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A new species of *Lepidocephalichthys* (Teleostei: Cobitidae) with distinctive sexual dimorphism and comments on relationships in southern lineages of Cobitidae

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Abstract

Lepidocephalichthys (Telostei:Cobitidae) is diagnosed as being unique among cobitids in having the 7–8th pectoral rays of mature males modified. Recently collected material from Thailand included a new species of *Lepidocephalichthys* in which mature males have a large (extending over ~75% of the fin-ray length) dorsally projecting and serrated flange and a ventrally projecting flange. The ventrally projecting structure is unique among cobitids. An expanded phylogenetic analysis of cobitids, including previously published sequences and new material including the new species, reinforces the monophyly of *Lepidocephalichthys*. Relationships within southern lineages of cobitids, and the unusual habitat of the new species are discussed.

Key words: Cypriniformes, loaches, phylogenetics, dichromatism, Thailand, Vietnam, Mun River, Mekong

Introduction

Species of *Lepidocephalichthys* (Cobitidae) are small, spined loaches with sexually dimorphic pectoral fins. They are widely distributed throughout South and Southeast Asia, including the islands of Java and Borneo. Recent systematic studies on *Lepidocephalichthys* have included a taxonomic revision of the genus (Havird & Page 2010) and an analysis of phylogenetic relationships within Cobitidae (Šlechtová *et al*. 2008). Šlechtová *et al*. (2008) examined relationships among cobitids using the mitochondrial cytochrome *b* gene (cyt *b*) and the nuclear recombination activation gene-1 (RAG-1). Both datasets supported a large monophyletic lineage referred to as the 'northern clade' and including species of *Cobitis*, *Iksookimia*, *Niwaella*, *Kichulchoia*, *Koreocobitis*, *Misgurnus*, *Paramisgurnus* and *Sabanejewia*. Most genera in this clade were not found to be monophyletic. Genera that fell outside the northern clade (*Acanthopsoides*, *Acantopsis*, *Canthophrys*, *Kottelatlimia*, *Lepidocephalichthys*, *Lepidocephalus*, *Neoeurirrhichthys* and *Pangio*) did not form a monophyletic group and were referred to as the 'southern lineages.' These genera were recovered as monophyletic groups based on mitochondrial (with the exception of *Acanthopsoides*) as well as nuclear DNA data. *Lepidocephalichthys* was found to be sister to *Pangio* in the RAG1 analysis, a relationship not recovered in earlier analyses of morphological data (Nalbant 1963, 1994; Sawada 1982).

Although several morphological characters distinguish genera in the southern lineages, sexually dimorphic traits are among the most useful (Table 1). In particular, mature males have modifications of the

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TABLE 1. Characteristics of the eight cobitid genera in the southern lineages. Numbers of specimens in parentheses. Lengths are mean ± standard deviation. NSP = numbers of species in the genus (following Šlechtová *et al.*, 2008), NSPE = numbers of species examined, PFSD = pectoral fin sexual dimorphism, TL = total length, PDL = predorsal length, HL = head length, SNL = snout length, BD = body depth, PL = pectoral-fin length; DRSL, PCTL, PLV, ANL, and CDL rays = numbers of branched rays in dorsal, pectoral, pelvic, anal, and caudal fins, respectively. Barbel length refers to all pairs of barbels compared across cobitid genera.

Character	*Acantopsis* (28)	*Acanthopsoides* (35)	*Kottelatlimia* (119)	*Lepidocephalus* (7)	*Canthophrys* (10)	*Pangio* (215)	*Lepidocephal-ichthys* (487)	*Neoeucirrhichthys* (1)
NSP/NSPE	~4/~5	3/6	2/3	2/2	1/1	22/~27	15/18	1/1
PFSD location	2nd pectoral ray	2nd pectoral ray	2nd pectoral ray	2nd pectoral ray	Medial rays	2nd pectoral ray	7th–8th pectoral rays	Medial rays
PFSD shape	Thickened ray, tubercles	Thickened ray, tubercles	Serrations on flange or thickened ray	Thickened ray	Thickened rays, covered with skin	Thickened ray	Variable: flange, thickening, or blade	Thickened rays, covered with skin, tubercles
Barbel length	Small	Small	Medium/ variable	Large	Small	Variable	Variable	None
Dorsal-fin origin	Anterior to pelvic-fin origin	Just anterior to pelvic-fin origin	Just anterior to pelvic-fin origin	Posterior to pelvic-fin origin	Posterior to pelvic-fin origin	Between anal- and pelvic-fin origins	At or near pelvic-fin origin	At pelvic-fin origin
TL/SL	118.6 ± 2.3	116.6 ± 2.9	122.3 ± 3.0	113.6 ± 1.1	117.9 ± 2.0	111.5 ± 2.3	120.8 ± 4.4	117.8
PDL/SL	50.2 ± 5.2	52.4 ± 2.0	52.5 ± 3.3	66.8 ± 2.6	55.5 ± 2.5	70.8 ± 2.9	53.9 ± 4.1	57.2
HL/SL	24.1 ± 1.5	19.3 ± 1.1	22.8 ± 1.8	18.6 ± 1.9	23.5 ± 0.8	14.1 ± 1.6	19.5 ± 1.6	19.9
SnL/SL	14.9 ± 1.8	7.8 ± 0.8	7.9 ± 1.1	4.7 ± 0.5	10.3 ± 1.1	4.5 ± 0.7	5.6 ± 0.8	6.2
BD/SL	11.0 ± 1.6	10.4 ± 1.2	14.7 ± 1.4	17.5 ± 1.2	15.1 ± 2.1	10.2 ± 2.1	17.2 ± 1.9	12.0
PL/SL	15.9 ± 1.4	12.9 ± 1.4	17.5 ± 2.4	20.3 ± 4.1	16.3 ±1.3	8.4 ± 2.0	16.3 ± 2.6	11.0
DRSL	> 7	7	6 or 7	> 7	8	5 or 6	6	7
PCTL	> 7	8	6 or 7	> 8	9	7–10	7	8
PLV	6	6	6	5–7	6	4–6	6	6
ANL	5	5	5	5	5	5	5	5
CDL	14	14	12–14	14	14	14	14	14
Scales on top of head	No	No	No	Yes	No	No	*L. kranos* and *L. irrorata* only	No
Scales on side of head	No	No	No	Yes	No	No	Usually embedded or absent	No
Lateral line	Complete	Incomplete	No/incomplete	Complete	Complete	None	None	None

pectoral-fin rays, forming a structure termed the lamina circularis, which varies among genera. *Lepidocephalichthys* is diagnosed as having the 7–8th pectoral-fin rays modified in mature males (Havird & Page 2010). In cobitids, variation exists in the location of the lamina circularis, the number of rays modified, and shape of the structure formed.

Here we describe a new species of *Lepidocephalichthys* from the Mekong River drainage with highly distinctive sexually dimorphic pectoral fins. We also present an expanded phylogeny of the southern lineages of cobitids to confirm the generic placement of the new species. A discussion of relationships and sexual dimorphism within cobitids is provided.

Methods

Lengths were measured to the nearest 0.1 mm using digital calipers. Most measurements and counts follow Hubbs and Lagler (1964), with modifications as described in Havird & Page (2010). Specimens were classified as adults if they had a standard length (SL) equal to or greater than the SL of the smallest specimen with modified pectoral fins (Table 2). Smaller specimens were classified as juveniles and were not included in morphometric analyses. Adults were interpreted as male if they had modified pectoral fins and as female if they lacked modifications. Since the sexes of most specimens could not be confirmed via dissection due to small sample sizes, some specimens classified as females may be immature males. Sexually dimorphic characteristics are those of adult males vs. those of large individuals without modified pectoral fins (most of which are likely females).

TABLE 2. Adult standard length (SL, mm) and relative pectoral-fin lengths (% SL) for cobitids with large sample sizes. Minimum adult SL is for the smallest specimen with a lamina circularis. *Acantopsis* spp. refers to pooled data for three described (*A. choirorhynchos*, *A. dialuzona*, and *A. octoactinotos*) and several undescribed species. See Havird and Page (2010) for data on previously described *Lepidocephalichthys*. P = p-value comparing male and female pectoral-fin lengths calculated with a Student's two-tailed, unpaired t-test assuming equal variance.

Species	Min	Adult SL Mean	Max	Male pectoral fin length	Female pectoral fin length	P
Acanthopsoides molobrion	32.0	45.9	62.5	14.2 (n = 11)	11.6 (n = 15)	< 0.001
Acantopsis spp.	39.0	98.6	153.4	16.6 (n = 14)	14.8 (n = 30)	0.001
Kottelatlimia pristes	23.6	31.1	42.9	18.9 (n = 49)	15.8 (n = 39)	< 0.001
Lepidocephalichthys zeppelini	14.1	19.4	25.8	23.3 (n = 37)	20.2 (n = 91)	< 0.001
Pangio cuneovirgata	27.1	32.9	38.9	8.8 (n = 14)	7.3 (n = 14)	< 0.001
Pangio doriae	59.8	70.5	91.2	5.2 (n = 7)	3.2 (n = 5)	0.002
Pangio kuhlii	38.6	50.2	67.2	9.5 (n = 13)	7.3 (n = 15)	< 0.001
Pangio malayana	36.7	40.7	47.1	8.9 (n = 13)	7.0 (n = 7)	< 0.001
Pangio mauraniformis	36.3	43.9	48.9	10.8 (n = 12)	7.2 (n = 7)	< 0.001
Pangio piperata	33.5	40.7	48.4	10.8 (n = 13)	7.6 (n = 15)	< 0.001
Pangio semicincta	42.8	50.8	62.7	9.5 (n = 7)	7.5 (n = 5)	0.015
Pangio shelfordii	39.6	48.4	57.6	10.7 (n = 11)	7.5 (n = 8)	< 0.001

Institutional abbreviations are listed at http://www.asih.org/codons.pdf. In total, 490 specimens of cobitids were examined, mostly within the southern lineages. Specimens examined in the recent review of *Lepidocephalichthys* (Havird & Page 2010) were used in this study but are not listed in Material Examined (unless novel GenBank numbers are given). Catalog numbers of specimens examined are followed by number of specimens and range in SL in parentheses. A tilde (~) before geographic coordinates indicates that they were estimated from general locality data. All statistics were calculated using Microsoft Excel 2003.

TABLE 3. New material included in phylogenetic analyses. Sequences from Šlechtová et al. (2008) were also analyzed, including outgroups. BO = Borneo, MY = Malaysia, TH = Thailand, and SU = Sumatra. Species marked with * indicate species not analyzed by Šlechtová et al. (2008), vial numbers (from Florida Museum of Natural History Genetic Resources Repository) with T indicate paratypes, vial numbers with § indicate holotypes.

Genus	Species	Vial #	Voucher	Origin (region, province, river)	Accession #	
					Cyt *b*	RAG-1
Acantopsis	*dialuzona**	2005-0882	UF 161621	SU, Lampung, Way Seputih	GQ174311	GQ174401
		2005-0883	UF 161621	SU, Lampung, Way Seputih	GQ174307	GQ174387
		2005-1006	UF 161717	SU, Lampung, Way Sekampung	GQ174308	GQ174390
		2005-1007	UF 161717	SU, Lampung, Way Sekampung	GQ174309	GQ174402
		2006-0666	UF 166890	SU, Selatan, Air Musi	GQ174310	GQ174388
		2008-0628	UF 173514	MY, Johor, Sungai Siam	GQ174316	–
		2008-0635	UF 173514	MY, Johor, Sungai Siam	GQ174318	GQ174403
		2008-0640	UF 173516	MY, Johor, Sungai Sayong	GQ174314	GQ174381
		2008-0641	UF 173516	MY, Johor, Sungai Sayong	GQ174317	GQ174386
		2008-0692	UF 173552	MY, Johor, Sungai Sedili Besar	GQ174315	GQ174382
		2008-0693	UF 173552	MY, Johor, Sungai Sedili Besar	GQ174304	GQ174389
		2008-0696	UF 173552	MY, Johor, Sungai Sedili Besar	GQ174305	GQ174391
		2008-0698	UF 173552	MY, Johor, Sungai Sedili Besar	GQ174306	GQ174412
	*sp.**	2008-0530	UF 172928	TH, Ubon Ratchathani, Mekong	GQ174319	GQ174407
Acanthopsoides	*molobrion**	2005-1016	UF 161609	SU, Lampung, Way Seputih	GQ174313	GQ174410
		2006-0570	UF 166898	SU, Lampung, Way Besai	GQ174325	GQ174409
		2008-0643	UF 173524	MY, Johor, Sungai Sayong	GQ174326	–
		2008-0645	UF 173524	MY, Johor, Sungai Sayong	GQ174327	GQ174414
		2008-0668	UF 173529	MY, Johor, Sungai Semberong	GQ174331	GQ174411
		2008-0695	UF 173553	MY, Johor, Sungai Sedili Besar	GQ174328	GQ174408
		2008-0697	UF 173553	MY, Johor, Sungai Sedili Besar	GQ174330	GQ174413
		2008-0699	UF 173553	MY, Johor, Sungai Sedili Besar	GQ174329	GQ174406
Kottelatlimia	*pristes*	–	ZRC uncat.	BO, Central Kalimantan	GQ174332	–
Lepidocephalichthys	*berdmorei*	2008-0620	UF 172931	TH, Aquarium fish, Ataran	GQ174338	GQ174396
		2008-0621	UF 172931	TH, Aquarium fish, Ataran	GQ174337	GQ174379
	hasselti	2007-1140	UF 170276	TH, Chanthaburi, Mekong	GQ174333	GQ174378

Continued next page

TABLE 3. (continued)

Genus	Species	Vial #	Voucher	Origin (region, province, river)	Accession #	
					Cyt *b*	RAG-1
		2005-0902	UF 161478	SU, Lampung, Way Seputih	–	GQ174392
		2005-0970	UF 161482	SU, Lampung, Way Seputih	–	GQ174393
		2008-0550	UF 171982	TH, Ubon Ratchathani, Mekong	GQ174334	GQ174400
		2008-0551	UF 171982	TH, Ubon Ratchathani, Mekong	GQ174336	GQ174394
		2008-0552	UF 171982	TH, Ubon Ratchathani, Mekong	GQ174335	GQ174395
	*kranos**	2007-1237†	UF 170286	TH, Ubon Ratchathani, Mekong	GQ174341	GQ174380
		2007-1238†	UF 170288	TH, Ubon Ratchathani, Mekong	GQ174339	–
		2007-1239†	UF 170288	TH, Ubon Ratchathani, Mekong	GQ174340	–
		2007-1241†	UF 170287	TH, Ubon Ratchathani, Mekong	GQ174343	–
		2008-0476§	UF 171980	TH, Ubon Ratchathani, Mekong	GQ174342	–
		2008-0477†	UF 173041	TH, Ubon Ratchathani, Mekong	GQ174344	–
	*zeppelini**	2008-0519†	UF 171981	TH, Ubon Ratchathani, Mekong	GQ174345	GQ174383
		2008-0520†	UF 171981	TH, Ubon Ratchathani, Mekong	GQ174347	GQ174399
		2008-0546†	UF 174130	TH, Ubon Ratchathani, Mekong	GQ174346	–
		2008-0547†	UF 174130	TH, Ubon Ratchathani, Mekong	GQ174349	–
		2008-0548†	UF 174130	TH, Ubon Ratchathani, Mekong	GQ174351	GQ174384
		2008-0549†	UF 174130	TH, Ubon Ratchathani, Mekong	GQ174348	GQ174385
		2008-0553†	UF 174130	TH, Ubon Ratchathani, Mekong	GQ174350	–
Pangio	*semicincta*	2005-0894	UF 161608	SU, Lampung, Way Seputih	GQ174320	–
		2008-0634	UF 173513	MY, Johor, Sungai Siam	GQ174312	GQ174404
	oblonga	2005-0994	UF 161607	SU, Lampung, Way Tulangbawang	GQ174321	–
		2006-0601	UF 166989	SU, Selatan, Air Musi	GQ174322	GQ174405
		2008-0869	UF 172938	TH, Aquarium fish, Salween	GQ174323	GQ174398
		2008-0870	UF 172938	TH, Aquarium fish, Salween	GQ174324	GQ174397

Because the sexually dimorphic pectoral fin of the new species is unique among cobitids, we performed a phylogenetic analysis with sequences from across Cobitidae to confirm that the new species grouped within *Lepidocephalichthys*. Recently collected cobitid tissues from Thailand, Sumatra, and Malaysia (Table 3) were analyzed along with published sequences (including outgroups) from Šlechtová *et al*. (2008). Whole genomic DNA was extracted from fin clips preserved in ethanol using a 5% Chelex solution and 3 µl of prteinase K with overnight digestion**.** An approximately 1140 bp region including the complete mitochondrial cyt *b* gene was amplified and sequenced using the primer pair Glu-L.Ca14337–14359 and Thr-H.Ca15568–15548 (Šlechtová *et al*. 2008). Approximately 910 bp of the RAG1 gene were amplified and sequenced using the primers RAG-1F and RAG-RV1 (Šlechtová *et al*. 2008). PCR cycling parameters were those used by Šlechtová *et al*. (2006) for cyt *b* and Šlechtová *et al*. (2007) for RAG1.

Bands were visualized with ethidium bromide staining on 1% agarose gels to verify that primers amplified fragments of the appropriate sizes. PCR products were sequenced at the Interdisciplinary Center for Biotechnology Research (ICBR), University of Florida, Gainesville. Chromatograms were viewed and consensus sequences were assembled using CodonCode Aligner. Final alignments were generated using Clustal X2 (Larkin *et al*. 2007) and corrected manually by eye.

A Bayesian phylogeny was generated using MrBayes, version 3.1.2 (Ronquist & Huelsenbeck 2003) with five million generations and 45,000 trees sampled after a 10% burn-in for two runs. Posterior probabilities were used as an indication of node support. The cyt *b* and RAG1 analyses were partitioned by codon position, and each position was subjected to Modeltest version 3.7 (Posada & Crandall 1998) to determine the best-fit model of sequence evolution using the Akaike Information Criterion. The GTR + I + G model was chosen for each cyt *b* position. For the RAG1 dataset, the GTR + I + G, HKY + I, and K81uf + G models were chosen for the first, second, and third positions, respectively.

A parsimony analysis was also performed using PAUP 4.0b10 (Swofford 2002) for the RAG1 and cyt *b* datasets. Heuristic searches with random addition and tree bisection and reconnection parameters were completed, and support values were generated based on 1000 bootstrap replicates. Tamura-Nei-corrected sequence divergence values were calculated using PAUP 4.0b10.

Results

Lepidocephalichthys zeppelini **Havird & Tangjitjaroen, new species**
(Fig. 1; Tables 2–5)

Holotype. UF 174131, 21.1 mm-SL male, Thailand, Ubon Ratchathani, Mun River (tributary of Mekong River), isolated pools in a rice field, Ubon Rajathanee University campus, 15°8’3.18”N, 104°55’27.78”E, 10 June 2008, L. M. Page, W. Tangjitjaroen, S. Udduang, and J. C. Havird.

Paratypes. CAS 219335, 8 males, 37 females, 17.0–25.8 mm SL, Thailand, Ubon Ratchathani market, ~15°9'23.73"N, ~105° 3'27.81"E, 11–13 Sept. 1990, T. R. Roberts. NIFI 3248, 1 male, 8 females, 15.5–23.1 mm SL, Thailand, Nong Khai, Beung Kan, Goot Ting marsh, ~18°13'34.15"N, ~103°39'0.33"E, 11 June 2003, C. Vidthayanon. NIFI 3249, 1 male, 8 females, 15.9–20.0 mm SL, Thailand, Nong Khai, Beung Kan, Goot Ting marsh, ~18°13'34.15"N, ~103°39'0.33"E, 23–27 March 1996, C. Vidthayanon. UF 171981, 3 juveniles, 11.3–12.7 mm SL, Thailand, Ubon Ratchathani, Mun River (tributary of Mekong River), rice field, 15°8’17.76”N, 104°55’30.54”E, 9 June 2008, L. M. Page, W. Tangjitjaroen, and J. C. Havird, GenBank GQ174345, GQ174347, GQ174383, GQ174399. UF 171983, 1 juvenile, 12.7 mm SL, Thailand, Amnat Charoen, Mekong drainage, small sandy stream, 15°54’13.56”N, 105°11’17.28”E, 10 June 2008, L. M. Page, W. Tangjitjaroen, and J. C. Havird. UF 174130, 10 males, 18 females, 4 juveniles, 12.1–22.8 mm SL, data as for holotype, GenBank GQ174346, GQ174348–51, GQ174384, 5. UF 174132, 1 female, 15.7 mm SL, Thailand, Ubon Ratchathani, Mun River (tributary of Mekong River), marsh near Ubon Rajathanee University campus, 15°10’45.84”N, 104°45’44.76”E, 10 June 2008, L. M. Page, W. Tangjitjaroen, and J. C. Havird. UMMZ 227583, 11 males, 22 females, 15.0–23.3 mm SL, Vietnam, Long Xuyen, Mekong drainage, rice paddy NW Long Xuyen, ~10°23'22.49"N, ~105°24'56.46"E, 22 July 1974, Rainboth, Smith, and Weidenbach. ZRC 51882, 3, 17.0–22.9 mm SL, data as for holotype.

Diagnosis. A species of *Lepidocephalichthys sensu* Havird & Page (2010). *Lepidocephalichthys zeppelini* is distinguished from other *Lepidocephalichthys* by having the 7–8th pectoral-fin rays of the mature male having a large (extending along > 75% of the length of the 7–8th pectoral rays) dorsally projecting, rounded rectangular flange with about 25 fine serrations and a smaller ventrally projecting, rounded flange (Fig. 1C, D); a forked caudal fin; small barbels (not reaching orbit); dark reticulations on caudal fin; and small size (to 25.8 mm SL).

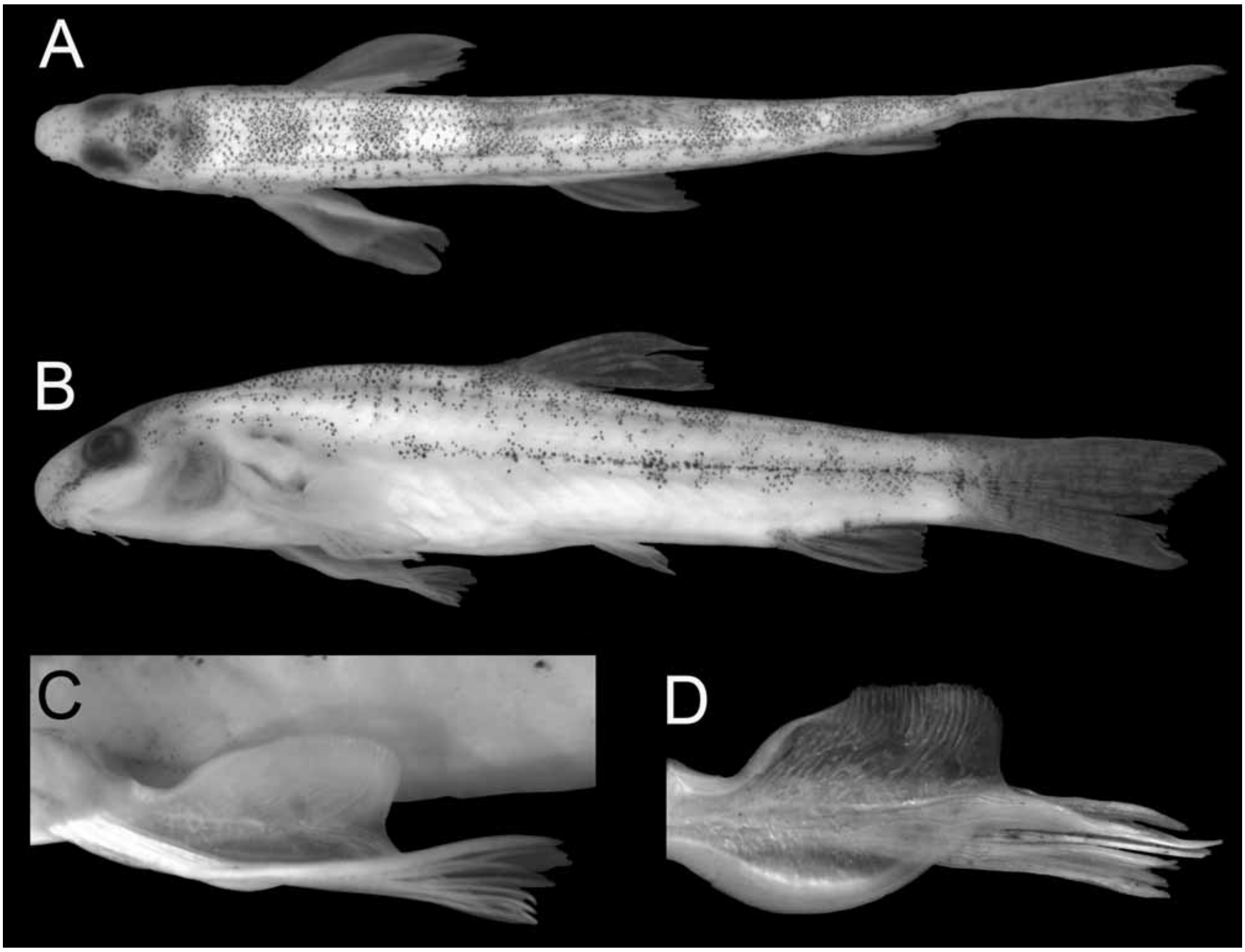

FIGURE 1. *Lepidocephalichthys zeppelini*, new species, UF 174131 (holotype), 21.1 mm-SL male, Thailand, Ubon Ratchathani, Mun River (tributary of Mekong River), isolated pools in a rice field, Ubon Rajathanee University campus: (A) dorsal view, (B) lateral view, (C) lamina circularis on pectoral fin, (D) medial view of pectoral fin removed from UF 174130 (22.2 mm-SL male paratype) showing lamina circularis.

Comparisons. *Lepidocephalichthys zeppelini* is distinguished from all other *Lepidocephalichthys* by having the 7–8th pectoral-fin rays forming a large, dorsally projecting, rounded rectangular flange and a smaller (although large compared to the dorsal projections of other species), ventrally projecting rounded flange (Fig. 1C, D). It is also distinguished from all other species of *Lepidocephalichthys* by its small adult body size (to 25.8 vs. 30.8 mm SL).

The new species is further distinguished from all other congeners except *L. manipurensis* Arunkumar, *L. furcatus* (de Beaufort), *L. goalparensis* Pillai & Yazdani, and *L. micropogon* (Blyth) by its forked (vs. rounded or truncated) caudal fin. It is distinguished from *L. micropogon*, *L. goalparensis*, and *L. manipurensis* by its darkly reticulated (vs. barred) caudal fin, and from *L. furcatus* by having fine serrations (vs. smooth edge) on the dorsal flange on the 7–8th pectoral-fin rays of males (Fig. 1C, D), barbels not reaching orbit (vs. barbels reaching orbit), fewer predorsal scales (about 40 vs. 50–60), and smaller size (to 25.8 vs. 30.8 mm SL).

Description. Morphometric data in Table 4; small adult size (averaging 19.4 mm SL); body depth increasing from snout to nape, then decreasing to caudal peduncle (Fig. 1B); dorsal fin with 2 unbranched, 6 branched rays, last branched ray split to base; anal fin with 2 unbranched, 5 branched rays, last branched ray split to base; pectoral fin with 1 unbranched, 7 branched rays; pelvic fin with 1 unbranched, 6 branched rays; 16 caudal rays (7 branched, 1 unbranched in each lobe); caudal fin forked; dorsal-fin origin anterior to pelvic-fin origin; in mature males 7–8th pectoral-fin rays with large (extending along > 75% of length of rays), dorsally projecting rounded rectangular flange with about 25 fine serrations and smaller, ventrally rounded flange (Fig. 1C, D); axial process in well-preserved specimens as small pocket of skin projecting from pectoral-fin base, not fused to rays; 30–46 predorsal scales (average about 40); no scales on top and side of head; anterior nostril on end of small outwardly projecting tube; suborbital bifid spine with anterior projection smaller than posterior; barbels: 2 rostral pairs, 1 maxillary pair at corner of mouth, medially split mandibular lobe forming 2 medially thickened mouth flaps; barbels small: first pair of rostral barbels not reaching anterior nostril, other pairs not reaching orbit; ventral mouth flaps usually without fringes.

Color in alcohol. *Lepidocephalichthys zeppelini* has pale yellow to white belly, background overlain with dark-brown marks on side, dorsum, head, and fins. Six–14 dark-brown blotches on side disconnected in females, connected by narrow stripe in males. Dark-brown chevron (<- shaped mark) at base of caudal fin points towards head, similar to that in *L. furcatus* (Kottelat & Lim 1992), but usually darker. Three to five predorsal and 3–6 postdorsal irregular dark blotches, chevrons, or bars on dorsum, with one at dorsal-fin base (Fig. 1A). Most specimens with small, inconspicuous dark spot on upper caudal-fin base spanning principal rays 4–7. Caudal, anal, and dorsal fins darkly reticulated. Dark stripe extends from snout, through eye, onto top of head, forming two dark spots on top of head where it terminates; otherwise, top of head with small dark-brown spots forming no pattern.

TABLE 4. Morphometric data for holotype and paratypes of *Lepidocephalichthys zeppelini*. Min = minimum, Max = maximum, SD = standard deviation.

	L. zeppelini (n = 128)				
Character	Holotype	Mean	Min	max	SD
Standard length (mm)	21.1	19.4	14.1	25.8	2.45
Percents standard length					
Total length	123.5	126.2	111.4	140.2	4.408
Predorsal length	47.8	50.8	45.9	57.2	2.20
Prepelvic length	51.5	54.5	42.7	63.7	2.96
Preanal length	77.2	80.8	73.6	94.2	3.57
Body depth	21.3	21.4	17.8	25.1	1.56
Body width	8.69	11.0	7.17	16.4	1.71
Pectoral-fin length (all)	–	21.1	13.1	28.4	2.89
Pectoral-fin length (male)	23.9	23.3	17.4	28.4	2.53
Pectoral-fin length (female)	–	20.2	13.1	26.6	2.50
Pelvic-fin length	16.4	16.7	5.34	22.5	2.26
Dorsal-fin height	22.5	22.0	6.37	29.1	3.23
Caudal penduncle depth	10.6	10.8	7.75	14.5	0.99
Head length	20.4	23.7	19.0	29.9	1.80
Percents head length					
Snout length	22.6	26.2	16.3	35.5	3.64
Orbit diameter	25.2	24.9	17.3	32.2	3.18
Anterior rostral-barbel length	14.5	11.3	5.41	19.6	3.20
Maxillary-barbel length	39.2	23.5	11.7	39.2	4.70
Interorbital width	23.3	18.5	10.9	31.1	3.75

Sexual dimorphism. In addition to the modified pectoral fins and sexual dichromatism described above, *L. zeppelini* has other sexual dimorphisms characteristic of *Lepidocephalichthys*. Males have significantly (P < 0.001, Student's two-tailed, unpaired t-test assuming equal variance) larger pectoral fins (Table 2) and pelvic fins (Table 5) than females. Males are also significantly (P < 0.001, Student's two-tailed, unpaired t-test assuming equal variance) smaller than females: males average 18.1 mm SL and reach 21.7 mm SL whereas females average 19.9 mm SL and reach 25.8 mm SL.

Relationships. Clades containing seven individuals of *L. zeppelini* for cyt *b* (Fig. 2A), and four individuals for RAG1 (Fig. 2B), were resolved as a distinct lineage within *Lepidocephalichthys* with 100% support in all analyses. In the cyt *b* analysis (Fig. 2A), *L. zeppelini* grouped most closely with *L. thermalis* (Valenciennes); RAG1 sequences suggested a closer relationship between *L. zeppelini* and *L. kranos* Havird & Page (Fig. 2B). The average intraspecific divergence for *L. zeppelini* was 0.1% for cyt *b* and 0.2% for RAG1. The average interspecific divergence between *L. zeppelini* and *L. thermalis* was 22.0% for cyt *b*, and between *L. zeppelini* and *L. kranos* was 8.9% for RAG1.

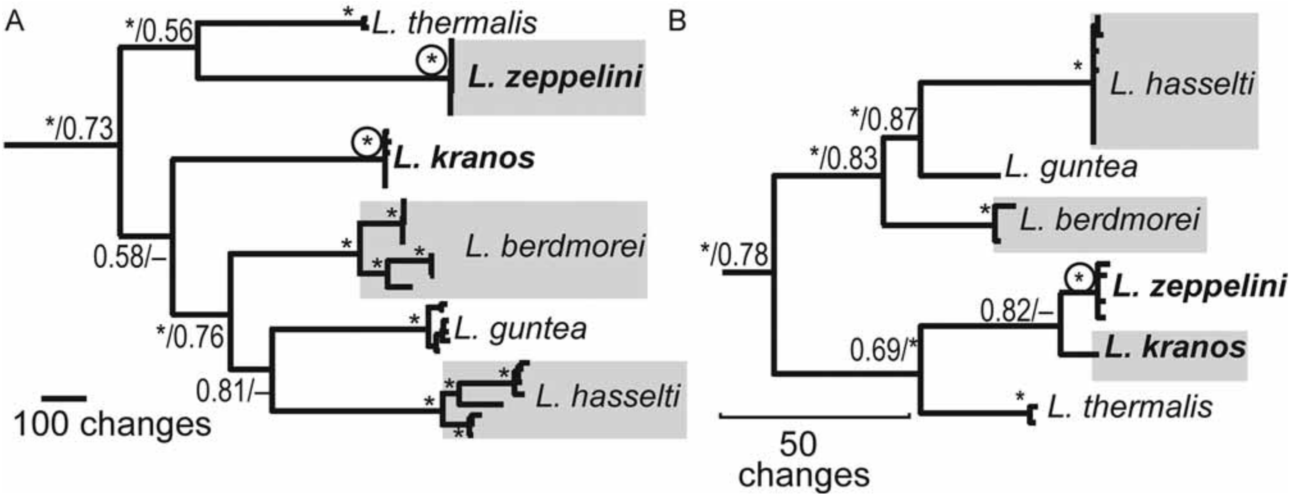

FIGURE 2. Phylogeny of species of *Lepidocephalichthys* based on Bayesian analysis of cyt *b* (A) and RAG1 (B). Clades of species are alternatively shaded. Since the parsimony analysis gave a very similar topology, support values for both analyses are presented at each node (numbers on left are posterior probabilities and numbers on right are bootstrap values). Asterisks indicate Bayesian support values of 0.95 or greater and parsimony support values of 0.90 or greater; single asterisks meet both criteria. Dashes indicate relationships were not supported in the parsimony analysis. *Lepidocephalichthys zeppelini*, n. sp. and *L. kranos*, recently described by Havird & Page (2010), are bolded and their support values are circled.

TABLE 5. Relative pelvic-fin lengths of adults of eight cobitid species with large sample sizes. Lengths are mean ± standard deviation. P = p-value comparing male and female pelvic-fin lengths calculated with a Student's two-tailed, unpaired t-test assuming equal variance.

	Pelvic Fin Length (% SL)		
Species	Male	Female	P
Acanthopsoides molobrion	12.1 ± 0.7 (n = 20)	11.1 ± 0.7 (n = 19)	< 0.001
Kottelatlimia pristes	15.6 ± 1.6 (n = 28)	14.6 ± 1.1 (n = 33)	0.008
Lepidocephalichthys berdmorei	15.1 ± 0.6 (n = 20)	13.2 ± 1.5 (n = 22)	0.001
L. guntea	16.0 ± 1.1 (n = 20)	14.0 ± 1.5 (n = 26)	< 0.001
L. hasselti	16.5 ± 1.5 (n = 32)	14.9 ± 1.2 (n = 29)	< 0.001
L. kranos	17.8 ± 2.8 (n = 9)	16.2 ± 1.9 (n = 20)	0.145
L. zeppelini	17.6 ± 2.1 (n = 25)	15.6 ± 2.2 (n = 27)	0.002
Pangio semicincta	8.0 ± 0.5 (n =9)	6.0 ± 0.7 (n = 14)	< 0.001
Eight species combined	15.9 ± 2.8 (n = 130)	14.0 ± 3.0 (n = 165)	< 0.001

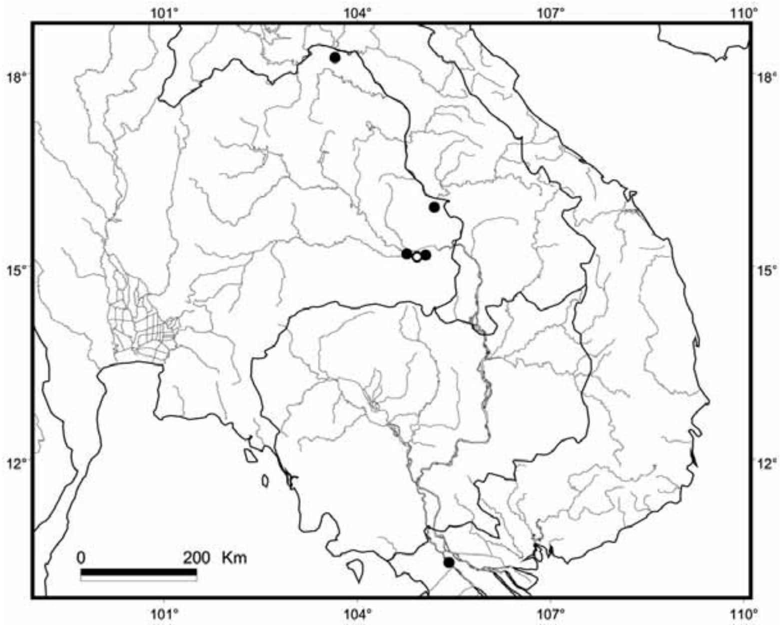

FIGURE 3. Distribution of *Lepidocephalichthys zeppelini*. Black dots represent localities for specimens examined; circle represents type locality.

FIGURE 4. Type locality of *Lepidocephalichthys zeppelini*. Individuals were in small ephemeral pools in otherwise dry agricultural fields. Most other specimens are from similar habitats.

Distribution and habitat. *Lepidocephalichthys zeppelini* is known from the Mekong drainage in Thailand and Vietnam (Fig. 3) where it has been collected with *L. hasselti* and *L. kranos*. It has been found mainly in agricultural fields in small shallow pools (Fig. 4). One juvenile was collected in a small sandy stream.

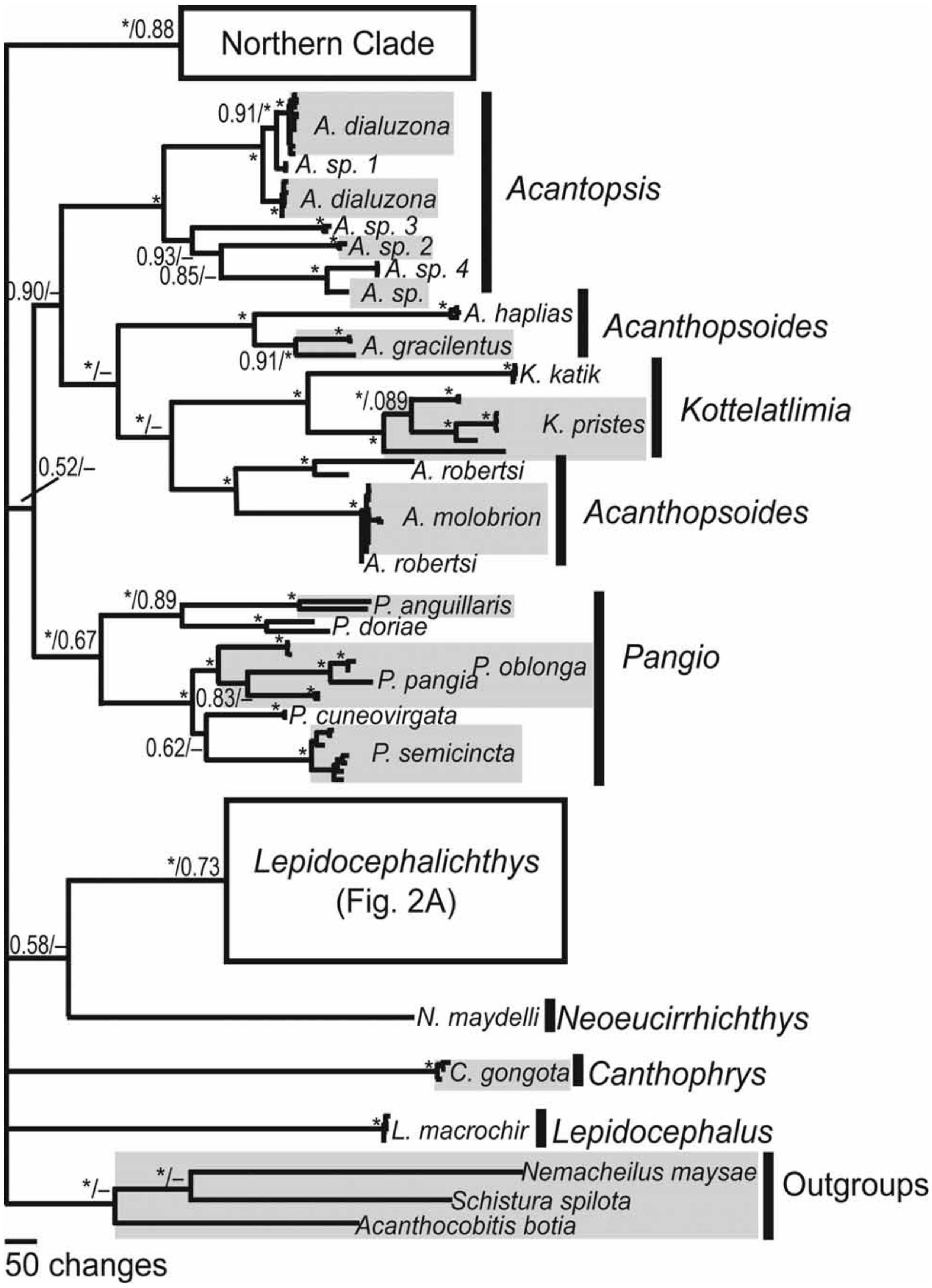

FIGURE 5. Phylogeny of cobitids based on Bayesian analysis of cyt *b*. Shading, support values, asterisks, and dashes as in Figure 2.

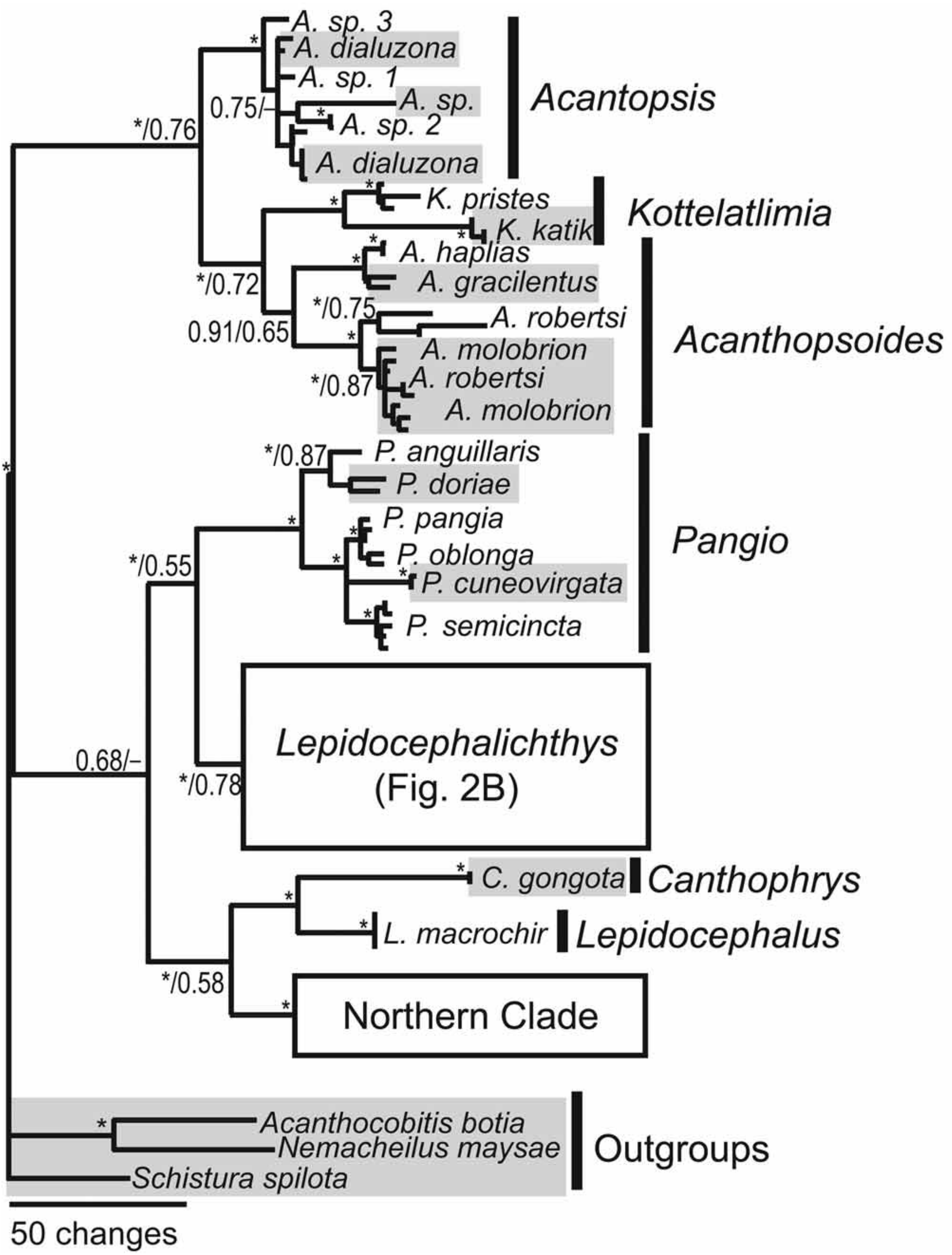

FIGURE 6. Phylogeny of cobitids based on Bayesian analysis of RAG1. Shading, support values, asterisks, and dashes as in Figure 2.

Previous collectors of *L. zeppelini* described its habitat as marshes or rice paddies. While collecting in Thailand in June at the beginning of the wet season, we originally targeted small streams, marshes, and flooded rice fields with little success, yielding only a few juveniles. However, when small ephemeral pools in otherwise dry agricultural fields were targeted, many adults were collected. At the type locality (Fig. 4), pools less than 9 m^2 contained the majority of *L. zeppelini* collected. *Lepidocephalichthys hasselti* was also abundant in these pools, along with other common Southeast Asian freshwater fishes including species of *Anabas, Puntius, Rasbora, Channa*, and *Hampala*.

Etymology. The species name *zeppelini* is a reference to the 1968–1980 band Led Zeppelin. Use of the Gibson EDS-1275 double-neck guitar by Jimmy Page reminded us of the diagnostic double lamina circularis of this species. It is Latinized as a noun in the genitive singular.

Discussion

In addition to supporting individuals of *L. zeppelini* as a distinct monophyletic clade within *Lepidocephalichthys*, our expanded phylogenetic analysis of cobitids—50 new sequences and five additional species from the southern lineages (Table 3) were added to the phylogenetic analysis of Šlechtová *et al*. (2008)—presents an updated analysis of cobitid relationships. Analyses of cyt *b* and RAG1 sequences included 1150 and 894 bps, respectively. Both gene trees had similar topologies and support values, and both strongly supported the northern clade and other relationships found in Šlechtová *et al*. (2008).

As in Šlechtová *et al*. (2008), the phylogeny based on cyt *b* (Fig. 5) gave poor resolution of intergeneric relationships among the southern lineages, but revealed within-species (geographical) structure in several species with large samples. For example, *Lepidocephalichthys hasselti* (Valenciennes) from east Thailand formed a clade distinct from that for samples from central Thailand. The RAG1 phylogeny (Fig. 6) gave strongly supported relationships among genera but failed to provide much intraspecific geographic resolution.

With new sequences from *Acanthopsoides molobrion* Siebert included, the specimen of *Acanthopsoides robertsi* Siebert from peninsular Malaysia (GenBank EF508482) included in the analysis by Šlechtová *et al*. is recognized as a likely misidentification (*A. robertsi* is not known from peninsular Malaysia). Similarly, including new sequences from *Pangio oblonga* (Valenciennes) resulted in the sample of *Pangio pangia* (Hamilton) (GenBank EF508583) from the analysis by Šlechtová *et al*. falling within the *P. oblonga* clade. This also may be due to misidentification, or it may indicate a lack of reciprocal monophyly for the two taxa.

Although discussions of sexual dimorphism in Cobitidae are often limited to modifications of the pectoral fins in males (Kim *et al*. 1997; Chen & Chen 2007; Kottelat & Tan 2008), other forms of dimorphism are common in cobitids. As reported for other *Lepidocephalichthys* (Havird & Page 2010), *L. zeppelini* has dark spots on the side of the body in the female and a narrow dark stripe in the adult male (Fig. 7G–I). Although most pronounced in *L. guntea* (Hamilton) (Fig. 7D–F), this dichromatism was present in several cobitids examined. *Canthophrys gongota* (Hamilton), *Cobitis choii* (Kim & Son), *Cobitis sinensis* Sauvage & Dabry de Thiersant (Fig. 7A–C), and *Acantopsis* sp. have conspicuous spots on the female and a stripe on the male. Males with the largest structure (lamina circularis) on their pectoral fins also have the most conspicuous stripes, suggesting that circulating levels of sex hormones control the expression of both traits. This hypothesis is supported by a study showing species of *Misgurnus* altering this structure in relation to sex hormone treatments (Kim *et al*. 1997). Small males sometimes have a large lamina circularis and a conspicuous stripe, and expression of the dimorphic traits does not seem to be strongly correlated with body size. In addition to the lamina circularis and distinguishing color patterns, males also have significantly longer pectoral fins (Table 2). Most males also have longer pelvic fins (Table 5) than do females.

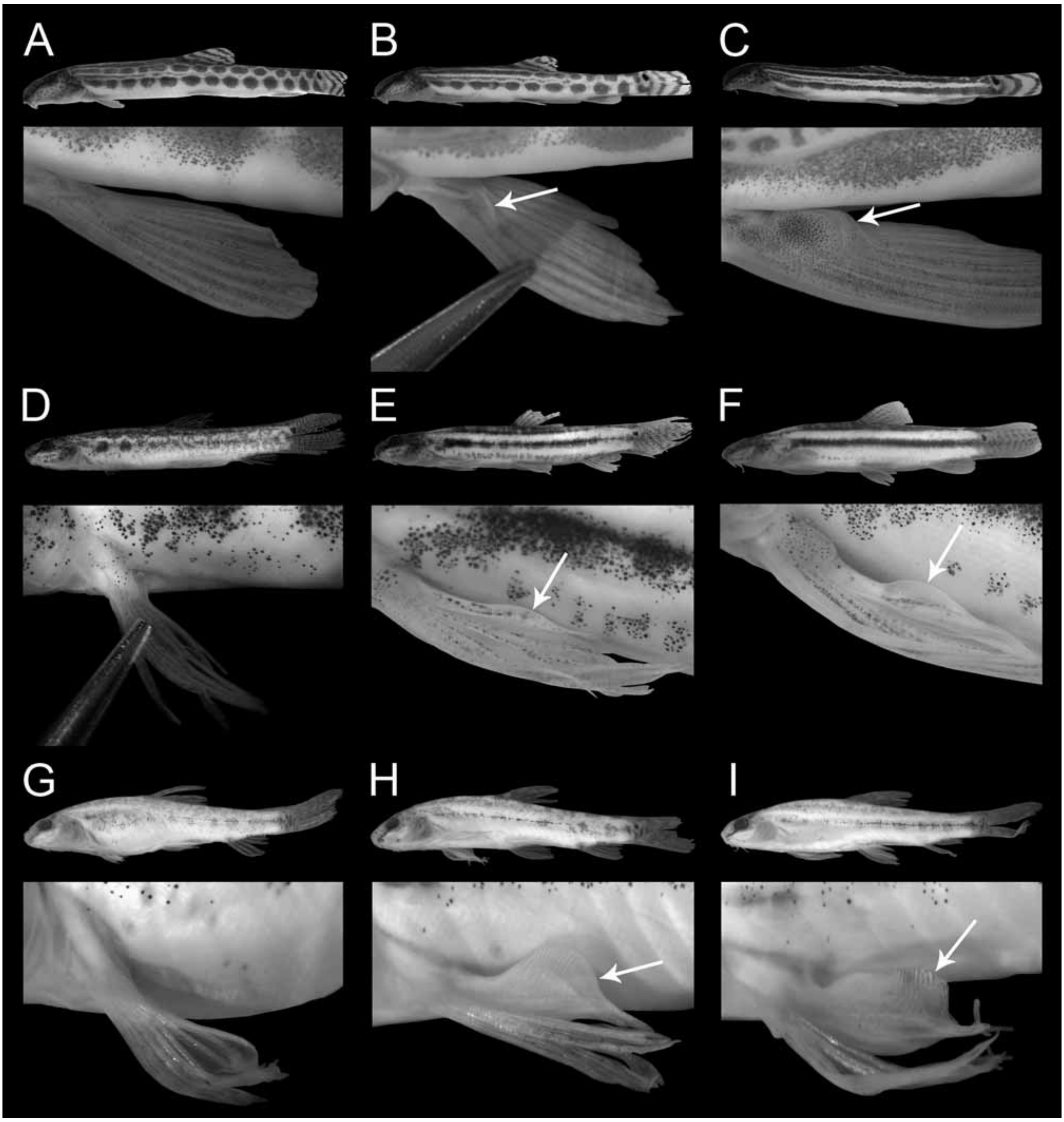

FIGURE 7. Relationship between color pattern (especially stripe intensity) and development of lamina circularis in three species of cobitids: (A–C) *Cobitis sinensis*, UMMZ 240028, (A) 66.0 mm-SL female, (B) 71.4 mm-SL male, (C) 55.0 mm-SL male; (D–F) *Lepidocephalichthys guntea*, KU 29353, (D) 46.7 mm-SL female, (E) 45.9 mm-SL male, (F) 53.4 mm-SL male; (G–I) *L. zeppelini*, UF 174130, (G) 21.9 mm-SL female, (H) 16.2 mm-SL male, (I) 21.9 mm-SL male.

The relatively dry agricultural fields where most specimens of *L. zeppelini* were found represent an interesting habitat for loaches in Southeast Asia. Only juveniles were collected from larger ponds, small streams, and marshes, suggesting either that juveniles were easier to catch or that adults were absent from these habitats. Adults may only be found in the pools of otherwise dry agricultural fields—which likely vanish completely during the dry season—begging an explanation for where the fishes go during the dry season. Some may survive by burrowing into the substrate (M. Kottelat, pers. comm.); others may migrate to more suitable habitat during the dry season. Long-term studies monitoring *L. zeppelini* and other species in these fields could determine seasonal changes in habitat use or behavior.

Material examined

Acanthopsoides hapalias Siebert: Cambodia–UMMZ 234697 (26, 32.6–35.0).

Acanthopsoides molobrion Siebert: Borneo–ZRC 38854 (1, 26.9). ZRC 39980 (2, 42.9–50.6). Malaysia–UF 173515 (12, 32.5–38.9). UF 173524 (17, 26.8–45.6), GenBank GQ174326, CQ174328, GQ174414. UF 173529 (2, 33.7–42.9), GenBank GQ174331, GQ174411. UF 173552 (27, 34.0–46.0). UF 173553 (27, 32.5–44.4), GenBank GQ174328–30, GQ174406, GQ174408, GQ174413. ZRC 1471 (2, 40–46.9). ZRC 9309 (1, 54.9). ZRC 11107 (1, 39.8). ZRC 13764 (1, 36.6). ZRC 25577 (2, 32.0–45.7). ZRC 27566 (2, 33.7–38.7). ZRC 28288 (1, 48.1). ZRC 29409 (2, 41.8–45.7). ZRC 29412 (2, 51.6–55.8). ZRC 39550 (4, 42.8–62.5). ZRC 40218 (2, 35.9–49.7). ZRC 42793 (1, 48.8). ZRC 42899 (1, 58.4). ZRC 42950 (1, 46.7). ZRC 44155 (1, 53.7). Sumatra–UF 161609 (3, 38.2–43.8), GenBank GQ174313, GQ174410. UF 161622 (21, 31.1–35.5). UF 166885 (6, 45.0–51.3). UF 166898 (2, 28.2–33.8), GenBank GQ174325, GQ174409.

Acanthopsoides robertsi Siebert: Borneo–ZRC 37872 (1, 42.0). ZRC 40054 (4, 29.4–36.4). Sumatra–UF 166897 (1, 41.9).

Acantopsis choirorhynchos (Bleeker): Malaysia–ZRC 1449 (1, 113.0). ZRC 1461 (1, 75.1). ZRC 1463 (2, 115.1–135.4). ZRC 1490 (2, 104.4–111.9). ZRC 5898 (1, 93.4). ZRC 5901 (1, 98.6). ZRC 5915 (1, 107.6). Myanmar: USNM 37844 (12, 36.3–90.4).

Acantopsis dialuzona van Hasselt: Malaysia–UF 173514 (2, 52.0–102.8), GenBank GQ174316, GQ174318, GQ174403. UF 173516 (4, 84.8–101.2), GenBank GQ174314, GQ174317, GQ174381, GQ174386. UF 173552 (8, 63.8–125.8), GenBank GQ174304–6, GQ174315, GQ174382, GQ174389, GQ174391, GQ174412. ZRC 1491 (1, 113.4). ZRC 7412 (1, 153.4). ZRC 11775 (1, 63.8). ZRC 21488 (2, 48.6–118.1). ZRC 27576 (2, 61.6–62.9). ZRC 44190 (1, 49.8). Sumatra–UF 161621 (5, 55.5–60.2), GenBank GQ174307, GQ174311, GQ174387, GQ174401. UF 161717 (9, 47.3–60.7), GenBank GQ174308–9, GQ174390, GQ174402. UF 166890 (11, 48.8–58.9), GenBank GQ174310, GQ174388. ZRC 41665 (1, 43.1). ZRC 42566 (1, 77.0). Thailand–ZRC 39328 (2, 82.1–112.4).

Acantopsis octoactinotos Siebert: Borneo–ZRC 37613 (1, 30.3). ZRC 37685 (1, 30.6). ZRC 40415 (2, 39.0–45.8).

Acantopsis spp. (several undescribed species): Aquarium–ZRC 50979 (4, 95.9–127.0). Malaysia–ZRC 1489 (2, 81.2–85.3). Myanmar–ZRC 43458 (1, 76.5). ZRC 43519 (1, 123.6). Thailand–UF 169951 (5, 59.6–122.8). UF 169952 (6, 81.1–95.1). UF 169953 (3, 70.9–75.4). UF 169954 (14, 65.1–129.2). UF 170195 (1, 54.1). UF 172925 (1, 116.8). UF 172928 (1, 92.4), GenBank GQ174319, GQ1744407. ZRC 40898 (1, 73.6). Sumatra–ZRC 38630 (2, 50.4–51.2).

Canthophrys gongota (Hamilton): Bangladesh–UF 172552 (2, 79.5–82.4). India–ZRC 38897 (4, 79.1–97.9). Nepal–KU 28604 (2, 65.3–72.1). KU 29113 (4, 49.2–115.4). KU 29361 (1, 96.4). KU 29561 (2, 82.8–84.2).

Cobitis bilineata Canestrini: Italy–UF 81156 (4, 42.9–58.0). UF 110731 (5, 45.6–65.8).

Cobitis calderoni Bacescu: Spain–UMMZ 212518 (10, 32.3–44.6).

Cobitis choii Kim & Son: Mongolia–ANSP 185225 (35, 21.0–55.0). ANSP 185388 (1, 42.9).

Cobitis elongata Heckel & Kner: Romania–UMMZ 185061 (2, 93.2–134.7). UMMZ 185062 (3, 108.5–199.5).

Cobitis lutheri Rendahl: South Korea–UMMZ 240027 (6, 51.3–71.7).

Cobitis macrostigma Dabry de Thiersant: China–FMNH 14807 (2, 75.3–92.9).

Iksookimia longicorpa (Kim, Choi & Nalbant): South Korea–UMMZ 240026 (6, 88.7–111.9).

Iksookimia koreensis (Kim): South Korea–FMNH 95966 (3, 80.8–103.8). UMMZ 240025 (6, 61.1–78.2).

Iksookimia pumila (Kim & Lee): South Korea–UMMZ 240024 (6, 48.6–67.4).

Kottelatlimia katik (Kottelat & Lim): Malaysia–ZRC 9344 (holotype) (1, 12.9). ZRC 9345 (paratypes) (3, 11.2–12.5).

Kottelatlimia pristes (Roberts): Borneo– CAS 49352 (paratype) (1, 36.0). MCZ 56064 (paratypes) (2, 30.5–31.1). USNM 230265 (paratype) (1, 31.4). BMNH 2000.10.18.70 (1, 25.6). BMNH 2000.10.18.95 (1, 22.0). CAS 219322 (2, 23.2–30.7). ZRC 22836 (2, 32.2–36.0). ZRC 22855 (1, 35.8). ZRC 27850 (2, 26.1–36.3). ZRC 29444 (3, 25.4–25.9). ZRC 29451 (2, 21.5–25.0). ZRC 37888 (1, 31.8). ZRC 38788 (3, 27.3–32.0). ZRC 39512 (3, 27.9–35.3). ZRC 39856 (3, 28.1–30.0). ZRC 39870 (4, 29.4–33.0). ZRC 39893 (3, 28.7–31.0). ZRC uncataloged (1, 28.0), GenBank GQ174332. Malaysia–ZRC 14916 (1, 35.0). ZRC 14921 (3, 27.4–30.2). ZRC 14926 (3, 24.4–25.7). ZRC 15141 (2, 25.1–28.2). ZRC 17844 (2, 32.9–36.8). ZRC 20763 (2, 28.1–37.1). ZRC 20836 (3, 29.1–35.1). ZRC 27723 (2, 27.7–35.3). ZRC 38281 (3, 30.7–36.9). ZRC 38437 (2, 21.5–22.6). ZRC 43658 (2, 21.5–27.9). Sumatra–MZB 15302 (26, 27.1–31.5). MZB 15303 (21, 27.9–36.5). UF 166980 (22, 29.7–35.6). UF 166981 (28, 23.6–31.2). UF 166984 (2, 29.2–34.5). ZRC 38514 (3, 30.2–34.6). ZRC 38522 (3, 26.7–33.4). ZRC 38567 (1, 40.8). ZRC 38585 (2, 29.3–30.0). ZRC 38600 (2, 23.4–32.5). ZRC 39084 (3, 25.3–33.5). ZRC 39153 (5, 30.3–31.4). ZRC 39177 (2, 33.9–34.3). ZRC 42259 (3, 30.0–40.0). ZRC 42318 (3, 36.6–39.0). ZRC 42400 (3, 28.1–38.4). ZRC 42437 (2, 20.7–29.7). ZRC 43029 (3, 30.9–42.9). ZRC 43089 (4, 31.1–40.1). ZRC 43128 (2, 24.6–31.0). ZRC 43140 (3, 28.4–35.1).

Lepdiocephalichthys berdmorei (Blyth): Thailand–UF 172831 (5, 56.3–74.1), GenBank GQ174337–8, GQ174379, GQ174396.

Lepdiocephalichthys hasselti (Valenciennes): Thailand–UF 170276 (1, 29.2), GenBank GQ174333, GQ174378. UF 171982 (51, 17.4–40.7), GenBank GQ174334–6, GQ174394–5, GQ174400. Sumatra–UF 161478 (1, 32.0), GenBank GQ174392. UF 161482 (2, 26.0–31.0), GenBank GQ174393.

Lepdiocephalichthys kranos Havird & Page: Thailand–UF 171980 (holotype) (1, 33.1), GenBank GQ174342. UF 170286 (paratypes) (2, 26.6–33.6), GenBank GQ174341, GQ174380. UF 170287 (paratypes) (4, 31.2–37.4), GenBank GQ174343. UF 170288 (paratypes) (10, 18.2–35.9), GenBank GQ174339–40. UF 173041 (paratypes) (1, 32.6), GenBank GQ174344.

Lepidocephalus macrochir (Bleeker): Sumatra–BMNH 1866.5.2.55 (syntype) (1, 77.7). Borneo–BMNH 2001.1.15.8066–8070 (4, 63.0–69.3). BMNH 2001.1.5.8071–8075 (1, 55.9).

Lepidocephalus spectrum Roberts: Borneo–USNM 230267 (paratype) (1, 50.3).

Misgurnus anguillicaudatus (Cantor): Florida–UF 143225 (1, 64.5). UF 148188 (10, 37.9–55.0). UF 163719 (4, 65.9–82.9).

Misgurnus fossilis (Linnaeus): Poland–UMMZ 185341 (8, 50.5–63.1).

Misgurnus mizolepis Günther: Taiwan–UMMZ 194439 (1, 71.0).

Misgurnus sp.: China–USNM 89204 (1, 94.0).

Neoeucirrhichthys maydelli Banarescu & Nalbant: Nepal–KU 29366 (1, 29.2).

Pangio agma (Burridge): Borneo–ZRC 8408 (1, 43.3). ZRC 31934 (2, 53.0–57.8). ZRC 40273 (2, 43.0–44.3). ZRC 42720 (2, 40.7–44.6).

Pangio alcoides Kottelat & Lim: Malaysia–ZRC 41923 (1, 39.0). ZRC 40200 (3, 37.7–46.4).

Pangio alternans Kottelat & Lim: Borneo–ZRC 35037 (2, 31.0–31.8).

Pangio anguillaris (Vaillant): Laos–UMMZ 241968 (7, 50.1–62.5). Malaysia–ZRC 34884 (2, 64.1–65.6). Thailand–ZRC 35647 (2, 42.4–44.3). Sumatra–ZRC 38629 (65.2–65.4).

Pangio cuneovirgata (Raut): Malaysia–ZRC 2060 (2, 33.2–36.5). ZRC 8414 (1, 28.6). ZRC 18461 (1, 37.2). ZRC 28178 (2, 31.7–34.6). ZRC 39553 (1, 36.9). ZRC 40179 (4, 27.1–38.9). ZRC 42774 (1, 33.2). ZRC 42795 (1, 31.2). ZRC 42820 (1, 32.4). ZRC 42945 (2, 33.0–33.2). ZRC 44189 (2, 32.5–35.1). Sumatra–ZRC 385642 (4, 27.9–33.6). ZRC 42299 (2, 29.6–31.5). Thailand–ZRC 42094 (4, 30.3–33.4).

Pangio doriae (Perugia): Malaysia–FMNH 62013 (1, 72.2). ZRC 1487 (2, 67.4–70.4). ZRC 14293 (1, 61.4). ZRC 42821 (2, 62.2–71.9). ZRC 42900 (2, 59.8–68.6). ZRC 42949 (1, 63.3). Sumatra–ZRC 41667 (4, 64.6–91.2).

Pangio filinaris Kottelat & Lim: Malaysia–ZRC 38742 (2, 33.3–35.7). ZRC 41872 (4, 34.4–49.0).

Pangio incognito Kottelat & Lim: Borneo–ZRC 39372 (1, 21.0).

Pangio kuhlii (Valenciennes): Borneo–ZRC 39431 (3, 42.0–56.0). Malaysia–ZRC 27946 (4, 43.4–54.3). ZRC 28029 (3, 38.6–51.3). ZRC 28217 (2, 57.1–61.9). ZRC 39552 (1, 67.2). ZRC 40199 (2, 35.3–42.9). ZRC 40222 (2, 47.2–50.0). ZRC 42772 (2, 47.8–50.9). ZRC 42792 (2, 40.5–43.4). ZRC 42817 (1, 63.1). ZRC

42931 (1, 57.0). ZRC 42944 (1, 50.5). Sumatra–UF 166987 (6, 29.7–43.9). ZRC 38568 (2, 50.3–51.5). ZRC 42038 (1, 46.4). ZRC 42422 (2, 43.2–46.7).

Pangio malayana (Tweedie): Malaysia–UMMZ 238933 (3, 34.3–41.9). ZRC 17744 (1, 45.7). ZRC 28053 (1, 34.7). ZRC 28177 (1, 32.4). ZRC 34899 (2, 45.5–47.1). ZRC 35033 (1, 37.5). ZRC 38236 (1, 40.0). ZRC 42775 (2, 37.0–37.9). ZRC 42796 (2, 36.7–38.5). ZRC 42823 (4, 35.6–41.6). ZRC 42924 (2, 43.1–46.3). ZRC 42946 (2, 39.1–39.7). ZRC 42961 (2, 40.1–43.0). ZRC 44202 (2, 37.7–41.3).

Pangio mariarum: Borneo–ZRC 37644 (2, 31.0–33.9).

Pangio muraeniformis: Malaysia–FMNH 68663 (7, 33.7–35.7). ZRC 44200 (1, 40.8). Singapore–ZRC 1186 (4, 36.3–48.9). Sumatra–ZRC 30799 (2, 40.8–47.7). ZRC 30941 (2, 34.2–35.4). ZRC 32914 (2, 36.4–48.7). ZRC 33040 (2, 46.5–48.1). ZRC 33389 (2, 40.2–43.4). ZRC 33622 (1, 46.4). ZRC 34296 (2, 39.7–46.8). ZRC 42455 (3, 40.5–45.6).

Pangio myersi: Thailand–UMMZ 209439 (6, 54.6–64.8). ZRC 35807 (1, 38.7). ZRC 47141 (2, 64.8–68.1).

Pangio oblonga: Java–ZRC 29150 (2, 54.8–56.1). Malaysia–ZRC 14322 (1, 36.6). ZRC 41038 (1, 45.3). Thailand–UF 172938 (3, 37.3–39.3), GenBank GQ174323–4, GQ174397–8. ZRC 41972 (1, 48.6). Sumatra–UF 161607 (2, 41.3–43.5), GenBank GQ174321. UF 166989 (4, 45.2–47.6), GenBank GQ174322, GQ174405.

Pangio pangia: Malaysia–ZRC 496 (1, 41.0). ZRC 497 (2, 37.1–41.4). Myanmar–ZRC 43504 (2, 34.3–35.7).

Pangio piperata: Malaysia–ZRC 34566 (1, 33.7). ZRC 38234 (2, 42.6–48.4). ZRC 38744 (4, 40.0–45.4). ZRC 39554 (2, 33.5–38.9). ZRC 40221 (2, 40.3–47.9). ZRC 41871 (1, 44.0). ZRC 41934 (2, 43.9–46.5). ZRC 42699 (2, 38.3–38.8). ZRC 42770 (2, 42.8–43.1). ZRC 42787 (2, 35.9–37.0). ZRC 42824 (2, 38.4–38.6). ZRC 42864 (2, 43.7–46.7). ZRC 42922 (2, 34.3–35.7). ZRC 42948 (2, 33.7–39.8).

Pangio pulla: Borneo–ZRC 35022 (1, 59.7).

Pangio sandakanensis: Borneo–FMNH 44800 (paratypes of *Acanthopthalmus sandakanensis*) (2, 17.4–23.5). FMNH 68159 (paratypes of *Acanthopthalmus sandakanensis*) (8, 24.8–35.5). FMNH 44798 (1, 27.3). ZRC 37645 (17, 26.1–35.6). ZRC 45473 (2, 21.2–22.1).

Pangio semicincta: Malaysia–UF 173513 (2, 36.7–44.0), GenBank GQ174312, GQ174404. ZRC 17703 (1, 51.1). ZRC 17708 (2, 42.8–62.7). ZRC 43659 (2, 44.3–51.2). ZRC 4585 (3, 51.0–55.5). Sumatra–UF 161608 (2, 45.3–48.1), GenBank GQ174320. ZRC 43095 (46.5–51.0). Thailand–ZRC 42095 (2, 47.9–50.9).

Pangio shelfordii: Borneo–ZRC 37870 (1, 45.0). ZRC 37884 (2, 46.3–52.9). ZRC 39448 (3, 47.6–52.5). Malaysia–ZRC 40233 (4, 45.4–53.7). ZRC 40255 (1, 47.4). ZRC 42771 (1, 46.2). ZRC 42825 (1, 43.0). ZRC 42836 (1, 57.6). ZRC 42850 (3, 47.1–55.6). Singapore–FMNH 60263 (5, 35.5–43.7). Sumatra–ZRC 37531 (2, 39.6–42.6).

Pangio sp.: Malaysia–ZRC 8916 (2, 34.7–42.0). Thailand–ZRC 39298 (1, 50.0). ZRC 41319 (1, 61.0).

Pangio superba: Borneo–ZRC 38787 (3, 30.9–36.4).

Sabanejewia larvata: Italy–UF 81157 (3, 28.7–43.6).

Sabanejewia romanica: Romania–UMMZ 185064 (10, 49.1–74.5).

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