

## Research



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## Evolutionary biology

# Mesozoic origin and 'out-of-India' radiation of ricefishes (Adrianichthyidae)

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The Indian subcontinent has an origin geologically different from Eurasia, but many terrestrial animal and plant species on it have congeneric or sister species in other parts of Asia, especially in the Southeast. This faunal and floral similarity between India and Southeast Asia is explained by either of the two biogeographic scenarios, 'into-India' or 'out-of-India'. Phylogenies based on complete mitochondrial genomes and five nuclear genes were undertaken for ricefishes (Adrianichthyidae) to examine which of these two biogeographic scenarios fits better. We found that *Oryzias setnai*, the only adrianichthyid distributed in and endemic to the Western Ghats, a mountain range running parallel to the western coast of the Indian subcontinent, is sister to all other adrianichthyids from eastern India and Southeast-East Asia. Divergence time estimates and ancestral area reconstructions reveal that this western Indian species diverged in the late Mesozoic during the northward drift of the Indian subcontinent. These findings indicate that adrianichthyids dispersed eastward 'out-of-India' after the collision of the Indian subcontinent with Eurasia, and

subsequently diversified in Southeast–East Asia. A review of geographic distributions of ‘out-of-India’ taxa reveals that they may have largely fuelled or modified the biodiversity of Eurasia.

## 1. Introduction

The Indian subcontinent geologically originated from Gondwana, a Neoproterozoic supercontinent composed of the present-day Africa, South America, Australia, Antarctica, Arabian Peninsula, Madagascar, and the Indian subcontinent [1]. During the breakup of Gondwana, the Indian subcontinent became isolated from Africa around 130–160 Ma, drifted northwards, and eventually collided with Eurasia, which originated from Laurasia, around 35–55 Ma (figure 1a) [2–7]. Though the origin of the Indian subcontinent differs geologically from that of Eurasia, many terrestrial animal and plant species on it have congeneric or sister species in other parts of Asia, especially in the Southeast [8–15].

The faunal and floral similarity between India and Southeast Asia has been attributed to dispersals from Eurasia to the Indian subcontinent [16,17]. One hypothesis on which this ‘into-India’ biogeographic scenario is based is the ‘Satpura hypothesis’ by S. L. Hora, an Indian ichthyologist [16,18], which considers that the westward dispersals of Southeast Asian fauna occurred through the central Indian Satpura hill ranges in the Pleistocene. In contrast, it is also theoretically possible that the Indian taxa originated on the Indian subcontinent, and that the dispersals occurred ‘out-of-India’, from India to Southeast Asia, after the collision of the Indian plate with Eurasia [19,20]. It is essential to evaluate the ‘into-India’ versus ‘out-of-India’ scenarios to understand how the biodiversity in these regions of different geological origins was formed [21–25].

Fauna and flora in the Western Ghats, a mountain range running parallel to the western coast of the Indian subcontinent, hold the key for the test of these two biogeographic scenarios. The Western Ghats harbour unique, evolutionarily distinct lineages of many taxa [26–30]. The unique fauna and flora in the Western Ghats suggest that they have long been isolated from other regions of the Indian subcontinent. If this isolation predates the collision of the Indian subcontinent, and if the Western Ghats clade is sister to all other clades, then the presence of their common ancestor in the Indian subcontinent is supported, consistent with the ‘out-of-India’ scenario (figure 1b). In contrast, if the Western Ghats taxa are nested within a larger phylogeny consisting of species from outside the region, and if the isolation of the Western Ghats postdates the collision of the Indian subcontinent, then the ‘into-India’ scenario is instead supported.

We examine which of these two biogeographic scenarios better fits a group of small-sized ricefishes (family Adrianichthyidae) comprising 37 species (figure 1c) distributed throughout Southeast and East Asia, and the Indian subcontinent [31], with one species, the Malabar ricefish, *Oryzias setnai*, (formerly *Horaichthys setnai*, named after S. L. Hora), endemic to the Western Ghats lowlands [32,33]. Though the endemism of *O. setnai* suggests long-term isolation, no study has investigated its phylogenetic position or evolutionary history. Using sequences of the complete mitochondrial genomes and five nuclear genes, we reconstruct a comprehensive phylogeny of the family Adrianichthyidae, including this Western Ghats endemic species, and

estimate divergence times and ancestral areas of major adrianichthyid lineages. We demonstrate that this family originated in India and subsequently dispersed east as far as Wallacea, the biogeographical transition zone between Indomalaya and Australasia, where it there became one of the most important elements of the region’s current freshwater ichthyofauna.

## 2. Materials and methods

### (a) Field collections

Twenty-two adrianichthyid species were collected from throughout the geographic range of this family (electronic supplementary material, table S1). Full details of field collections are provided in the electronic supplementary material.

### (b) Mitochondrial and nuclear sequencing of *O. setnai*

Total DNA was extracted from one *O. setnai* individual from an aquarium strain. The entire length of the mitogenome was *de novo* assembled using long PCR (electronic supplementary material, table S2) [34,35] and shotgun-sequencing (electronic supplementary material, figure S1). We also Sanger-sequenced five nuclear genes (electronic supplementary material, table S3). Full details of sequencing are provided in the electronic supplementary material.

### (c) Whole-genome sequencing of other adrianichthyids

Whole-genome sequencing was performed for wild or laboratory individuals of 10 adrianichthyid species (electronic supplementary material, table S1). Reads were mapped to a reference genome assembly of *O. latipes* (ASM223467v1) or *O. javanicus* (OJAV\_1.1), and bases were called across each reference mitochondrial genome and across the five nuclear genes of each reference. Each mitogenome sequence was annotated using MitoAnnotator [36,37]. Full details of sequencing are provided in the electronic supplementary material.

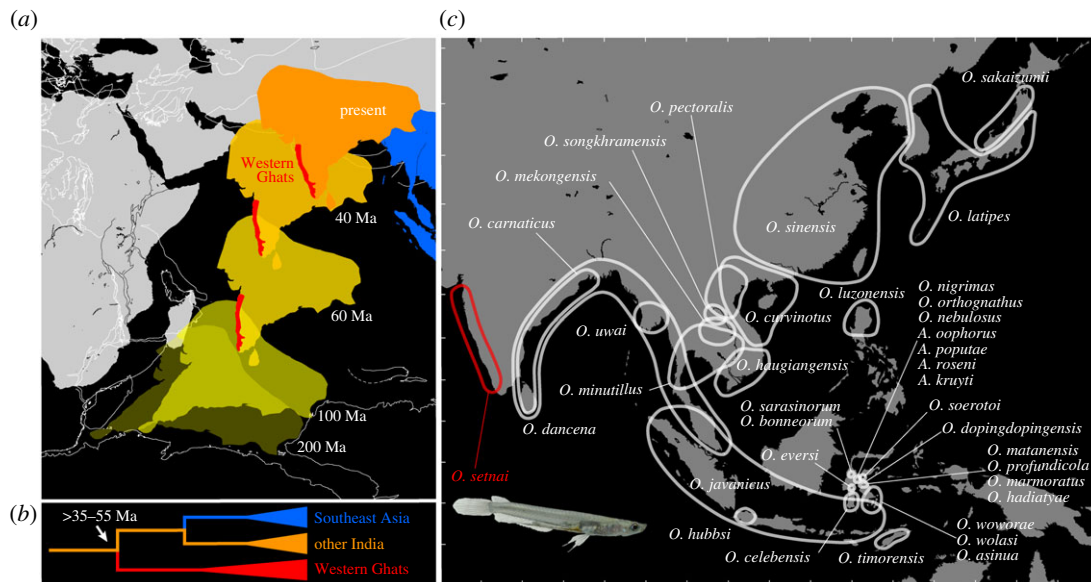
### (d) Phylogenetic analysis

Sequences of the mitogenomes and the five nuclear genes were obtained for an additional 20 adrianichthyid taxa, using short read sequences of the whole genome retrieved from DDBJ-DRA (electronic supplementary material, table S1); reads were mapped to a reference genome assembly of *O. celebensis* (OryCel\_1.0) or *O. latipes*, and bases were called. For two species (*O. javanicus* and *O. dancena*), mitogenome sequences retrieved from DDBJ were used (electronic supplementary material, table S1). Sequences of mitogenomes and nuclear genes of five beloniform, seven cyprinodontiform, five atheriniform and two cichlid (perciform) species were also retrieved from DDBJ (electronic supplementary material, table S1).

Alignments were performed separately for each gene. For mitochondrial genes, we excluded ambiguously aligned regions in the rRNA and tRNA genes, the third codon positions from the protein-coding genes, and the whole NADH dehydrogenase subunit 6, resulting in sequences of a total 11 233 bp. Alignments of nuclear genes resulted in sequences of a total 4204 bp. A maximum-likelihood phylogeny was estimated separately for the mitochondrial, nuclear and concatenated sequences using raxml-GUI v. 1.31 [38]. Full details of phylogenetic analyses are provided in the electronic supplementary material.

### (e) Divergence time estimation

Lognormal relaxed clock analyses were performed separately on the 11 233 bp mitochondrial and 4204 bp nuclear sequences using



**Figure 1.** (a) Time sequence of drifting continental blocks at each age from 200 Ma to present (map provided by and modified from [2] with permission). (b) Schematic phylogeny under the scenario ‘out-of-India’. (c) Map depicting the geographic distributions of all species in the family Adrianichthyidae.

BEAST v. 2.5.2 [39]. We employed three fossil records: (i) †*Mahengechromis* (the minimum age 45.46 Ma) [40] for the node between the two cichlids [41], (ii) †*Rhamphexocoetus volans* (the minimum age 49.11 Ma) [42] for the branch leading to the flying-fish [41], and (iii) †*Lithopoeilus brouveri* (the minimum age 5.33 Ma) [43] for the node between *Oryzias sarasinorum* and *Oryzias eversi* [44], and the opening of the Makassar Strait, ca 45 Ma [45–47], to time-calibrate the phylogenetic tree (figure 2). Appropriate substitution models were selected for each gene (for rRNA and tRNA genes) and codon (for coding genes). Full details on the divergence time estimation are provided in the electronic supplementary material.

### (f) Ancestral area reconstruction

The geographic range of Adrianichthyidae was divided into five geological areas: (A) Western Ghats, (B) Indian subcontinent (excluding the Western Ghats), (C) Southeast Asia (excluding Wallacea and New Guinea), (D) East Asia, and (E) Wallacea and New Guinea. Using the tree obtained from the BEAST analysis above, ancestral areas at each node of the tree were reconstructed under different biogeographical models with RASP v. 4.2 [48]. Likelihood under each model was estimated, and the fit of each model to the data was compared by consulting Akaike information criteria corrected for a small sample size. Full details on the ancestral area reconstruction are provided in the electronic supplementary material.

## 3. Results

### (a) Phylogeny of Adrianichthyidae

All phylogenies revealed *O. setnai* to be a sister to all other members of the family Adrianichthyidae (figure 2 and electronic supplementary material, figure S2). The branch of *O. setnai* in these phylogenies was disproportionately longer compared with other adrianichthyids. The latter were composed of three main clades—the ‘*latipes*’, ‘*javanicus*’, and ‘*celebensis*’ species groups. The *latipes* species group comprises species distributed mainly in the inland areas of the Indochinese Peninsula, Philippines and East Asia; the *javanicus* species group occurs in the eastern part of India and throughout Southeast Asia; and the *celebensis* species group is endemic

to Sulawesi Island (figure 2). Among the three species groups, the *latipes* species group is sister to the other two.

### (b) Divergence time estimates

Adrianichthyidae was estimated to have separated from other members of the order Beloniformes around 89 Ma (73–107 Ma in 95% HPD; figure 2, node 1). The divergence time of *O. setnai* was estimated at around 74 (60–88) Ma (node 2) in the late Mesozoic (see also electronic supplementary material, figure S3). Thereafter, the *latipes* species group split off around 52 (45–60) Ma (node 3), and the subsequent split between the *javanicus* and *celebensis* species groups occurred around 47 (41–52) Ma (node 4).

### (c) Reconstruction of ancestral areas

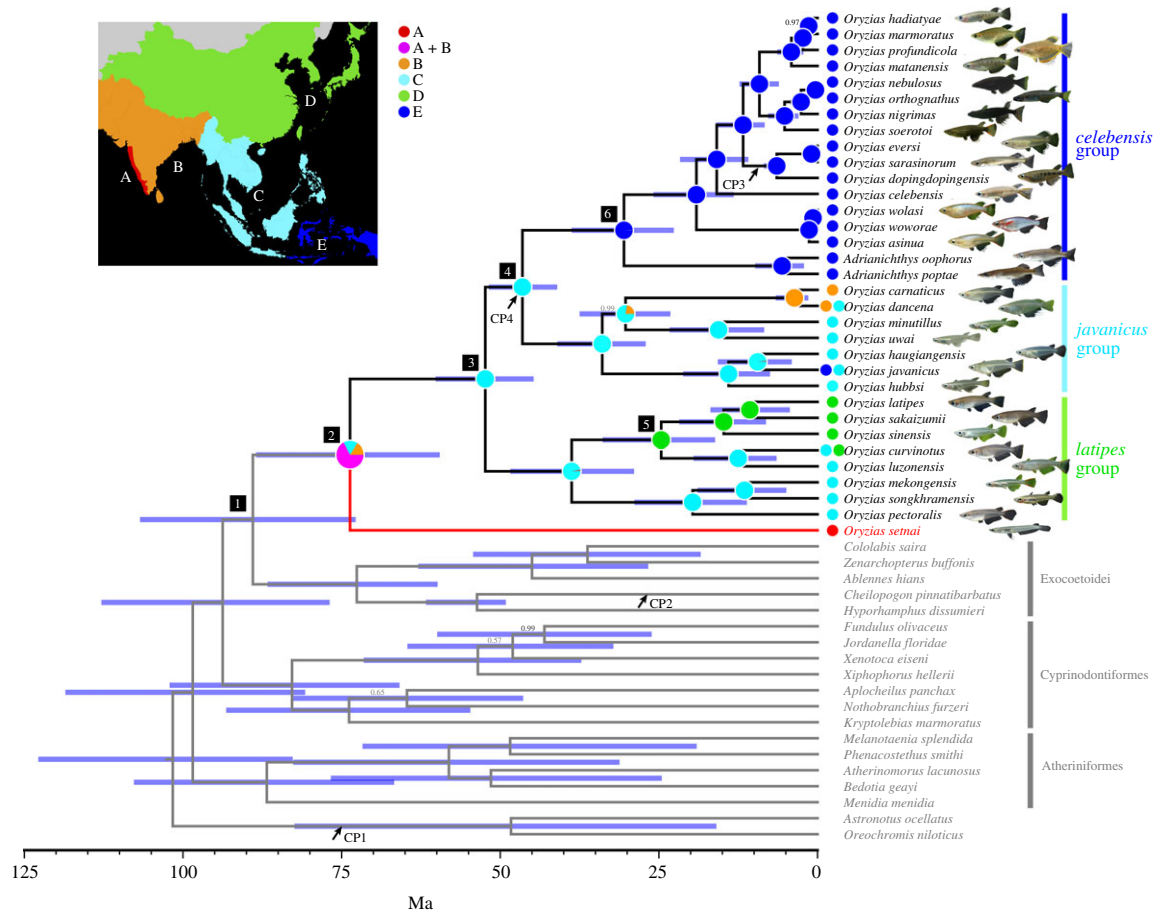
The best biogeographical model (Dispersal-Extinction Cladogenesis with founder event speciation model: DEC + J; electronic supplementary material, table S4) estimated that the most probable distribution area for the common ancestor of adrianichthyids was on the Indian subcontinent (i.e. the Western Ghats and other parts of India) (figure 2, node 2). The common ancestor of the *latipes*, *javanicus* and *celebensis* species groups was estimated to be distributed in Southeast Asia (node 3). Thereafter, dispersals from Southeast Asia to East Asia and to Wallacea occurred within the *latipes* species group (node 5), and in the most recent common ancestor of the *celebensis* group (node 6), respectively.

## 4. Discussion

### (a) Origin and dispersal history of the Adrianichthyidae

We found that *O. setnai*, endemic to the Western Ghats western plains, is sister to all other Adrianichthyidae taxa, which comprise three major groups (the *latipes*, *javanicus* and *celebensis* species groups) [49,50]. Our results also reveal that the divergence time of this species (60–88 Ma) predates the collision of the Indian subcontinent with Eurasia (35–55 Ma [2–7]), and that the common ancestor of the Adrianichthyidae was





**Figure 2.** Bayesian chronogram of adrianiichthyid taxa based on mitochondrial and nuclear sequences. Bars represent 95% high posterior density (HPD). Ancestral areas reconstructed using a DEC + J model are shown as pies at each node. Numbers on branches are Bayesian posterior probabilities (BPPs); branches with no number represent BPP = 1. Arrows indicate calibration points; CP1: †*Mahengechromis* for the node between the two cichlids, CP2: †*Rhamphexoetus volans* for the branch leading to the flyingfish, CP3: †*Lithopoeilus brouweri* for the node between *Oryzias sarasinorum* and *Oryzias eversi*; and CP4: the opening of the Makassar Strait (see text for details).

estimated to have been distributed on this ancient subcontinent. This lends credibility to the hypothesis that the split of *O. setnai* occurred on the Indian subcontinental 'raft', supporting the 'out-of-India' hypothesis.

The divergence of *O. setnai* and its endemism to western India may be related to the formation of the Western Ghats mountain ranges. The western coast of India could have appeared as an abrupt cliff some 1000 m in elevation ca 65–90 Ma after the Indian subcontinent broke away from Madagascar [51], becoming the present-day Western Ghats. This long (1600 km) and high mountain range running parallel to the southwestern coast of the Indian subcontinent may have acted as a physical barrier preventing the migration of species between the western and eastern coasts. We think that the common ancestor of Adrianiichthyidae was divided into the west and east by this mountain range, and that the western population would have evolved in isolation as *O. setnai*. The common ancestor of the Eurasian clade probably diverged from the eastern population.

The branch leading to *O. setnai* is, notably, disproportionately long, indicating an acceleration in evolutionary rate (electronic supplementary material, figure S2). This acceleration might be related to the geological history of the Western Ghats. It is well known that large-scale, long-term volcanic eruptions occurred along the western coast of the Indian subcontinent during its northward drift, forming the Deccan Traps [52]. It is, therefore, no wonder that *O. setnai* has

repeatedly experienced strong bottlenecks caused by recurring eruptions. According to the nearly neutral theory of molecular evolution [53], evolutionary rates of protein-coding genes increase with decreasing population size, which may explain this long branch. A detailed demographic history of *O. setnai* using the nuclear genome is required to test this hypothesis.

The split between the Adrianiichthyidae and other members of the Beloniformes, that is, Exocoetoidei, estimated at 73–107 Ma (figure 2, node 1), perhaps occurred in conjunction with the separation of the Indian subcontinent from Africa and Madagascar. Since most extant species in the Exocoetoidei: Belonidae (needlefishes), Exocoetidae (flyingfishes), Hemiramphidae (halfbeaks) and Zenarchopteridae (viviparous halfbeaks) are marine [54], the expansion of coastal areas following the breakup of the Indian subcontinent may have increased opportunities for a common ancestor of Exocoetoidei to pioneer new habitat. In contrast, Adrianiichthyidae pioneered the inland areas of the Indian subcontinent, and subsequently those in Eurasia, probably spreading via coastal areas.

## (b) Conclusion: Eurasian biodiversity fuelled by 'out-of-India' dispersals

Contrary to Hora's hypothesis [16,18], Hora's fish and its relatives originated on the Indian subcontinent and subsequently dispersed east into Southeast and East Asia, where they have

**Table 1.** Geographic distributions of taxa demonstrated to be ‘out-of-India’ by molecular studies (i.e. ‘out-of-India’ taxa demonstrated solely by taxonomic and/or palaeontological studies are not included). Numbers represent the numbers of species in each geographic area. Bold numbers represent modes. See electronic supplementary material, table S5 for the list of species and genera used, and their geographic ranges.

taxon [reference]	geographic area				
	Western Ghats (A)	Indian subcontinent (B)	Southeastern Asia (C)	Eastern Asia (D)	Wallacea and New Guinea (E)
<b>plants</b>					
Allioideae <sup>a</sup> [55]	0	0	0	<b>3</b>	0
<i>Paliurus</i> [56]	0	0	0	<b>4</b>	0
Crypteroniaceae [20]	0	2	<b>11</b>	1	2
Dipterocarpaceae <sup>a</sup> [57]	3	7	<b>10</b>	3	4
<b>invertebrates</b>					
Theotiminae (spiders) [58]	0	1	<b>49</b>	7	7
Heterometrinae (scorpions) [59]	5	<b>31</b>	9	0	0
oriental <i>Rhysida</i> (centipedes) [60]	<b>8</b>	6	2	0	0
tribe Dacini (fruit flies) [61]	44	78	238	75	<b>384</b>
<b>freshwater fishes</b>					
<i>Scleropages</i> [62]	0	0	<b>5</b>	0	0
Notopteridae [63]	0	2	<b>6</b>	0	0
Channoidei [64]	5	<b>23</b>	22	6	0
Aplocheilidae [65]	4	<b>6</b>	1	0	1
Adrianichthyidae [this study]	1	2	11	4	<b>22</b>
<b>amphibians</b>					
Ichthyopiidae [66]	13	11	<b>31</b>	1	0
Microhylidae [14]	16	22	<b>58</b>	13	2
Ranoidea <sup>a</sup> [67]	19	23	<b>43</b>	25	15
<b>reptiles</b>					
Agamidae <sup>a</sup> [68]	8	15	<b>26</b>	10	10

<sup>a</sup>The number of genera was used for the taxon.

greatly diversified. Our review of geographic distributions (electronic supplementary material, table S5) reveals that other ‘out-of-India’ taxa have also diversified more or less in Southeast and East Asia (table 1). This probably reflects that ‘out-of-India’ taxa were newcomers to Eurasia, where they may have found empty niches and/or competitively excluded native Laurasian taxa. The biodiversity of Eurasia may have been largely fuelled or modified by these taxa which came on the subcontinental raft.

**Ethics.** Field collections were conducted based on the Memorandum of Agreement between the Kerala University of Fisheries and Ocean Studies (KUFOS) and the University of the Ryukyus, the Research Permits issued from the Ministry of Research, Technology, and Higher Education, Republic of Indonesia (394/SIP/FRP/SM/XI/2014 and 106/SIP/FRP/E5/Dit.KI/IV/2018), and the Memorandum of Agreement between the Hanoi National University of Education and the Okinawa Institute of Science and Technology Graduate University. Field collections in Laos and Myanmar were supported by the Living Aquatic Resources Research Center and the Ministry of Natural Resources and Environmental Conservation, respectively. We followed the Regulations for Animal Experiments at the University of the Ryukyus for handling the fish, and all experiments were

approved by the Animal Care Committee of the University of the Ryukyus (2018099 and 2019084).

**Data accessibility.** Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.931zcrjkg> [69].

**Authors’ contributions.** All authors substantially contributed to this study. K.Y., Y.Take. and R.R. conceived the study; K.Y., H.K., R.T., K.M., H.D.T., N.K., S.M., V.B., K.W., P.M., S.T., L.K.C.Y., K.W.A.M., V.K.A. and R.R. conducted fieldwork; S.A., H.Y., T.K., J.M., H.K. and J.K. performed laboratory work; and K.Y., S.A., H.Y., J.M., R.Ka., S.F., R.Ki., Y.Take., D.H.E.S. and Y.Taka. conducted analyses. K.Y., S.A., D.H.E.S., K.W., R.R. and J.K. drafted the manuscript, and all authors were engaged in editing and/or revising the manuscript. All authors are accountable for the work performed and approved the final manuscript.

**Competing interests.** We declare we have no competing interests.

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