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## Molecular evidence for diphyly of the Asian catfish family Amblycipitidae (Teleostei: Siluriformes) and exclusion of the South American Aspredinidae from Sisoroidea

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**ABSTRACT.** — Amblycipitidae Day, 1873 is an Asian family of catfishes (Siluriformes) usually considered to contain 28 species placed in three genera: *Amblyceps* (14 spp.), *Liobagrus* (12 spp.) and *Xiurenbagrus* (2 spp.). Morphology-based systematics has supported the monophyly of this family, with some authors placing Amblycipitidae within a larger group including Akysidae, Sisoridae and Aspredinidae, termed the Sisoroidea. Here we investigate the phylogenetic relationships among four species of *Amblyceps*, six species of *Liobagrus* and the two species of *Xiurenbagrus* with respect to other sisoroid taxa as well as other catfish groups using 6100 aligned base pairs of DNA sequence data from the *rag1* and *rag2* genes of the nuclear genome and from three regions (*cyt b*, CO1, ND4 plus tRNA-His and tRNA-Ser) of the mitochondrial genome. Parsimony and Bayesian analyses of the data indicate strong support for a diphyletic Amblycipitidae in which the genus *Amblyceps* is the sister group to the Sisoridae and a clade formed by genera *Liobagrus* and *Xiurenbagrus* is the sister group to Akysidae. These taxa together form a well supported monophyletic group that assembles all Asian sisoroid taxa, but excludes the South American Aspredinidae. Results for aspredinids are consistent with previous molecular studies that indicate these catfishes are not sisoroids, but the sister group to the South American doradoid catfishes (Auchenipteridae + Doradidae). The redefined sisoroid clade plus Bagridae, Horabagridae and (*Ailia* + *Lalides*) make up a larger monophyletic group informally termed “Big Asia.” Likelihood-based SH tests and Bayes Factor comparisons of the *rag* and the mitochondrial data partitions considered separately and combined reject both the hypothesis of amblycipitid monophyly and the hypothesis of aspredinid inclusion within Sisoroidea. This result for amblycipitids conflicts with a number of well documented morphological synapomorphies that we briefly review. Possible nomenclatural changes for amblycipitid taxa are noted.

### INTRODUCTION

With over 3000 valid living species in freshwater and marine environments across the globe and extraordinary diversity in their morphologies and ecologies, the catfishes (Order Siluriformes) are one of the world's great teleost radiations. Asia harbors 15 family-level catfish groups (Sullivan et al., 2006, fig. 2, appendix A), ten of which

are endemic to the continent. Three of these, Sisoridae, Akysidae and Amblycipitidae, belong to a higher clade named Sisoroidea (de Pinna, 1996). Heightening recent interest in sisoroid catfishes is a high rate of discovery of new species (see lists in Ferraris, 2007) and the hypothesis that a South American family, the Aspredinidae, belongs to this otherwise all-Asian group (Chen, 1994; de Pinna, 1996; de Pinna and Ng, 2004; and Diogo, 2005). In the

context of ongoing molecular higher-level phylogenetic studies of the major groups of catfishes (Hardman, 2005; Sullivan et al. 2006) and the opportunity afforded by new samples representing additional species, we investigate here the monophyly and extra-group relationships of one of the sisoroid families: Amblycipitidae.

Amblycipitids are small-sized catfishes inhabiting moderately to swiftly flowing rivers across southern and eastern Asia. Until recently the family has included three genera and 28 species: *Amblyceps* Blyth, 1858, with 14 species, *Liobagrus* Hilgendorf, 1878, with 12, and *Xiurenbagrus* Chen and Lundberg, 1995, with two (Ferraris, 2007). Nguyen and Vo (in Nguyen 2005) described a new amblycipitid genus, *Nahangbagrus*; as of this writing we have seen neither specimens nor the original description. In the most taxon-complete morphology-based phylogenetic study of Amblycipitidae, Chen (1994) and Chen and Lundberg (1995) found evidence for monophyly of the family and recognition of three genera, with *Xiurenbagrus* newly created for a species that had been originally placed in *Liobagrus*. *Amblyceps* plus *Liobagrus* were recovered as sister taxa with *Xiurenbagrus xiurenensis* basal to these. Chen's (1994) analysis of higher-level sisoroid relationships recovered Amblycipitidae and Akysidae as sister taxa subtended first by Sisoridae and then by the South American Aspredinidae. Amblycipitid monophyly is supported in other recent morphological investigations with *Xiurenbagrus* included (Friel, 1994; Ng, 2006) or not (de Pinna, 1993, 1996; de Pinna and Ng, 2004; Diogo, 2005).

To date, molecular phylogenetic analyses aimed at resolving major clades of catfishes at and above the family level have sampled few species of Amblycipitidae or suffered from insufficient sequence data to provide robust phylogenies. The first suggestion of amblycipitid non-monophyly is from Hardman (2005) who found in both parsimony and Bayesian analysis of 170 catfish cytochrome *b* (cyt *b*) sequences that two species of *Liobagrus* clustered with the akysid *Acrochordonichthys* and not with the single included species of *Amblyceps*. In the parsimony analysis *Amblyceps* appeared as sister to species of Aspredinidae and the bagrid *Batasio*, and in the Bayesian analysis as the sistergroup to sisorid taxa. Also in Hardman's (2005) Bayesian analysis, Aspredinidae appeared not in or near Asian sisoroids, but sister to doradoid catfishes (Auchenipteridae + Doradidae). The nearly family-complete dataset of nuclear recombination activating genes 1 and 2 (*rag1* and *rag2*) gene sequences assembled by Sullivan et al. (2006) include a single species of *Amblyceps* so that monophyly of its family could not be tested. All analyses of the combined *rag* data, however, yielded strong and consistent support for an exclusively

Asian Sisoroidea within which *Amblyceps* is sister to Sisoridae, for a larger all-Asian clade containing Sisoroidea, Bagridae, Horabagridae and (*Ailia* + *Laides*), as well as for a separate South American clade uniting aspredinids and doradoids. Ng (2006) generated data sets for mitochondrial cytochrome oxidase 1 (CO1) and nuclear *rag2* genes containing two species of *Amblyceps*, several representatives of other sisoroid families including Aspredinidae, plus various other catfishes as outgroups. Ng's parsimony analysis of the *rag2* data and separate maximum likelihood analyses of the two genes recovered the two *Amblyceps* as monophyletic. In line with the results of Sullivan et al. (2006), Ng's *rag2* data place *Amblyceps* sister to Sisoridae, whereas CO1 does not resolve relationships of *Amblyceps* among the sisoroid families.

The present molecular phylogenetic study of Amblycipitidae includes representatives of three genera, both species of *Xiurenbagrus*, better species-level representation of *Amblyceps* and *Liobagrus* than previous studies, and molecular datasets containing large nuclear and mitochondrial partitions. Taxon sampling at the species level within and outside Amblycipitidae is far from complete, but sufficient to examine the monophyly of the family and the relationships of these catfishes among sisoroids. Additionally, we include supplemental taxa needed to examine the two competing hypotheses for the phylogenetic position of the South American Aspredinidae: (1) that they are sisoroids and (2) that they are the sister group to the South American doradoid catfishes.

## MATERIALS AND METHODS

*Taxon sampling.*—The specimens used in this study are listed in Appendix A. We included four (of the 14) species of *Amblyceps*, six (of the 12) species of *Liobagrus* and the two species of *Xiurenbagrus*. We lack *Amblyceps caecutiens* Blyth 1858 and *Liobagrus reinii* Hilgendorf 1878, the type species for their respective genera. However given the robust morphological diagnoses of both genera (Chen and Lundberg, 1995) we expect the non-monophyly of either one to be unlikely. In the case of *Liobagrus obesus* we obtained mitochondrial sequences from GenBank (DQ321752) and did not sequence it ourselves. (*Rag* sequences were not available for this taxon.) For seven of these 12 ingroup taxa we sequenced two or more individuals. We included two individuals of the same amblycipitid species in the analyses if their combined sequences differed by at least four base pairs. In the case of *Amblyceps foratum* a second sequenced individual that differed by only three base pairs from the first specimen sequenced was not included in the matrix. We included five species and genera of Sisoridae and four species and three genera of Akysidae.

We included four species and genera of Aspredinidae. We also include representatives of the bagrids, horabagrids, *Ailia* and *Laides*, that made up the remainder of the informally named “Big Asia” clade in Sullivan et al. (2006). Outgroup taxa include *Ictalurus punctatus*, *Plotosus lineatus*, and *Rita rita*. Finally, the doradoids *Acanthodoras cataphractus*, *Ageneiosus ucayalensis*, *Trachelyopterus galeatus*, and *Centromochlus heckelii* were included as additional outgroups to test the hypotheses outlined above regarding the phylogenetic affinities of the Aspredinidae.

**Marker selection and laboratory methods.**—We obtained sequences of the three *rag* gene fragments (two from *rag1*, one from *rag2*) used in Sullivan et al. (2006) for the 14 taxa examined here that were not included in that study. Primer sequences and PCR conditions are provided in that publication. We added to this nuclear dataset with data from the complete *cyt b* gene (1137 bases), a portion of the CO1 gene (626 bases), and a third mitochondrial fragment including a part of the NADH dehydrogenase subunit 4 (ND4) gene (587 bases) plus a 128-base portion of the adjoining transfer RNAs (tRNA-Histidine and tRNA-Serine). PCR and sequencing primers (in 5' to 3' orientation) for these markers are as follows: for *cyt b*, L14724: GAC TTG AAA AAC CAC CGT TG & H15915: CTC CGA TCT CCG GAT TAC AAG AC; for CO1, CO1F(L): TCT CAA CCA ACC ATA AAG ACA TTG G, CO1R(H): TAT ACT TCT GGG TGC CCA AAG AAT CA; for ND4 plus t-Leu & t-Ser: L11958 GGA GGC TAC GGC ATA ATA CGA A, H12780: GGT TCC TAA GAC CAA CGG ATG.

We carried out PCR in 10 or 20  $\mu$ l reactions with components at the following concentrations: 1x Sigma PCR buffer (Sigma-Aldrich, St. Louis, MO), 0.02 U/ $\mu$ l Sigma JumpStart *Taq*, 2mM MgCl<sub>2</sub>, 0.4  $\mu$ M of forward and reverse primer, 200  $\mu$ M of each dNTP and approximately 200pg/ $\mu$ l template DNA. We used an initial denaturation step of 1 min at 94°C followed by 30 or 35 cycles of 94°C for 30s, annealing at temperatures between 48 and 57°C for 30s, and extension at 72°C for 1.5 min. This was followed by a final 5 minute, 72 °C extension step. We evaluated amplification success on ethidium bromide-stained agarose gels, purified PCR products using ExonucleaseI and Shrimp Alkaline Phosphatase and performed dye-deoxy termination cycle sequencing using ABI Big Dye chemistry (PE Applied Biosystems, Foster City, CA). We cleaned these sequencing reactions on Sephadex columns prior to running them on an ABI capillary sequencer. We edited and combined sequences into contigs for each fragment with Sequencher 4.2.2 (GeneCodes Corporation, Ann Arbor, MI). For the nuclear DNA sequences, heterozygous nucleotides were assigned IUPAC ambiguity codes.

Sequence alignment for the *rag* fragments was ac-

complished readily by eye with the aid of an amino acid translation. Alignment for *cyt b*, CO1 and ND4 included no indels and was unambiguous. The 128 base pair fragment of t-RNA sequence downstream of the ND4 fragment includes several short indels resulting in an ambiguous alignment for 14 bases that were excluded from the analyses.

**Phylogenetic Analysis.**—To infer phylogenies, we used Bayesian methods as implemented in MrBayes 3.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003), maximum likelihood in GARLI 0.95 (Zwickl, 2006) and maximum parsimony as implemented in PAUP\* 4.0b10 (Swofford, 2002). We ran analyses on the combined nuclear and mitochondrial partitions as well as on each separately.

To optimize the fit of model parameters to the data in the Bayesian analyses, we estimated parameters separately for each data partition. As in Sullivan et al. (2006), we divided the combined *rag1* and *rag2* data into three partitions corresponding to the three codon positions. Similarly for the mitochondrial data, we partitioned the combined *cyt b*, ND4 and CO1 data by codon position and treated the tRNA data as a separate partition, for a total of seven partitions. We determined the appropriate model of evolution to be used for each partition in MrBayes by calculating AIC scores (Posada and Buckley, 2004) for all models in MrModelTest 2.2 (Nylander, 2004). Based on these scores, we assigned GTR+I+ $\Gamma$  models to all but the mitochondrial second codon position partition to which we assigned a HKY85+I+ $\Gamma$  model, and the tRNA partition to which we assigned a GTR+ $\Gamma$  model.

To search for the most parsimonious tree or trees in PAUP\*, we conducted full heuristic (TBR-branch swapping) searches in which starting trees were obtained by 1000 stepwise addition replicates, all characters and character state transformations were weighted equally. To assess support for nodes, we performed 1000 bootstrap replicates with 10 stepwise additions of taxa per replicate. Additionally we obtained decay (Bremer) support values for the *rag* and mitochondrial data partitions for nodes in the tree using TreeRot (Sorenson, 1999).

In MrBayes 3.1, we ran two independent sets of MCMC chains, each with three heated and one unheated chain for 8x10<sup>6</sup> generations. These were sampled every 1000 generations. All analyses employed the default flat Dirichlet priors. We assessed stationarity by monitoring the convergence of the standard deviation of split frequencies and by graphing posterior probabilities of both runs against generations. We excluded trees and parameter values from the pre-convergence “burn-in” phases of the runs. For the likelihood analyses in GARLI, we retained the results of highest log likelihood from three independent runs using

random starting trees and the default GTR+I+ $\Gamma$  model, with all other settings at their default value.

In addition to these unconstrained analyses of the data, we formally examined two hypotheses of relationship: (1) amblycipitid monophyly and (2) the existence of a clade consisting of the Aspredinidae and the other “sisoroid” catfishes in parsimony, likelihood and Bayesian analyses by comparing the best tree obtained by each method to the best obtainable consistent with the appropriate single topological constraint. We compared the difference in the number of steps between the hypotheses in parsimony, used the non-parametric SH-test (Shimodaira and Hasegawa, 1999) to compare likelihood scores and compared Bayes Factors from analyses in MrBayes 3.1 (Kass and Raftery, 1995). We repeated this procedure for the nuclear and mitochondrial data partitions considered separately and as well as combined to investigate whether results were gene, or genome-specific.

## RESULTS

*Sequence characteristics.*—The dataset consisted of 6100 aligned bases: 3633 aligned bases of *rag1* and *rag2*, and 2467 aligned bases of concatenated *cyt b*, CO1, and ND4+tRNA mitochondrial sequence. While the dataset is largely complete, we include six terminal taxa (out of 50) for which amplification of one of the six sequence fragments failed, and one taxon retrieved from GenBank, *Liobagrus obesus*, for which we have no *rag* data (Table 1). This taxon is included in analyses of the mt dataset by itself and in the combined analyses, but obviously not in the analyses of the *rag* data. No other taxon is missing more than one of the six sequenced gene fragments and every ingroup genus is represented by some completely sequenced taxa. Missing data on this small scale is unlikely to affect phylogenetic analysis significantly (Wiens, 2003).

Plotting pairwise uncorrected mitochondrial genetic distances (“p”-distances) against the corresponding distances from the combined *rag1* and *rag2* partitions illustrates increasing saturation of the mt genes at greater *rag* distances (Fig. 1). The model parameters estimated by MrBayes for each of the seven data partitions are shown in Table 1.

*Phylogenetic results.*—There are 1479 and 1122 informative characters for parsimony from the nuclear and the mitochondrial partitions, respectively. Parsimony analysis of the complete dataset resulted in a single most parsimonious tree of 15720 steps and a C.I. of 0.30 when uninformative characters are excluded. The likelihood analysis in GARLI and the Bayesian analysis in MrBayes 3.1 yielded tree topologies identical to each other and similar to that produced by parsimony, differing only with respect to

several outgroup relationships. (These points of difference not being of immediate interest here, we forgo discussion of them.) The tree shown in Fig. 2 includes those nodes common to all three analyses of the full dataset. Fig. 3 shows a phylogram from the Bayesian analysis illustrating the sisoroid taxa only. All analyses indicate that the amblycipitid taxa do not form a monophyletic group; instead a clade of the four *Amblyceps* species appears as the sister group to a clade consisting of the five sisoroid taxa, while the genera *Xiurenbagrus* and *Liobagrus*, each respectively monophyletic and each other’s sister group, are together the sister group to the four akysid taxa. Partitioned decay (Bremer) support values in the combined data parsimony analysis reveal that these two nodes are supported by characters within both the nuclear and the mitochondrial partitions (Fig. 2). For the *Amblyceps* + sisoroid node, the parsimony decay value is 14, for which nine of the total are contributed by the nuclear partition, and five from the mitochondrial partition. For the (*Liobagrus*, *Xiurenbagrus*) + akysid node, the decay value is 30, of which 20 are contributed by the nuclear partition and ten from the mitochondrial partition. These two nodes are also recovered

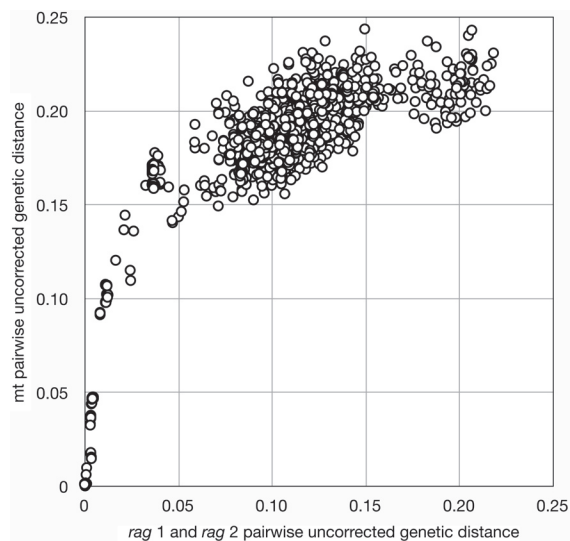


Fig. 1. Comparative evolutionary rates of the mitochondrial versus nuclear markers used in this study. The combined mitochondrial (*cyt b*, CO1, ND4 and tRNA-His, tRNA-Ser) uncorrected genetic distances (p-distances) calculated in all possible pairwise comparisons of the taxa used in this study are plotted against the corresponding values for the combined *rag1* and *rag2* data. The non-linear relationship reflects increasing saturation of variable sites in the mitochondrial sequences relative to variable sites in the *rag* sequences. Saturation of variable sites is likely one factor that contributes to the mitochondrial markers’ poorer resolution of deep nodes in phylogenetic analyses relative to *rag1* and *rag2*.

Table 1. Model parameters (mean  $\pm$  variance) estimated by MrBayes 3.1 during Bayesian analysis of  $8 \times 10^6$  post burn-in generations (15602 samples from two runs). Appropriate models for each partition were determined by AIC scores calculated in MrModelTest 2.2. Arithmetic mean of log likelihoods = -71805.74.

MODEL	PARTITION 1	PARTITION 2	PARTITION 3	PARTITION 4	PARTITION 5	PARTITION 6	PARTITION 7
PARAMETER	GTR + I + $\Gamma$	GTR + I + $\Gamma$	GTR + I + $\Gamma$	GTR + I + $\Gamma$	HKY + I + $\Gamma$	GTR + I + $\Gamma$	GTR + $\Gamma$
	<i>rag</i> 1st codon position	<i>rag</i> 2nd codon position	<i>rag</i> 3rd codon position	mt coding, 1st position	mt coding, 2nd position	mt coding, 3rd position	mt non-coding (tRNA)
kappa	–	–	–	–	6.1549 $\pm$ 0.9154	–	–
A < – > C	0.1719 $\pm$ 0.0002	0.1017 $\pm$ 0.0001	0.0898 $\pm$ 0.0000	0.0266 $\pm$ 0.0000	–	0.0085 $\pm$ 0.0000	0.0350 $\pm$ 0.0002
A < – > G	0.2521 $\pm$ 0.0003	0.3181 $\pm$ 0.0005	0.3720 $\pm$ 0.0002	0.1710 $\pm$ 0.0005	–	0.5586 $\pm$ 0.0006	0.2585 $\pm$ 0.0028
A < – > T	0.1023 $\pm$ 0.0001	0.1003 $\pm$ 0.0001	0.0750 $\pm$ 0.0000	0.0630 $\pm$ 0.0001	–	0.0124 $\pm$ 0.0000	0.0451 $\pm$ 0.0002
C < – > G	0.0770 $\pm$ 0.0001	0.1254 $\pm$ 0.0002	0.0653 $\pm$ 0.0000	0.0015 $\pm$ 0.0000	–	0.0247 $\pm$ 0.0001	0.0474 $\pm$ 0.0003
C < – > T	0.2993 $\pm$ 0.0004	0.2771 $\pm$ 0.0005	0.3345 $\pm$ 0.0002	0.7102 $\pm$ 0.0008	–	0.3526 $\pm$ 0.0006	0.5781 $\pm$ 0.0038
G < – > T	0.0974 $\pm$ 0.0001	0.0773 $\pm$ 0.0001	0.0635 $\pm$ 0.0000	0.0277 $\pm$ 0.0000	–	0.0433 $\pm$ 0.0002	0.0359 $\pm$ 0.0002
p(A)	0.2976 $\pm$ 0.0001	0.3370 $\pm$ 0.0002	0.2858 $\pm$ 0.0001	0.2833 $\pm$ 0.0002	0.1664 $\pm$ 0.0002	0.4464 $\pm$ 0.0001	0.3726 $\pm$ 0.0015
p(C)	0.2140 $\pm$ 0.0001	0.2056 $\pm$ 0.0001	0.1929 $\pm$ 0.0000	0.3199 $\pm$ 0.0002	0.2866 $\pm$ 0.0002	0.3086 $\pm$ 0.0001	0.1916 $\pm$ 0.0007
p(G)	0.2774 $\pm$ 0.0001	0.1956 $\pm$ 0.0001	0.1937 $\pm$ 0.0001	0.2304 $\pm$ 0.0002	0.1314 $\pm$ 0.0001	0.0552 $\pm$ 0.0000	0.1782 $\pm$ 0.0008
p(T)	0.2110 $\pm$ 0.0001	0.2619 $\pm$ 0.0001	0.3277 $\pm$ 0.0001	0.1665 $\pm$ 0.0001	0.4157 $\pm$ 0.0003	0.1898 $\pm$ 0.0000	0.2576 $\pm$ 0.0009
alpha	1.3757 $\pm$ 0.2797	0.7459 $\pm$ 0.0907	4.1179 $\pm$ 0.3367	0.8542 $\pm$ 0.0089	0.6387 $\pm$ 0.0334	0.9275 $\pm$ 0.0017	0.5316 $\pm$ 0.0076
p-invariant	0.3205 $\pm$ 0.0072	0.3930 $\pm$ 0.0092	0.0521 $\pm$ 0.0002	0.6016 $\pm$ 0.0005	0.7721 $\pm$ 0.0010	0.0088 $\pm$ 0.0000	–
m	0.1016 $\pm$ 0.0001	0.0678 $\pm$ 0.0000	0.3219 $\pm$ 0.0003	0.4467 $\pm$ 0.0024	0.0514 $\pm$ 0.0000	6.4688 $\pm$ 0.0056	0.3749 $\pm$ 0.0021



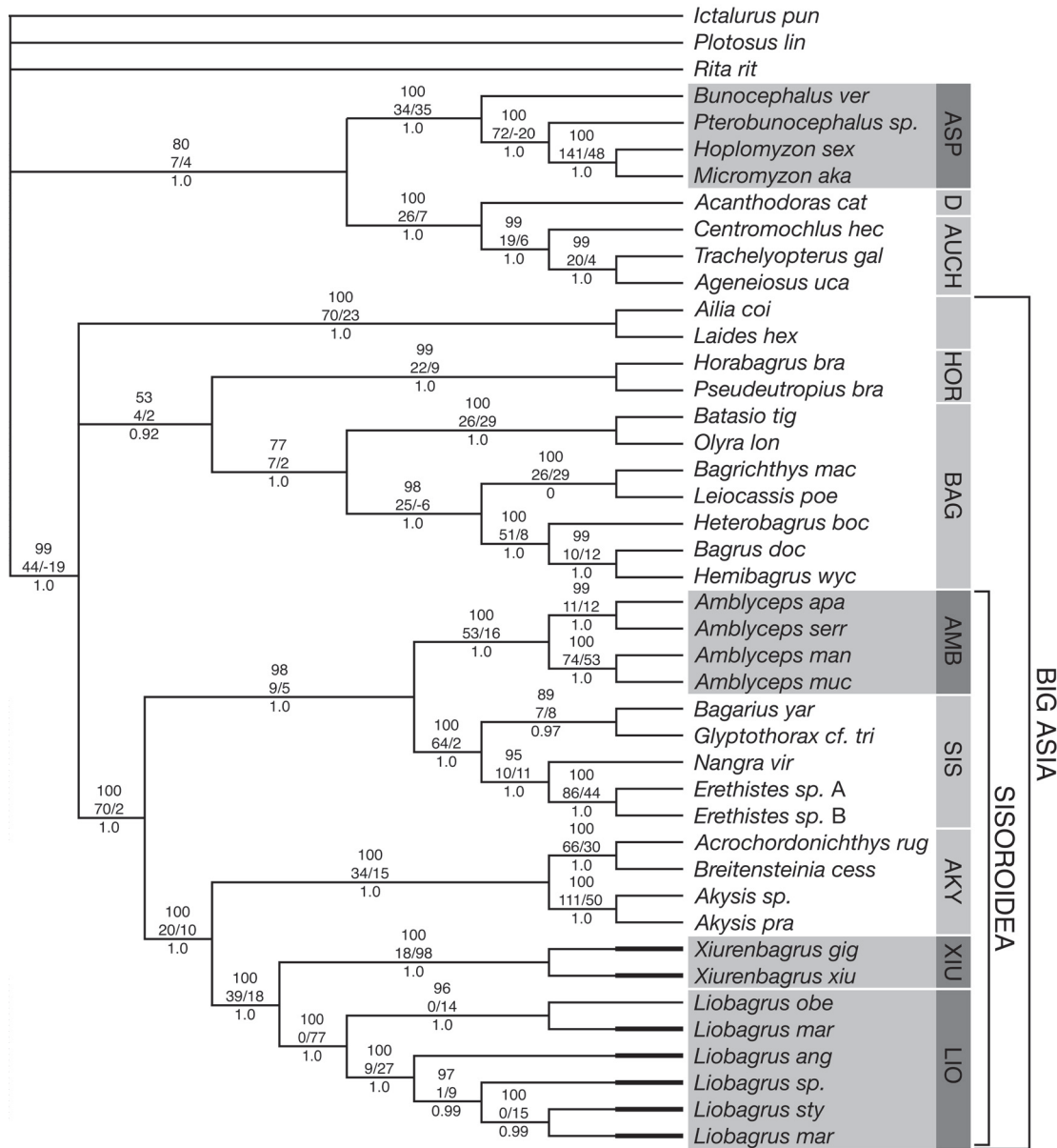


Fig. 2. Phylogenetic tree of amblycipitid catfishes, other sisoroid taxa and outgroups derived from an unweighted parsimony analysis and a partitioned, mixed-model Bayesian analysis of 6100 aligned bases of nuclear (*rag1* & *rag2*) and mitochondrial (*cyt b*, CO1, ND4 and tRNA) data. Nodes common to both analyses are illustrated. Amblycipitid and Aspredinid taxa indicated by shading. Top value shown above branches is the parsimony bootstrap proportion under which the decay (Bremer) value for the *rag* data partition and the decay value for the mitochondrial data partition separated by a “/” are shown. (The total decay value is the sum of the two partitioned decay values. A partitioned decay value may be a negative integer.) Below branches are shown Bayesian posterior probabilities. Sisoroid clade is nested within a larger clade including (*Ailia* + *Laidex*), bagrids and horabagrids. Aspredinidae are sister to doradoid species outside of the “Big Asia” clade. Among sisoroid taxa, Amblycipitidae are diphylectic: *Amblyiceps* is sister to Sisoridae and (*Liobagrus* + *Xiurenbagrus*) is sister to Akysidae. Terminal taxa with thickened lines represent sample size of two sequenced individuals. Full names of terminal taxa are in Appendix A. ASP = Aspredinidae, D = Doradidae, AUCH = Auchenipteridae, HOR = Horabagridae, BAG = Bagridae, AMB = *Amblyiceps*, SIS = Sisoridae, AKY = Akysidae, XIU = *Xiurenbagrus*, LIO = *Liobagrus*.

in parsimony and Bayesian analyses of the nuclear (*rag*) partition by itself. When the mitochondrial data partition is analyzed separately, only one of these nodes, (*Liobagrus*, *Xiurenbagrus*) + akysids, is recovered. In these analyses the taxon *Bagarius yarrelli* falls outside the sisoridae, with the species of *Amblyceps* forming the sistergroup to the remaining sisorid taxa.

Returning to the full dataset analyses depicted in Fig. 2, all of the sisoroid taxa together (minus Aspredinidae) constitute a monophyletic group. These sisoroids plus the bagrids, horabagrids, *Laides* and *Ailia* together form a larger monophyletic group with respect to the aspredinids and outgroups that corresponds to the Big Asia clade of Sullivan et al. (2006). Within Big Asia, a basal polytomy remains among (*Ailia* + *Laides*), the sisoroids and a clade consisting of bagrids plus the horabagrids. The Big Asia clade does not appear in the analyses of the mitochondrial data alone, but no alternative large clades receive high support in these analyses.

Finally, both in the analyses of the full dataset as well as in analyses of the nuclear and mitochondrial partitions separately, the doradoid taxa and the aspredinid taxa are

recovered as monophyletic sister groups. In analyses of the full dataset, the parsimony bootstrap support value is 80 and the decay value is 11, with seven decay steps contributed from the *rag* partition and four from the mitochondrial partition.

Within *Amblyceps*, the recovered relationships among species (Figs. 2, 3) are: ((*A. mangois*, *A. mucronatum*), (*A. apangi*, *A. serratum*)). Both sister group pairs are further defined by autapomorphic deletions in the *rag* sequence. Within *Liobagrus*, the recovered relationships are: (((*L. stanyani*, *L. marginatoides*), *L. sp.*), *L. anguillicauda*), (*L. obesus*, *L. marginatus*)).

*Tests of alternate topologies.*—Using parsimony analysis of the full dataset, the shortest tree obtainable that contains a monophyletic Amblycipitidae is 48 steps longer than the shortest unconstrained tree (Table 2). Similarly, the shortest tree containing a monophyletic Sisoroidea that includes Aspredinidae is 55 steps longer than the unconstrained tree. Using the likelihood-based SH-test, we find that both of these alternate hypotheses have significantly lower likelihood than the unconstrained topologies. Comparison of the Bayes factors between the constrained and unconstrained topologies likewise compels rejection of the alternate hypotheses. When these comparisons and tests are repeated on the nuclear (*rag*) and the mitochondrial data separately, we find evidence to reject the hypothesis of amblycipitid monophyly and a Sisoroidea including aspredinids in both data partitions, although it is stronger in the *rag* partition. Only the SH test of amblycipitid monophyly using mitochondrial data returned a non-significant value. However given the difference in length of the two hypotheses in parsimony (eight steps) and a value greater than 10 for twice the natural log of the Bayes factor (Kass and Raftery, 1995), there appears to be sufficient evidence in the mitochondrial partition alone to reject amblycipitid monophyly.

## DISCUSSION

*Major clades.*—We find strong molecular support for a diphyletic origin of the catfish genera now comprising Amblycipitidae (Fig. 4), corroborating Hardman's (2005) tentative finding from *cyt b* sequences alone. This result is obtained from separate analysis of the nuclear and mitochondrial data partitions as well as from the combined dataset and is robust with respect to the method of analysis (Table 2). Similarly strong is the result that the South American Aspredinidae are not close relatives of sisoroid or other Big Asia catfish groups, but instead appear close to the South American doradoid catfishes (Fig. 4). This result is consistent with a Bayesian analysis in Hardman (2005) and in parsimony and Bayesian analyses in Sullivan et al.

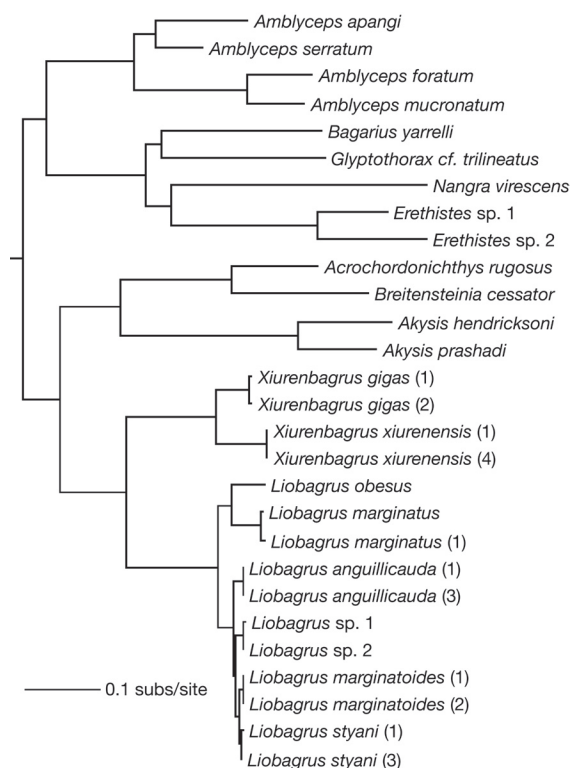


Fig. 3. Phylogram depicting relationships and genetic distances among sisoroid taxa used in this study from the partitioned, mixed-model Bayesian analysis of the complete dataset (see Table 1).



(2006). The analysis here shows the aspredinid-doradoid relationship to be robust to larger samples of aspredinid and sisoroid taxa than were used in the earlier studies and to be supported by data from both the nuclear and mitochondrial genomes.

*Morphology-based systematics of Amblycipitidae.*—*Amblyceps* and *Liobagrus* usually have been exclusively united since Hora (1936) moved *Akysis* and *Acrochordonichthys* out of Amblycipitidae into their own family Akysidae. While it is beyond our scope of this paper to verify and review the morphological characters reported by previous authors, below we summarize and call attention to the body of work that precedes ours.

The early characterizations of Amblycipitidae, as for all catfish families, were not explicitly phylogenetic and many of the features used are either plesiomorphic, homoplastic or of uncertain significance (Regan, 1911; Hora, 1936; Tilak, 1966; Chardon, 1968). Recent morphology-based investigations have identified potential synapomorphic characters that support monophyly of Amblycipitidae comprising *Amblyceps* and *Liobagrus*, and, after its recognition, *Xiurenbagrus*. Thus, Mo (1991) briefly described, but did not illustrate, a possibly unique bony process on the fourth transverse process of the Weberian complex as a synapomorphy shared by *Amblyceps* and *Liobagrus*. For these same taxa de Pinna's (1993) parsimony analysis suggested as synapomorphies three characters: L-shaped endopterygoid bones, continuous cartilaginous posterior and medial margins of the pelvic girdle, and horn-shaped postero-medial process of cartilage from the pelvic girdle. Chen (1994) observed that none of the synapomorphies listed by Mo (1991) and de Pinna (1993) were unique to *Amblyceps* and *Liobagrus*. Further, Chen (1994; see also Chen and Lundberg, 1995) reported three unique plus three non-unique but unambiguous synapomorphies shared by *Amblyceps*, *Liobagrus* and *Xiurenbagrus*.

1. Fan-shaped expansion of the posterodorsal corner of the hyomandibular (see Chen and Lundberg, 1995, fig. 2, p. 782; and several figures in Chen, 1994).

2. Posterodorsal narrow projection of the interopercle (see Chen, 1994, fig. 17, p. 341 and fig. 48, p. 383).

3. Oblique orientation and deep subcutaneous position of the middle nuchal plate (see Chen, 1994, fig. 22, p. 347 and fig. 24, p. 349).

4. Fusion of the adjacent basal elastic cartilages of the inner and outer mental barbels (see Chen and Lundberg, 1995, fig. 7, p. 784).

5. Dorsoposterior expansion of the jaw adductor muscles onto the skull roof (see Chen, 1994, fig. 14, p. 337).

6. Formation of a sharp transverse crest at the occiput on which the jaw muscles originate (see Chen, 1994, figs.

9, 11, pp. 332, 334).

In 1996 de Pinna described three more unique features shared by *Amblyceps* and *Liobagrus* involving the metapterygoid-ectopterygoid ligament (fig. 8, p. 13), hypobranchial shape (fig. 19, p. 24) and basket-like arrangement of the branchiostegal bones. A few other morphological characters potentially supporting amblycipitid monophyly are discussed by de Pinna (1996), Diogo (2005) and Ng (2006), but none of these authors made direct observations on *Xiurenbagrus*.

Within Amblycipitidae Chen's study recovered *Amblyceps* and *Liobagrus* as a clade with *Xiurenbagrus* basal to them (Chen, 1994; Chen and Lundberg, 1995). The evidence producing this topology includes ten unique or nearly unique but unambiguous characters of the skeleton, external morphology, lateralis sensory canals and body proportions.

1. The posterior limb of the L-shaped endopterygoid is long, slender and straight or medially arched (Chen and Lundberg, fig. 17, p. 794). Contrary to de Pinna (1993), Chen interpreted the presence of the L-shaped endopterygoid as a synapomorphy supporting a more inclusive clade of Amblycipitidae + Akysidae.

2. *Amblyceps* and *Liobagrus* have a cuplike skin flap on the anterior margin of the pectoral girdle behind the gill membrane (Chen and Lundberg, fig. 15, p. 792).

3. The parietal branch of supraorbital sensory canal is absent (Chen and Lundberg, fig. 4, p. 783).

4. The premaxilla has a posteriorly directed sublateral process (Chen and Lundberg, fig. 13, p. 787).

5. Metapterygoid-hyomandibular joint is overlapping or abutting, rather than deeply interdigitating (Chen and Lundberg, fig. 2, p. 782).

6. The distal, unfused pectoral-fin spine segments are greatly elongated distally and overlapping (Chen and Lundberg, fig. 11, p. 786).

7. A subpteryotic process of supracleithrum is present (Chen and Lundberg, fig. 16, p. 793).

8. The inner mental barbels are long (terminating posterior to the gill membrane).

9. The lateral line is short (terminating below the dorsal-fin origin).

10. The antorbital and first infraorbital are not fused and lie side by side in parallel (Chen and Lundberg, fig. 12, p. 786).

The morphological and the molecular data clearly offer conflicting signals on amblycipitid monophyly and interrelationships of its three known genera. Both data sources appear to offer robust evidence. The morphology includes apparently unique and unreversed synapomorphies in skeletal and soft anatomy supporting amblycipitid monophyly, and the *Amblyceps* + *Liobagrus* subgroup. The

Table 2. Comparison of best, unconstrained trees (a) obtained using maximum parsimony (MP), maximum likelihood (ML) and Bayesian methods to trees in which amblycipitid monophyly is constrained (b) and aspredinid taxa and sisoroid taxa are constrained to form a clade (c). Trees were calculated using the full dataset and for the nuclear (*rag*) and mitochondrial partitions separately. MP analyses were conducted in PAUP\*4.0b, ML analysis was conducted in GARLI v.0.951 with GTR +  $\Gamma$  + I model (best score from three runs). SH tests were conducted with 10,000 RELI bootstrap replicates in PAUP\*, with trees and parameters obtained in GARLI. Partitioned Bayesian analyses conducted in MrBayes 3.1 as described in text.

Tree Description	Maximum Parsimony			Maximum Likelihood			Bayesian	
	steps	$\Delta$ steps	#trees	InL score	$\Delta$ inL	P(SH)	In marg. L <sup>a</sup>	$2(\ln B_{10})^b$
ALL DATA								
(a) Unconstrained	15720		1	-76024.654			-71864.06	
(b) Amblycipitidae monophyly constrained	15768	+48	1	-76123.214	-98.506	<0.001*	-71949.84	171.56
(c) Aspredinidae constrained within Sisoroidea	15775	+55	2	-76162.805	-138.152	<0.001*	-71994.15	260.18
RAG DATA ONLY								
(a) Unconstrained	5638		2	-33887.921			-33249.33	
(b) Amblycipitidae monophyly constrained	5673	+35	2	-33959.543	-71.622	<0.001*	-33317.41	136.16
(c) Aspredinidae constrained within Sisoroidea	5677	+39	2	-34007.511	-119.591	<0.001*	-33372.84	247.02
MT DATA ONLY								
(a) Unconstrained	10030		1	-39746.030			-38344.28	
(b) Amblycipitidae monophyly constrained	10038	+8	3	-39759.646	-13.616	0.163	-38357.02	25.48
(c) Aspredinidae constrained within Sisoroidea	10052	+22	1	-39769.388	-23.358	0.035*	-38358.59	28.62

\*Significant at the 5% level or better.  
<sup>a</sup> estimated from harmonic mean of log likelihoods from post-burn in trees.  
<sup>b</sup> $B_{10}$  = Bayes Factor. Values greater than 10 for  $2(\ln B_{10})$  are strong evidence against the alternative hypothesis (Kass & Raftery, 1995).

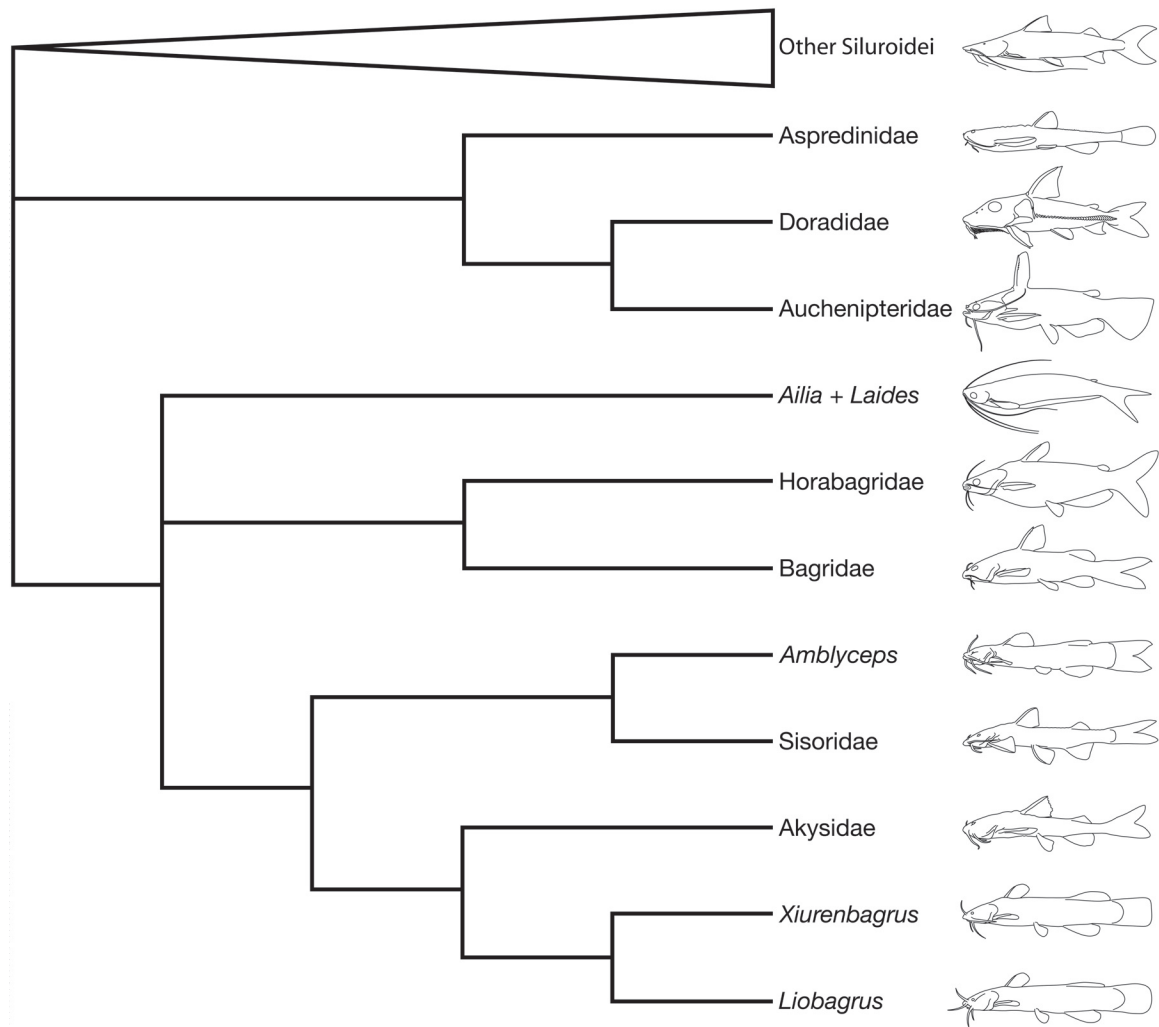


Fig. 4. Summary cladogram showing phylogenetic results with respect to catfish genera and families included in this study. Amblycipitidae is diphylectic: *Amblyceps* is sister to Sisoridae and (*Xiurenbagrus* + *Liobagrus*) is sister to Akysidae. These taxa together make up an all-Asian Sisoroidea. The South American family Aspredinidae is sister to the South American doradoids (Doradidae + Auchenipteridae). Catfish illustrations by Kyle Luckenbill.

molecular data includes nuclear and mitochondrial gene sequences that, combined and partitioned, recover well-supported clades: *Liobagrus* + *Xiurenbagrus* most closely related to akysids, and *Amblyceps* most closely related to sisorids.

*Composition of Sisoroidea and the position of Aspredinidae.*—In much recent morphological work the South American banjo catfish family Aspredinidae is placed near or among the Asian sisoroids (Ferraris, 1989; de Pinna 1993, 1996; Chen, 1994; de Pinna and Ng, 2004; Diogo, 2005; Diogo et al. 2001, 2002, 2003a,b).

De Pinna (1996) united the Amblycipitidae, Akysidae, Sisoridae, “erethistids” (now a subgroup of Sisoridae) and Aspredinidae into the superfamily Sisoroidea Bleeker. There is wide consensus among morphological and molecular studies that *Amblyceps*, *Liobagrus*, and *Xiurenbagrus* are sisoroids, but there is a mixed bag of topologies of these genera within the larger clade. De Pinna’s (1996) analysis recovered Amblycipitidae as the basal sister to all sisoroids, and Aspredinidae distal in the tree as the sister group of “erethistids” Diogo’s (2005) results were similar, but the akysid branch was unresolved. Chen’s

(1994) and Ng's (2005) morphological analyses recovered Amblycipitidae and Akysidae as sister taxa subtended first by Sisoridae and then more basally by the South American Aspredinidae.

On the other hand, Friel (1994) described shared derived features suggesting that aspredinids are most closely related to doradoids and African mochokids, and for sisoroids he placed amblycipitids sister to Akysidae plus Sisoridae. As previously reported by Sullivan et al. (2006), nuclear *rag* gene sequences recover aspredinids as the sister clade to South American doradoids, i.e., without African mochokids. That result is clearly confirmed in the present study of both *rag* and mt DNA sequences. Based on this evidence, we consider Sisoroidea to be a monophyletic group restricted to the Asian Akysidae, Amblycipitidae and Sisoridae.

*Biogeography of Amblyceps, Liobagrus and Xiurenbagrus.*—As pointed out by Zhao et al. (2004), all three amblycipitid genera are largely allopatrically distributed with respect to each other. *Amblyceps* occurs in drainages on the Indian subcontinent and the Malay Peninsula, but not east of the Mekong River basin. Species of *Liobagrus* occur in the Changjiang (Yangtze) River basin, on the Korean Peninsula, and on the islands of Japan and Taiwan. The two species of *Xiurenbagrus* occur in the Zhujiang (Pearl) River basin in southern China. This allopatry is not complete, however, as the second author collected an undetermined species of *Liobagrus* (*Liobagrus* sp. used in this study) within a part of the Zhujiang basin. *Liobagrus* may have entered this basin by means of the Lingqu Canal constructed in the late Third Century BCE.

Reappraising biogeography in light of the phylogenetic relationships recovered by the analysis of the molecular data, one notes that the distributions of the sister groups Akysidae and the clade *Liobagrus* + *Xiurenbagrus* are non-overlapping. Akysidae are distributed from Burma east to the Malay Peninsula and onto to Java, Sumatra and Borneo. Akysids are not distributed east of the Indochinese Peninsula on continental Asia (Ng and Sabaj, 2005). This distributional information and the relationships (Akysidae, (*Liobagrus*, *Xiurenbagrus*)) imply a north-south division in the common ancestor of *Liobagrus* and *Xiurenbagrus* following an earlier east-west split between the common ancestor of this clade and Akysidae. Estimating the ages of these clades and their correlation with important geological events on the Asian continent may be an interesting subject of future studies. Biogeographical interpretation is less clear-cut for *Amblyceps* and its sister group, Sisoridae, since sisorids broadly overlap and extend far beyond the range of *Amblyceps*.

*Classification of Amblycipitidae.*—Given the unresolved conflict between morphological and molecular

datasets with regard to amblycipitid monophyly, we defer making taxonomic changes here. However, if further study of Asian Sisoroidea is supportive of our results, then revision of the current family level classification will be necessary. The most sweeping alternative would be to combine the three currently recognized families of Asian sisoroids (i.e., Akysidae Gill, 1861, Amblycipitidae Day, 1873 and Sisoridae Bleeker, 1858) into a single family Sisoridae (from Bleeker, 1858, Ferraris and de Pinna, 1999). On the other hand, the clade of *Liobagrus* + *Xiurenbagrus* can be given family rank and named after the older generic name *Liobagrus*, or the two main clades of Asian Sisoroidea, (*Liobagrus* + *Xiurenbagrus*, Akysidae) and (*Amblyceps*, Sisoridae), could each be recognized as families.

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Appendix A. Taxonomic specimen data and GenBank sequence numbers for the 50 siluriform specimens used in this study. For species represented by two sequences, specimen identifiers enclosed by parentheses. Missing data indicated by a “—”.

Family Group	Terminal taxon	Catalogue Number	Locality	5' rag1	3' rag1	rag2	ND4+rRNA	Cyt b	COI
	<i>Alilia coila</i>	Private collection, H.H. Ng	India, Ganges basin	DQ492541	DQ492452	DQ492340	EU490804	EU490901	EU490852
	<i>Lalides hexanema</i>	Private collection, H.H. Ng	Sumatra, Batang Hari basin	DQ492601	DQ492453	DQ492341	EU490817	EU490915	EU490866
Akysidae	<i>Acrochordontichthys rugosus</i>	INHS 93578	Thailand	DQ492539	DQ492444	DQ492332	EU490802	EU490899	EU490850
Akysidae	<i>Akysis prashadi</i>	UMMZ 245488	Myanmar, Irrawaddy basin	EU490942, EU490960	EU490978	EU490998	EU490806	EU490903	EU490854
Akysidae	<i>Akysis hendricksoni</i>	INHS 93579	Thailand	DQ492542	DQ492445	DQ492333	EU490805	EU490902	EU490853
Akysidae	<i>Breitensteinia cessator</i>	Private collection, H.H. Ng	Asia, Aquarium fish trade	EU490941, EU490959	EU490977	EU490997	EU490803	EU490900	EU490851
Amblyceipitidae	<i>Amblyceps apangi</i>	UMMZ 247456	India, West Bengal	EU490943, EU490961	EU490979	EU490999	EU490825	EU490922	EU490873
Amblyceipitidae	<i>Amblyceps mucronatum</i>	Private collection, H.H. Ng	Asia, Aquarium fish trade	EU490945, EU490963	EU490981	EU491001	EU490827	EU490925	EU490876
Amblyceipitidae	<i>Amblyceps serratum</i>	Private collection, H.H. Ng	Asia, Aquarium fish trade	EU490944, EU490962	EU490980	EU491000	EU490828	EU490923	EU490874
Amblyceipitidae	<i>Amblyceps foratum</i>	INHS 93530	Thailand, Bangkok basin	DQ492543	DQ492451	DQ492339	EU490826	EU490924	EU490875
Amblyceipitidae	<i>Liobagrus anguillicauda</i> (1)	IBH S0404266	China, Fujian, Minjiang basin	EU490946, EU490964	EU490982	EU491002	EU490829	EU490926	EU490877
Amblyceipitidae	<i>Liobagrus anguillicauda</i> (3)	IBH S0404268	China, Fujian, Minjiang basin	EU490947, EU490965	EU490983	EU491003	EU490830	EU490927	EU490878
Amblyceipitidae	<i>Liobagrus marginatoides</i> (1)	IBH S0404263	China, Sichuan, Upper Yangtse basin	EU490948, EU490966	EU490984	EU491004	EU490831	EU490928	EU490879
Amblyceipitidae	<i>Liobagrus marginatoides</i> (2)	IBH S0404264	China, Sichuan, Upper Yangtse basin	EU490949, EU490967	EU490985	EU491005	EU490832	EU490929	EU490880
Amblyceipitidae	<i>Liobagrus marginatus</i>	UMMZ 246862	China, Sichuan, Upper Yangtse basin	EU490950, EU490968	EU490986	EU491006	EU490833	EU490930	EU490881
Amblyceipitidae	<i>Liobagrus marginatus</i> (1)	IBH S0411127	China, Sichuan, Upper Yangtse basin	EU490951, EU490969	EU490987	EU491007	EU490834	EU490931	EU490882
Amblyceipitidae	<i>Liobagrus obesus</i>	GenBank sequence	unknown	—	—	—	DQ321752	DQ321752	DQ321752
Amblyceipitidae	<i>Liobagrus sp.</i> (1)	IBH S0404260	China, Guangxi, Lijiang, Pearl basin	EU490954, EU490972	EU490990	EU491010	EU490837	EU490934	EU490885
Amblyceipitidae	<i>Liobagrus sp.</i> (2)	IBH S0404261	China, Guangxi, Lijiang, Pearl basin	EU490955, EU490973	EU490991	EU491011	EU490838	EU490935	EU490886
Amblyceipitidae	<i>Liobagrus stayani</i> (1)	IBH S0404066	China, Hunan, Yuanjiang, Yangtse basin	EU490952, EU490970	EU490988	EU491008	EU490835	EU490932	EU490883
Amblyceipitidae	<i>Liobagrus stayani</i> (3)	IBH S0408036	China, Hubei, Hanjiang, Yangtse basin	EU490953, EU490971	EU490989	EU491009	EU490836	EU490933	EU490884
Amblyceipitidae	<i>Xiurenbagrus gigas</i> (1)	IBH S2003151	China, Guangxi, Hongshuihe, Pearl basin	EU490956, EU490974	EU490992	EU491012	EU490839	EU490936	EU490887
Amblyceipitidae	<i>Xiurenbagrus gigas</i> (2)	IBH S0305032	China, Guangxi, Hongshuihe, Pearl basin	EU490957, EU490975	EU490993	EU491013	EU490840	EU490937	EU490888
Amblyceipitidae	<i>Xiurenbagrus xiurenensis</i> (1)	IBH S0404027	China, Guangxi, Hongshuihe, Pearl basin	—	EU490994	EU491014	EU490841	EU490938	EU490889

Appendix A. cont. For species represented by two sequences, specimen identifiers enclosed by parentheses.

Family Group	Terminal taxon	Catalogue Number	Locality	5' <i>rag1</i>	3' <i>rag1</i>	<i>rag2</i>	ND4+rRNA	Cyt <i>b</i>	COI
Aspredinidae	<i>Bunocephalus verrucosus</i>	CU 91989	South America, aquarium fish trade	EU490940, EU490958	EU490976	EU490996	—	EU490894	EU490846
Aspredinidae	<i>Hoplosternon xiphirostratum</i>	CU 82559	Venezuela, Portuguesa River, Orinoco basin	DQ492592	DQ492536	DQ492423	EU490798	EU490891	EU490843
Aspredinidae	<i>Micromyzon akamai</i>	ANSP 182777	Brazil, Amazon basin	DQ492644	DQ492537	DQ492424	EU625515	EU490892	EU490844
Aspredinidae	<i>Pterobunocephalus</i> sp.	ANSP 182774	Brazil, Amazon basin	DQ492621	DQ492487	DQ492374	EU625514	EU490893	EU490845
Auchenipteridae	<i>Ageneiosus ucayalensis</i>	INHS 52920	Peru, Napo basin	DQ492540	DQ492463	DQ492351	EU490800	EU490898	EU490849
Auchenipteridae	<i>Centromochlus heckelii</i>	ANSP 182773	Brazil, Amazon basin	DQ492562	DQ492465	DQ492353	EU490799	EU490896	—
Auchenipteridae	<i>Trachelyopteris galeatus</i>	INHS 49034	Guyana, Mahaita basin	DQ492634	DQ492464	DQ492352	—	EU490897	EU490848
Bagridae	<i>Bagrichthys macropus</i>	INHS 93680	Thailand, Mekong basin	DQ492554	DQ492456	DQ492344	EU490807	EU490905	EU490856
Bagridae	<i>Bagrus doanaki</i>	CU 90408	Tanzania, Luiche River basin	DQ492555	DQ492458	DQ492346	EU490808	EU490906	EU490857
Bagridae	<i>Batasio tigrinis</i>	INHS 93643	Thailand, Chao Phraya basin	DQ492556	DQ492460	DQ492348	EU490809	EU490907	EU490858
Bagridae	<i>Hemibagrus wyckoides</i>	INHS 93682	Thailand, Mekong basin	DQ492587	DQ492461	DQ492349	EU490813	EU490911	EU490862
Bagridae	<i>Heterobagrus bocourti</i>	INHS 93586	Thailand	DQ492589	DQ492462	DQ492350	EU490814	EU490912	EU490863
Bagridae	<i>Letocassis poecilopterus</i>	Private collection, H.H. Ng	Sumatra, Batang Hari basin	DQ492603	DQ492457	DQ492345	EU490818	EU490916	EU490867
Bagridae	<i>Olyra longicaudatus</i>	Private collection, H.H. Ng	India, Brahmaputra basin	—	DQ492459	DQ492347	EU490820	EU490918	EU490869
Bagridae	<i>Rita rita</i>	Private collection, H.H. Ng	India, Ganges basin	DQ492616	DQ492518	DQ492405	EU490824	EU490921	EU490872
Doradidae	<i>Acanthodoras cataphractus</i>	ANSP 179854	Guyana, Rupununi basin	DQ492538	DQ492466	DQ492354	EU490801	EU490895	EU490847
Horabagridae	<i>Horabagrus brachysoma</i>	INHS 93585	India,	DQ492593	DQ492522	DQ492409	EU490815	EU490913	EU490864
Horabagridae	<i>Pseudotropheus brachypterus</i>	Private collection, H.H. Ng	Sumatra, Batang Hari basin	DQ492624	DQ492455	DQ492343	EU490823	EU490920	EU490871
Ictaluridae	<i>Ictalurus punctatus</i>	ANSP 180368	USA, Pennsylvania	DQ492595	DQ492511	DQ492398	EU490816	EU490914	EU490865
Plotosidae	<i>Plotosus lineatus</i>	ANSP 182776	Pacific Ocean, Aquarium fish trade	DQ492626	DQ492531	DQ492418	EU490822	EU490919	EU490870
Sisoridae	<i>Bagarius yarrelli</i>	INHS 93673	Thailand, Mekong basin	DQ492552	DQ492446	DQ492334	EU503228	EU490904	EU490855
Sisoridae	<i>Erethistes</i> sp. (A)	INHS 94106	Asia, Aquarium fish trade	DQ492576	DQ492449	DQ492337	EU490810	EU490908	EU490859
Sisoridae	<i>Erethistes</i> sp. (B)	ANSP 182781	Asia, Aquarium fish trade	DQ492584	DQ492450	DQ492338	EU490812	EU490910	EU490861
Sisoridae	<i>Glyptothorax cf. trilineatus</i>	INHS 93545	Thailand	DQ492580	DQ492447	DQ492335	EU490811	EU490909	EU490860
Sisoridae	<i>Nangra virescens</i>	No voucher	Asia, Aquarium fish trade	DQ492642	DQ492448	DQ492336	EU490819	EU490917	EU490868

