshening of warm surface waters of the Arctic and adjacent oceans may have facilitated the intercontinental dispersion of non-marine organisms. These northern pathways are novel predictive hypotheses for explaining disjunct distributions of tropical freshwater fishes such as the relictually endemic *Lacantunia* and its African sister clade.

INTRODUCTION

The unexpected discovery of a widely disjunct intercontinental distribution for a group of freshwater organisms is a significant event since, upon investigation, it stands to challenge or inform existing views on the assembly of continental faunas.

Catfishes (Order Siluriformes), with a global distribution, over 3000 recognized species (Ferraris, 2007) and a fossil record extending to the Late Cretaceous, have radiated into a remarkable array of forms and ecologies to become one of the most successful groups of teleost fishes. Because all but two of the 38 extant and two extinct families of catfishes are confined to freshwaters, their modern distribution has been determined by a complex interrelationship between their phylogenesis and continental earth history. Thus, in addition to their interesting ecology and evolution, siluriforms are key subjects in biogeography on all scales from regional to global (Lundberg et al., 2000).

Knowledge of the interrelationships of catfish families is expanding and there is notable consensus among the well-supported results from morphological (Mo, 1991; de Pinna, 1998; Rodiles-Hernández et al., 2005a,b; Diogo, 2004) and recent molecular (Hardman, 2005; Sullivan et al., 2006) studies. Although relationships among catfish families remain incompletely resolved, support in Sullivan et al. (2006) for several large multifamily clades, each endemic to single continents, suggests a long history of predominantly intracontinental diversification within catfishes. Against this background, the unanticipated finding of an intercontinental relationship involving a previously unknown family-level lineage represented by a single, narrowly distributed species becomes particularly noteworthy.

Following its recent discovery in the Reserva de la Biosfera Montes Azules, in southern México's Río Usumacinta basin, Rodiles–Hernández et al. (2005a) de-

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scribed the "Chiapas catfish" as a new species, genus and family. *Lacantunia enigmatica* possesses extraordinary diagnostic features of its cranial musculo–skeleton and gas bladder (Rodiles–Hernández et al., 2005a; Lundberg and Luckenbill, 2006). A first phylogenetic evaluation of *Lacantunia* using morphological characters (Rodiles–Hernández et al., 2005b) placed the Chiapas catfish above the phyletically deep diplomystid and fossil hypsidorid catfishes and among 22 unresolved groups in a large clade containing the other 30+ siluriform families. Among the few characters found that individually suggest its relationships, *Lacantunia* shares with African Claroteidae, Auchenoglanididae (sensu de Pinna, 1998) and some South American Cetopsidae a highly modified autopalatine bone and hypertrophied palatine cartilage. However, with available morphological data these families were not recovered together as a clade.

Catfishes in the families Ictaluridae, Heptapteridae and Ariidae are sympatric with *Lacantunia* in the Río Usumacinta. These families, like most freshwater taxa in the mixed biota of Mesoamerica (Rosen, 1975; Savage, 1982; Bussing, 1985; Miller et al., 2005), have broader biogeographic relationships to the faunas of North America (ictalurids), or South/Central America (heptapterids), or coastal marine waters (ariids). The Chiapas catfish shares no exclusive morphological synapomorphies with any of these families. Furthermore, each of these taxa has well-supported relationships with other catfish families (see Sullivan et al., 2006): Ictaluridae with Asian Cranoglanididae, Heptapteridae with South American Pimelodidae, Pseudopimelodidae and *Conorhynchos*, and Ariidae with the Anchariidae of Madagascar. Thus, as a divergent, narrowly endemic and unresolved lineage, the Chiapas catfish has had an uncertain history and implication for the assembly of the Mesoamerican biota. To address these questions we added *Lacantunia* to an ongoing investigation of catfish family–level phylogeny and biogeography using nuclear *rag1* and *rag2* gene sequences (Sullivan et al., 2006). Finding that *Lacantunia* has a novel African relationship (Fig. 1), we use relaxed clock molecular dating methods calibrated with fossils to test alternative paleogeographic routes for the intercontinental passage of this catfish lineage into the New World.

MATERIALS AND METHODS

Institutional abbreviations follow ASIH (2006) plus ECO–SC for El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México.

Data acquisition and phylogenetics.— From two specimens of *Lacantunia enigmatica*, we obtained sequences for two fragments of the *rag1* gene (1182 and 1494 bases, respectively) and one fragment of the *rag2* gene (945 bases). These differ in a single third–position site in the 5' *rag1* fragment. The sequences of specimen ECOSC 4339 (GENBANK EF078914–EF078916) were added to the existing dataset of 3660 aligned nucleotides for 110 siluriform species representing 36 families (for specimen and Genbank data see Appendix A of Sullivan et al., 2006). Also, more complete sequences for the African schilbid *Parailia congica* (GENBANK EF078917–EF078919) were added to the dataset. Sequence alignment and methods of phylogenetic analysis with maximum parsimony (MP), maximum likelihood (ML) and Bayesian methods are identical to those described in Sullivan et al. (2006). We subsequently tested the strength of signal in the data to reject hypotheses of relationship for *Lacantunia enigmatica* that differ from the one recovered. To do this we used the likelihood-based SH test (Shimodaira and Hasegawa, 1999) and Bayes factors (Kass and Raftery, 1995) to compare optimal tree(s) with a given topological constraint against the optimal unconstrained tree(s). Methods for performing these tests are given in Sullivan et al. (2006).

Molecular dating.— Likelihood ratio–relative rates tests carried out in the software r8s version 1.70 (Sanderson, 2004) confirm that substitution rates are significantly different between many sister lineages within the *rag1*/*rag2* catfish tree. Therefore, to estimate the age of the lacantuniid–claroteid ancestor, we used two approaches that do not assume a molecular clock and that can incorporate multiple fossil calibrations: the Bayesian relaxed clock (BRC) method implemented with the software ESTBRANCHES and MULTIDIVTIME (Thorne and Kishino, 2002) and Penalized Likelihood (PL, Sanderson, 2002) implemented in r8s (Sanderson, 2004). For both BRC and PL, we used the tree topology obtained from our partitioned–by–codon (3P) analysis in MrBayes 3.1.

Our BRC analyses followed the steps outlined in Rutschmann (2004) and the guidelines provided in the "readme" files included in the software distribution by J. Thorne. BRC analysis includes three stages: first, estimation of the F84 + G model parameters (Kishino and Hasegawa, 1989) in BASEML, part of the PAML version 3.14 package (Yang, 2004). Second, maximum likelihood estimation of branch lengths and a variance/covariance matrix using ESTBRANCHES. Third, a Bayesian MCMC analysis in MULTIDIVTIME to approximate the posterior distributions of substitution rates, divergence times, their standard deviations and 95% credibility intervals. We set MULTIDIVTIME priors for all analyses as follows: 1.44 (=144 mya) for the time from the root of the input tree to the tips and its standard deviation (parameters rttm and rttmsd), 2.05 (=205 mya, or the Triassic/Jurassic boundary) for the parameter "bigtime." As recommended by Thorne,

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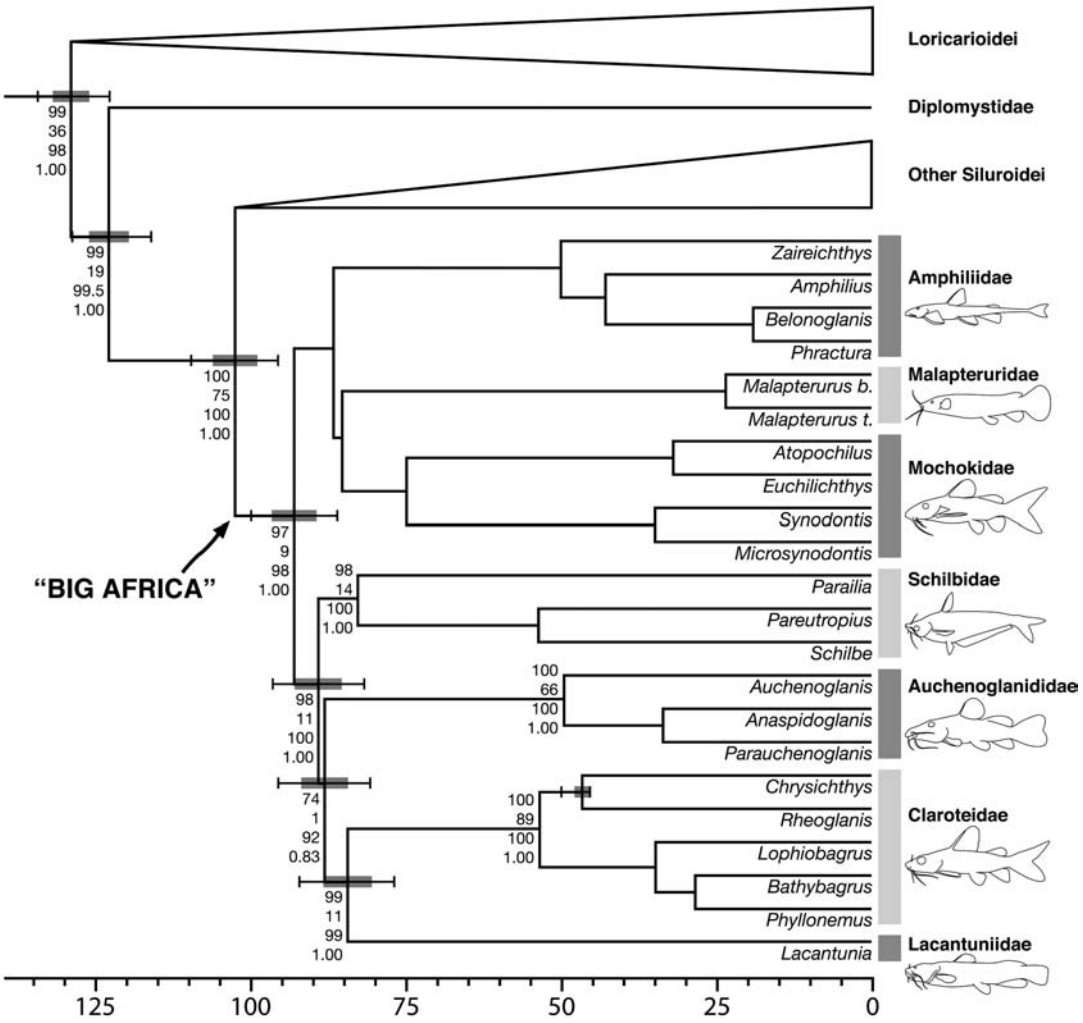


Fig. 1. The phylogenetic relationships of *Lacantunia* drawn as a MULTIDIVTIME chronogram tree emphasizing its closest relationships in the "Big Africa" clade and within a summary higher–level topology of catfishes. Horizontal scale = millions of years before present. Gray bars at selected nodes subtending and proximate to *Lacantunia* span time between estimates based on median and oldest fossil calibration ages, and thin lines are 95% credibility intervals. Four support indices are shown for selected nodes, respectively MP bootstrap proportion, decay (Bremer) index, ML bootstrap proportion and Bayesian posterior probability.

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we set the prior for the molecular evolutionary rate (rtrate) to a value equal to the median root-to-tip length of all branches from the ESTBRANCHES analysis divided by the value of rttm (rtrate=0.122). We set the prior for the standard deviation of this rate (rtratesd) equal to the same value. Finally, we set the priors for the mean and standard deviation of the autocorrelation parameter (brownmean and brownsd) both equal to 1.0. All other parameters were left at their default values.

We performed analyses in which the combined *rag1* and *rag2* dataset was treated as a single partition (1P) and others in which the data were partitioned into three datasets (3P) corresponding to codon positions in order to determine if potentially improved fit of the model to the data would significantly affect results. For the 3P analyses, model parameters, branch lengths and a variance/covariance matrix were calculated separately for each partition in BASEML and ESTBRANCHES prior to the MCMC procedure in MULTIDIVTIME. MCMC settings for all runs were: 100k cycles of burn-in, followed by one million cycles in which the Markov chain was sampled at 100 cycle intervals. For each analysis, we carried out two independent runs from different random starting seeds to confirm the convergence of the Markov chain onto the distribution of posterior probabilities. In order to gauge the relative contribution of the data versus the priors and constraints to the age estimate, we performed one MCMC run in which priors and constraints were set up identically, but with no data included. For this run, we lengthened the number of burn-in cycles by 10x.

For the PL analyses in r8s, we used the identical tree topology as for BRC, but used the branch lengths determined by the 3P analysis of our data in MrBayes 3.1. We used the TN algorithm (recommended for PL in r8s manual) and chose the log penalty over the additive penalty due to the former's better performance in estimating ages of deep nodes from more terminal calibration points (Sanderson pers. comm.). We found an optimal value of the smoothing parameter (=100) by means of the cross-validation procedure. We checked the uniqueness of each analysis result through use of the "checkgradient" command and by running each analysis three times from randomly altered starting conditions.

Calibration Points and constraints.— The calibration points used in the BRC and PL analyses are fossil–determined minimum ages applied as constraints on seven tree nodes (Fig. 2). Where the position of a fossil is basal or uncertain within its genus or higher taxon, we apply the age constraint to the node below that taxon.

1. The African fossil *Chrysichthys mahengeensis* is an Eocene claroteid dated at 45–46 mya (Murray and Budney, 2003; Harrison et al., 2001). The minimum age constraint is applied to the common ancestor of *Chrysichthys* and *Rheoglanis*.

2. A minimum age of 68–73 mya is assigned to the divergence of Ariidae and Anchariidae based on bone and otolith fossils assignable to Ariidae sp. of Late Campanian–Early Maastrichtian age from South and North America (Gayet and Meunier, 2003).

3. A minimum age of 65–71 mya is assigned to the divergence of Doradoidea and Aspredinidae based on an unnamed doradoid fossil of Maastrichtian age from Bolivia (Gayet and Meunier, 2003).

4. The oldest fossil bullhead catfish *Ameiurus pectinatus* (Lundberg, 1975) is from the Florissant Formation, Colorado, dated as Late Eocene (Evanoff and de Toledo, 1999) or 34–38 mya. This fossil species is basal within its genus and we apply the minimum age constraint to the ancestral node for *Ameiurus*, *Ictalurus* and *Noturus*.

5. The oldest ictalurid stem fossil *Astephus* sp. (Lundberg, 1975) occurs in the Polecat Bench Formation, Wyoming, dated as Early Paleocene (Hartman, 1986) or 63–65 mya. This minimum age is applied to the divergence of Ictaluridae and Cranoglanididae.

6. Two fossil species of the bagrid genus *Mystus* are reported from the Eocene of China (Chang and Zhou, 1993). Although *Mystus* is not in our taxon sample, the analyses of Mo (1991) and Ng (2003) recover the genus below *Hemibagrus+Bagrus*. We thus apply an Eocene age constraint of 34–56 mya to the common ancestral node of *Hemibagrus+Bagrus* and *Heterobagrus*.

7. The oldest callichthyid fossil *Corydoras revelatus* (Reis, 1998) is from Argentina in the Mais Gordo Formation dated as Late Paleocene (Marshall et al., 1997) or 58.2–58.5 mya. The unresolved systematic position of *C. revelatus* within its genus thus sets the minimum age for ancestral node of Corydoradinae plus Callichthyinae.

For both BRC and PL analyses we explored the effect of placing/removing a maximum-age constraint of 144 mya (Jurassic/Cretaceous boundary) for the stem of the siluriform lineage (= siluriform+gymnotiform node). Our choice of 144 mya is admittedly arbitrary, as are all such constraints, but conservatively informed by the fossil record of actinopterygians (see Discussion). To avoid circularity in testing biogeographic hypotheses we did not use paleogeographic–based ages as calibration points for dating catfish clades.

RESULTS

Phylogenetics.— The major catfish clades recovered in MP, ML and Bayesian phylogenetic analyses of the *rag1* and *rag2* data with *Lacantunia* added are essentially identical to those of our previous study without this species (Fig.

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2, this paper, cf. Sullivan et al., 2006, figs. 1-2, pp. 640-641). The central new finding here is that *Lacantunia* is the sistergroup of Claroteidae within the clade informally named "Big Africa" (Fig. 1): ((((*Lacantunia*, Claroteidae) Auchenoglanididae) African Schilbidae) (Mochokidae, (Malapteruridae, Amphiliidae))). Except for *Lacantunia*, "Big Africa" contains only endemic family–level groups of African freshwater catfishes accounting for about 90% of the catfish species there. Otherwise the only difference between the results here vs. Sullivan et al. (2006) is a swap of the positions of Auchenoglanididae and African Schilbidae relative to Claroteidae. The tree topology throughout "Big Africa" with *Lacantunia* added receives high bootstrap support in MP and ML, and high Bayesian posterior probabilities (Fig. 1). Further, the topology constraining monophyly of "Big Africa" without *Lacantunia* is rejected by both the SH (Shimodaira–Hasegawa) test and Bayes factors in favor of ((*Lacantunia*, Claroteidae) Auchenoglanididae) (Table 1). We also used MP tree length difference, SH tests and Bayes factors to compare the *Lacantunia*+Claroteidae node to the three alternative constraint topologies wherein the Chiapas catfish is placed, in turn, as the sistergroup to one of the families also present in the Río Usumacinta, i.e. *Lacantunia*+Ictaluridae, *Lacantunia*+Heptapteridae, *Lacantunia*+Ariidae. The trees produced by these constraints are rejected by all tests in favor of *Lacantunia*+Claroteidae (Table 1).

Two important nodes in "Big Africa" also receive support by unique and unreversed amino acid substitutions. First, the *Lacantunia*+Claroteidae node is marked by the synapomorphic replacement of plesiomorphic methionine by arginine at amino acid position 8 of the 5' *rag* fragment. Second, and also in 5' *rag* fragment, the entire "Big Africa" clade including *Lacantunia* has the synapomorphic substitution of glutamine for plesiomorphic glutamic acid at position 128.

A review of diagnostic morphological characters reported for *Lacantunia* by Rodiles–Hernández et al. (2005a), and claroteids and auchenoglanines (Mo, 1991) confirms and extends the similarities of their autopalatine bones and cartilages (Fig. 3). In the phylogenetic framework recovered in this study, these morphological features are unambiguously interpreted as two nested synapomorphies in the subtree ((*Lacantunia*, Claroteidae) Auchenoglanididae). No other unambiguous morphological synapomorphies are known for *Lacantunia*+Claroteidae.

Dating.—The most direct evidence bearing on the minimum age of divergence between the lacantuniid lineage and Claroteidae is the oldest known fossil belonging to either one. This is a mid-Eocene claroteid, *Chrysichthys mahengeensis*, from Mahenge, Tanzania dated at 45–46 mya (Murray and Budney, 2003; Harrison et al., 2001).

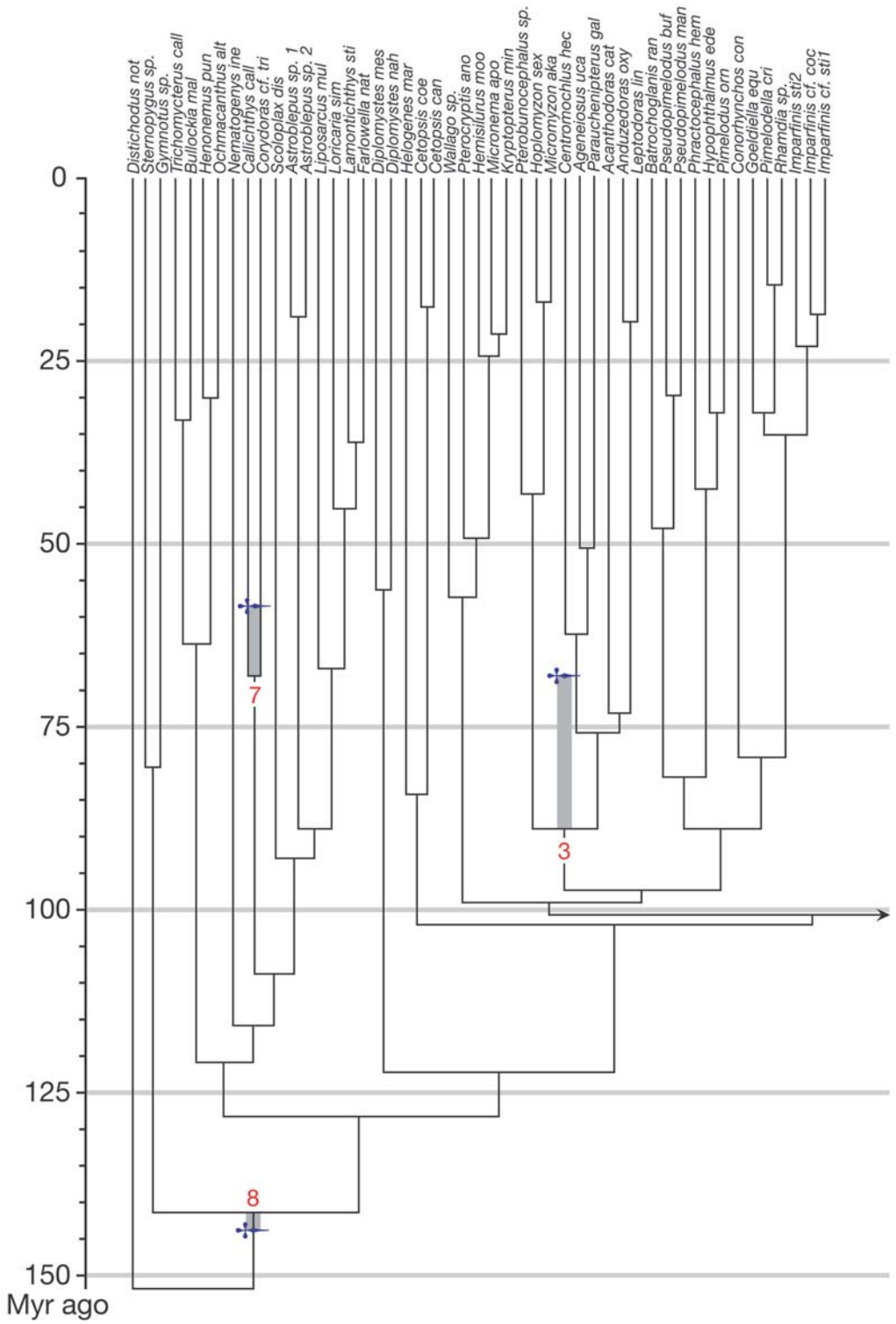
BRC analyses of the 1P *rag* data with a constraint of 144 mya (Jurassic/Cretaceous boundary) applied both as a prior and a maximum–age on the origin of Siluriformes estimates that Lacantuniidae and Claroteidae diverged between 83 and 86.5 mya. The variation depends on whether median or oldest fossil calibration ages (see Materials and Methods) are used. The 95% credibility interval for this divergence is 75–94 mya (Table 2, Figs. 1, 2). BRC analysis without a maximum–age constraint, produces older estimates: 102 mya (90–115 mya 95% credibility interval) for the divergence time of Lacantuniidae and Claroteidae, 191 mya (Early Jurassic) for the age of origin of the stem siluriform lineage, and 198 mya (earliest Jurassic) for the age of the characiphysan root node. BRC analyses of the 3P *rag* data gave results closely similar to 1P data (Table 2).

The PL analysis with r8s requires either a maximum–age or fixed–age constraint placed on a node somewhere in the tree. If any of the seven nodes associated with a fossil–based minimum age constraint is set to a fixed age constraint, the estimated age for origin of siluriforms becomes >300 mya, i.e. minimally Pennsylvanian. With a 144 mya maximum-age constraint placed on the origin of catfishes the estimates for the origin of Lacantuniidae in PL analyses range from 81.2 to 83.3 mya for median and oldest calibration ages, respectively. These estimates are slightly younger than the similarly constrained BRC point estimates but fall within the credibility range of the BRC results.

DISCUSSION

The phylogenetic placement of *Lacantunia* within "Big Africa" and with four sequential African outgroups is robust and carries two clear biogeographic implications: the lacantuniid lineage came out of Africa and had a much wider past distribution. The difficult question is how *Lacantunia* got to Chiapas and for this the age of its lineage is central. We infer from *Chrysichthys mahengeensis* that claroteids and lacantuniids diverged by mid-Eocene (45–46 mya). The BRC and PL analyses estimate that this split is much older in the Cretaceous, and of course earlier origins are implied for progressively more inclusive clades of siluroids, siluriforms, characiphysans, otophysans, ostariophysans and clupeocephalans. Without a maximum-age constraint BRC and PL analyses extend siluriform origins into early Jurassic and late Pennsylvanian respectively. The unconstrained estimates are starkly contradicted by the fossil record of actinopterygians across this vast span of time, an ample record that includes stem groups, divergent and extinct side branches, and late Triassic to late Jurassic fossils that are transitional to basal teleosts (Arratia, 1999, 2004). A few high-level crown clades of teleosts first appear in the latest Jurassic and earliest Cretaceous. Among these are the old-

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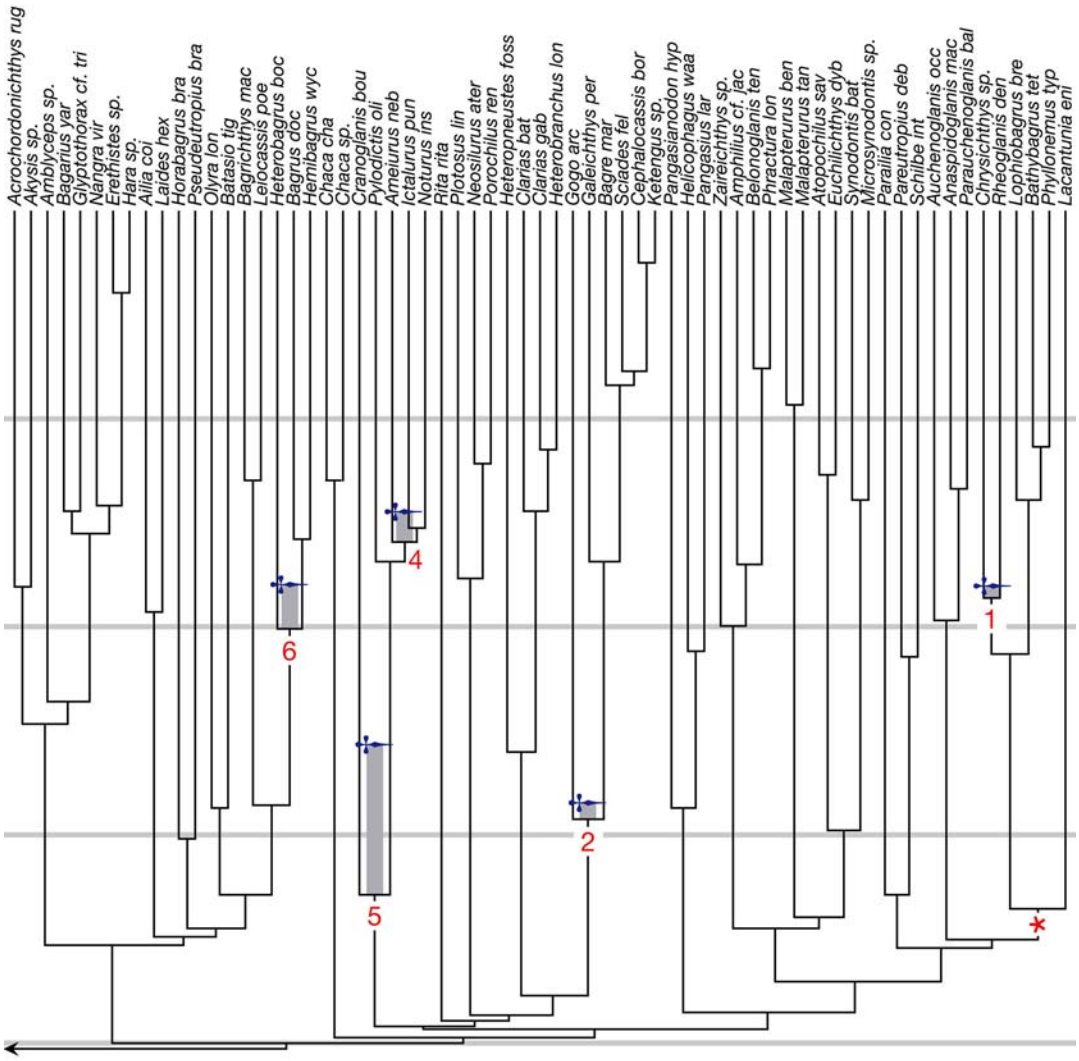


Fig. 2. The MULTIDIVTIME chronogram tree showing BRC mean fossil ages (Table 2) for catfishes. Numbers 1–7 label minimum–age constraint nodes based on fossils (see Materials and Methods); number 8 labels maximum–age constraint node for origin Siluriformes. Daggers mark position of fossil or maximum age constraint, gray bars span time interval between constraint age and MULTIDIVTIME estimated age, asterisk labels *Lacantunia*–Claroteidae divergence node. For full terminal taxon names, and specimen and Genbank data see Appendix A of Sullivan et al. (2006).

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est known ostariophysan in the Late Jurassic, and stem clupeiforms in the Early Cretaceous (Arratia, 1999, 2004). The oldest characiphysan is the Albian stem fossil *Santanichthys* (Filleul and Maisey, 2004). The oldest records of crown group siluriforms and characiforms are latest Cretaceous (Campanian and Maastrichtian), and the oldest crown cypriniforms are Paleogene (Wilson, 1977; Grande et al., 1982). In light of the minimum ages provided by fossils for higher clades, our application of a 144 mya maximum-age constraint on the origin of Siluriformes provides liberal scope for catfish diversification by doubling the time from the earliest fossil catfishes back to the Jurassic/Cretaceous boundary when fossils first record a few crown group teleosts. Coincidentally, Briggs (2005) posited a roughly similar age for siluriforms based on strict adherence to a biogeographic model requiring Pangaean–Gondwanan non–marine dispersion to achieve their present global distribution. With the 144-mya constraint in place, our BRC and PL estimates for the divergence time between *Lacantunia* and Claroteidae are Late Cretaceous between 75 to 94 mya (Figs. 1, 2, Table 2).

In line with the freshwater restriction of *Lacantunia* and all other catfishes in "Big Africa," we disfavor an *a priori* untestable scenario of salt-water dispersal for these fishes. Instead, using the estimated age of the lacantuniid lineage, we consider the locations and ages of possible freshwater routes linking Africa with the Americas (Fig. 4). No fossil or living intermediates mark the lacantuniid path. Most fossil catfishes from North and South America belong to living families endemic to either continent. However, there is also fossil evidence for a greater diversity of catfish clades in the Americas during the Late Cretaceous—Paleogene (Lundberg, 1975, 1992, 1993, 1998; Gayet, 1991; Gayet and Meunier, 1998, 2003; Grande and de Pinna, 1998). Despite their poorly resolved relationships, the South American Andinichthyidae, North American Hypsidoridae and *Rhineastes*, and on both continents a number of unnamed fossils suggest that the history of catfishes on these continents was more complex than we would suppose from the modern faunas alone. Because there was never a direct connection between Africa and Middle America, all routes via past inland waters would have crossed either North or South America. Generalized biotic tracks from North and South America into Mesoamerica are well documented (Rosen, 1975; Savage, 1982; Raven and Axelrod, 1974; Stehli and Webb, 1985).

The Pangean union between Africa and the Americas was enormously broad from Late Paleozoic into Early Jurassic. Opening of the Central Atlantic at ca. 180 mya would have fragmented a Jurassic biota spanning northwest Africa–eastern North America. The distributions and diversification of some dinosaurian groups has been variously linked (Upchurch et al., 2002), or not (Sereno, 2000), to fragmentation of Pangea. Few living vertebrate groups are suggested to have vicariantly diversified as a result of Pangean breakup, e.g. deep clades of crown group "archeobatrachian" frogs (Roelants and Bossuyt, 2005), scleroglossan and iguanian lizards (Estes, 1983), gar fishes of the genus *Atractosteus* (Wiley, 1976), and ostariophysan and otophysan teleosts including catfishes (Briggs, 2005; Kumazawa et al., 1999; Saitoh et al., 2003; Peng et al., 2006; Diogo, 2004). The postulated Pangean dates for ostariophysans and otophysans, some as old as Permian and Triassic respectively, and of catfishes as Jurassic, rest on fitting present phylogeographic distributions to continental drift/vicariance models (Briggs, 2005) and/or on a molecular clock chronology for Ostariophysi and Otophysi that was also calibrated with a continental drift model (Kumazawa et al., 1999). Like our age–unconstrained results with BRC and PL, these approaches ignore or dismiss the pertinent and tangible fossil record of actinopterygians. The temporal and phylogenetic evidence from paleontology, and our molecular dating suggest that the origin of Siluriformes and consequently the lacantuniid–claroteid subclade long postdated Pangean rifting of Africa and North America.

Africa and South America remained united as part of western Gondwana until late Early Cretaceous when, between about 105 –119 mya (Koutsoukos, 1992; Maisey, 2000; McLoughlin, 2004), a continuous South Atlantic seaway opened. Vicariant divergence resulting from this undoubtedly protracted drift event is the most common explanation for continental clades with disjunct distributions in Africa and South America (Stehli and Webb, 1985; Goldblatt, 1993). Had lacantuniids originated in this way on South America these catfishes would have found more than one opportunity for dispersal into Middle America (Fig. 4). The Pliocene (ca. 3 mya, Coates and Obando, 1996) emergence of the Isthmus of Panama allowed many taxa, including fishes, to migrate northward from South into Central America (Bussing, 1985; Bermingham and Martin, 1998). Before this, in Late Cretaceous or Early Tertiary, several South American ("Old Southern") groups of reptiles, amphibians and freshwater fishes moved into Middle America (Savage, 1982; Bussing, 1985; Miller et al., 2005). The older routes between South and Middle America are suggested by paleogeographic reconstructions of the Caribbean region (Pindell, 1994; Iturralde–Vinent and MacPhee, 1999). Island arcs developing and drifting eastward on the Caribbean plate may have functioned as land bridges or stepping-stones between the Americas in Late Cretaceous (ca. 70–80 mya). For example, Chakrabarty (2006) proposed derivation of the cichlid fishes of Middle America, Cuba and Hispaniola by dispersal along a Cretaceous Island Arc into these areas before the Eocene separation of the Carib-

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Table 1. Optimal tree scores and tests of alternate hypotheses of *Lacantunia* sister-group identity. The maximum parsimony (MP), maximum likelihood (ML) and Bayesian analyses of the *rag1*/*rag2* data were conducted in PAUP*, TreeFinder and MrBayes 3.1 respectively, to find optimal tree(s) compatible with each constraint. These trees were then compared to the optimal unconstrained trees. Asterisks indicate significant differences at the 5% level. SH tests with 50,000 RELL bootstrap replicates. ML analysis conducted with single GTR + I + G model, Bayesian analyses conducted with the *rag1*/*rag2* data partitioned by codon position and unlinked GTR + I + G models estimated for each partition.

	maximum parsimony			maximum likelihood			Bayesian		
constraint description	steps	O steps	#trees	lnL score	O lnL	P (SH)	ln marg. L[1]	$2(\ln B_{10})^2$	conclusion
BEST TREE (UNCONSTRAINED)	16465		8	-84551.416			-83340.12		
1: (Lacantunia, Heptapteridae)	16538	+73	10	-84762.590	-211.174	<0.0001*	-83520.21	360.18	reject
2: (Lacantunia, Ictaluridae)	16500	+35	6	-84660.934	-109.518	0.002*	-83436.16	192.08	reject
3: (Lacantunia, Ariidae)	16557	+92	66	-84814.245	-262.829	<0.0001*	-83602.83	525.42	reject
4: Lacantunia, ("Big Africa" taxa)	16490	+25	2	-84604.809	-53.393	0.124	-83385.24	90.24	reject

[1] natural log of marginal likelihood estimated from harmonic mean of log likelihoods from post-burn in trees.
[2] B_{10} = Bayes Factor. Values > 10 for $2(\ln B_{10})$ are strong evidence against constrained topology.

Table 2. Age estimates of the lacantuniid/claroteid common ancestor calculated by Baysian Relaxed Clock (BRC) method and Penalized Likelihood (PL) in r8s. BRC analyses conducted with both mean and oldest fossil age estimates and with data analyzed in a single partition (1P) or in three partitions (3P) by codon position. One BRC run was performed with no branch length data, only tree topology and priors. In a repeat analysis all estimated node ages were within 250 Ka of the first run.

analysis	time (mya)	s.d.	95% credibility interval	
			lower	upper
BRC-1P mean fossil ages	84.51	3.91	77.03	92.27
BRC-3P mean fossil ages	83.07	4.08	75.09	91.03
BRC-1P oldest fossil ages	86.50	3.83	79.07	94.04
BRC-3P oldest fossil ages	85.64	4.19	77.43	94.05
BRC-median fossil ages, no data	70.37	11.20	51.69	94.51
PL-youngest fossil ages	79.03			
PL-mean fossil ages	81.20			
PL-oldest fossil ages	83.28			

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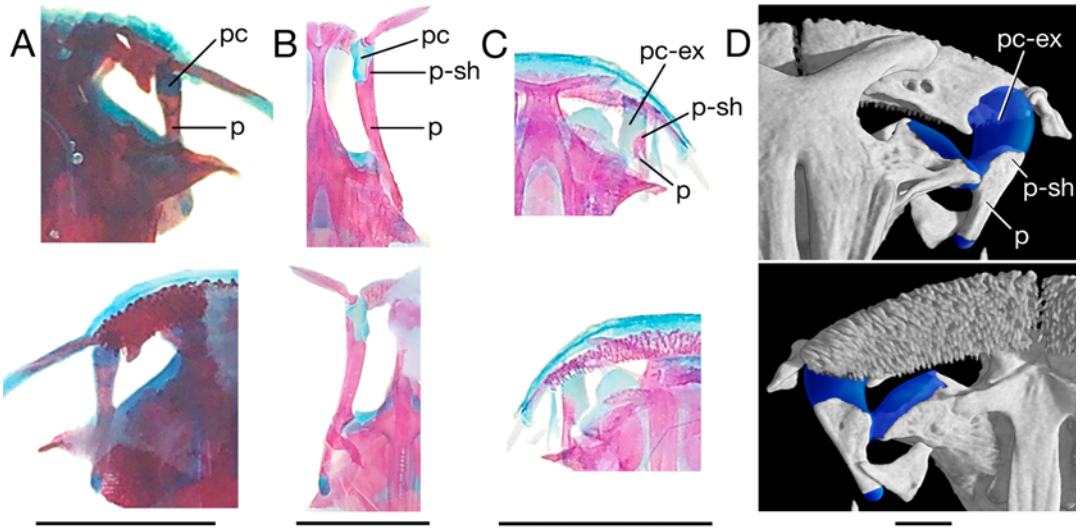


Fig. 3. Autopalatine bones and associated skeletal elements in representative siluroid catfishes; right side elements in dorsal (upper row) and ventral views (lower row). A, *Ameiurus serracanthus*, Ictaluridae, illustrating plesiomorphic character states of anteriorly truncated autopalatine bone and small anterior palatine cartilage, Academy of Natural Sciences, Philadelphia specimen ANSP 185358. B, *Parauchenoglanis* sp., Auchenoglanididae, illustrating synapomorphic bony autopalatine sheath together with plesiomorphic small palatine cartilage, Cornell University Museum of Vertebrates specimen CU 80568. C, *Chrysichthys* sp., Claroteidae, illustrating synapomorphic bony autopalatine sheath in combination with synapomorphic expanded anterior cartilage, CU 91685. D, *Lacantunia enigmatica*, Lacantuniidae, character states as in Claroteidae, based on HRXRCT image of Texas Natural History Collections specimen TNHC 29072 and dissection of ANSP 178696. Abbreviations: P–autopalatine; P–SH–autopalatine bony sheath; PC–small anterior palatine cartilage; PC–EX–expanded palatine cartilage. Scale bars = 5 mm.

bean Plate, including the Greater Antilles, from the North American Plate and Yucatan. "GAARlandia", a Late Eocene–Oligocene (ca. 33–35 mya) land bridge from South America to the Greater Antilles, was proposed to account for fossil and modern Antlillean mammals (Iturralde–Vinent and MacPhee, 1999). Because "GAARlandia" postdated separation of Cuba and Hispaniola from Yucatan it would have been a "cul–de–sac" for South American emigrants and too late to serve as a route for freshwater taxa to enter Mesoamerica.

As attractive as African–South American drift vicariance is for explaining tropical trans–Atlantic distributions, many clades showing the distributional pattern are too young and are otherwise accounted for (Lundberg, 1993; Lavin and Luckow, 1993; Davis et al., 2003, 2004; Poux et al., 2006). Here also our molecular dating estimates that the lacantuniid lineage is too young to be a product of Gondwanan vicariance dating from or before the final opening of the South Atlantic.

If, as the age estimates suggest, the lacantuniid lineage originated no more than 94 mya in Late Cretaceous, and in the Old World, the Holarctic routes from Asia and Europe to North America offer alternative "boreotropical" hypotheses. The Beringian land bridge (Fig. 4) was a corridor for biotic exchange between eastern Asia and western North America at various times during the long period from late Early Cretaceous (ca. 100 mya) to Pliocene when the Bering Strait opened about 3.5 mya, and again during the Illinoian and Wisconsinan glacial periods. Despite its northern latitude, Beringia's climate was considerably warmer in the Cretaceous and until the Late Miocene (Bowen et al., 2002; Min, 2005; Tiffney and Manchester, 2001), then cooling to arctic conditions in the Pleistocene. A great variety of taxa are known or suspected to have crossed Beringia in one direction or the other: plants (Tiffney and Manchester, 2001, Wen, 1999), dinosaurs (Gangloff et al.1995), plethodontid salamanders (Min et al., 2005), and mammals (Beard, 1998; Wallace and Wang, 2004). Freshwater fishes moved at different times between Asia and North America across the Bering bridge. Among the most recent are about 30 species narrowly distributed on both sides of Bering Strait (Lindsey and McPhail, 1986) plus more widely–ranging Holarctic species. Earlier (Cretaceous to Paleogene) freshwater fish migrants between Asia and North America in-

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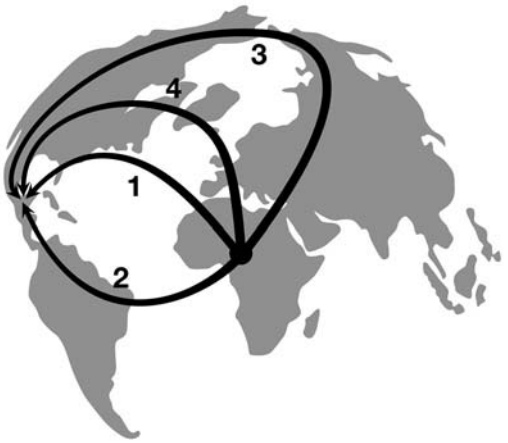


Fig. 4. Schematic alternative hypotheses for freshwater dispersion from Africa to Mesoamerica. 1) Pangean: Africa to North America before opening of the Central Atlantic and then to Mesoamerica, 2) Gondwana: Africa to South America before opening of the South Atlantic and then to Mesoamerica, 3) Bering land bridge: Africa to Asia to North America during Late Cretaceous to Late Miocene warm climate and then to Mesoamerica, 4) North Atlantic land bridge: Africa to Europe to North America during Late Cretaceous to Late Paleogene warm climate and then to Mesoamerica. Freshened surface waters of the Arctic and adjacent northern oceans during the middle Eocene raises a possibility of direct open–water dispersion from Europe or Asia to North America.

clude polyodontid paddlefishes (Grande and Bemis, 1991), hiodontiforms (Wilson and Williams, 1992), catostomid suckers (Smith, 1992), more than one group of phoxinin cyprinids (Coburn and Cavender, 1992) and ictaluroid catfishes (Hardman, 2005; Sullivan et al., 2006).

High latitude eastern North America was joined to western Europe by land bridges during opening of the North Atlantic (Fig. 4) from Late Cretaceous into Eocene (McKenna, 1983; Tiffney, 1985; Lavin and Luckow, 1993; Sanmartín et al., 2001). The Thulean land bridge between southern Europe, the British Isles, Greenland and North America had a warm temperate to subtropical climate into the Eocene (Wolfe, 1992; Moran et al., 2006; Sluijs et al., 2006). The De Geer land bridge between Scandinavia, northern Greenland and North America persisted until ca. 39 mya. Lavin and Luckow (1993) and Sanmartín et al. (2001) report many cases of Tertiary trans–North Atlantic migrations, and other recently proposed examples include tropical Malpighiaceae (Davis et al., 2003) and hummingbirds (Mayr, 2004). Living and fossil freshwater fishes shared by North America and Europe that may have made North Atlantic land bridge dispersals are leusiscine cyprinids of the *Notemigonus–Scardinius* clade (Coburn and Cavender, 1992), mudminnows (López et al., 2004), *Romanichthys*–Etheostomini percids (Wiley, 1992), amiine bowfins (Grande and Bemis, 1998) and gars of the *Lepisosteus oculatus* group (Wiley, 1976). During mid-Eocene (ca. 50 mya) the warm surface waters of the Arctic Ocean and adjacent seas underwent significant freshening (Brinkhuis et al., 2006). Such an event, estimated to have lasted ~800,000 yr, could have facilitated coastal or open water movement of freshwater organisms among northern continents. Our results indicate that lacantuniids existed when the North Atlantic land bridges and dilute northern seas were available dispersal routes.

Of course the first step for the lineage ancestral to *Lacantunia* would have been off of Africa and onto Europe or Asia in time to profit from one of the freshwater routes to North America. Lacking direct evidence from fossils of a wider distribution for this clade we are left to speculate about how and when this took place. Beringia, the corridor in place for the longest period, does not require lacantuniids in Asia before the Neogene, whereas to exploit a North Atlantic land bridge and/or the freshened northern seas, lacantuniid-claroteids would have needed to debut in Europe by the mid Eocene. Northern Africa was remote from Asia during Late Cretaceous through the early Tertiary (Plaziat, 1981; Blakey, 2006). Freshwater transit from Africa to Asia except through Europe would have been impossible until Early Neogene. However, Africa was proximate to southern Europe, existing then as an archipelago, from Late Cretaceous until the Miocene (Plaziat, 1981; Blakey, 2006). Fossils reveal the presence of freshwater fish clades of African origin in Europe starting in the early Eocene and until Miocene or Pliocene. These include alestid characiforms (De la Peña Zarzuelo, 1996; Zanata and Vari, 2005), cichlids (Murray, 2001; Carnevale et al., 2003; Chakrabarty, 2004) and bagrid, clariid and possibly claroteid catfishes (Gayet and Meunier, 2003). The last are fossil fin spines of Miocene age from southern Europe reported as "cf. *Chrysichthys* sp." (Antunes, 1989). If correctly identified these mark dispersion of the lacantuniid sister clade out of Africa, but given their age these could not represent a species ancestral to *Lacantunia*.

CONCLUSIONS

Over great scales of landscape and time lineages spread and diversify, go extinct or contract into distant disjunct distributions. Seen in its phylogenetic context *Lacantunia* is a striking case of disjunction. Similar African-Mesoamerican distributions are known among plants and

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insects (Sanmartín et al., 2001). Historical explanations for this biogeographic pattern are fraught with the uncertainty attending missing evidence and its congruence with multiple hypotheses. The Gondwanan and even more ancient Pangean scenarios, despite their relative simplicity of geography and vicariance, assign doubtfully deep ages onto low–ranked taxa and force vastly older beginnings on their containing clades for which their is no paleontological signal. Alternatively, on timing, Beringia, the North Atlantic land bridges and freshened northern seas were periodically available from Late Cretaceous and Tertiary when our estimates suggest lacantuniids had diverged from their closest African relatives. On climate, the Bering and Thulean bridges and Arctic–North Atlantic seas were at times suitable passageways for warmwater fishes. On biogeographic plausibility, the Holarctic land bridges are well documented as migration routes for a diversity of continental taxa including freshwater fishes and, for fishes, diluted coastal or open seas could have speeded range expansion. With more character evidence the phylogenetic hypothesis relating *Lacantunia* to "Big Africa" catfishes can be further tested. With some luck future discoveries will locate fossil or living intermediates in the lacantuniid lineage, or clades with matching distributions plus intermediates that illuminate the intercontinental path or at least reduce the alternatives. A search could begin with reevaluations of the several incompletely known Cretaceous and Paleogene catfishes from North and South America. The discovery of the Chiapas catfish was unexpected in the first place, and finding its deep African roots is an additional surprise. No matter how and when *Lacantunia enigmatica* came to be narrowly situated in southern México, this species will remain aptly named.

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