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Recognition of the lamprey genus *Occidentis* Carim *et al.*, 2024 as distinct from *Lampetra* Bonnaterre, 1788

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Lamprey molecular phylogenies to date have relied on mitochondrial (mt) DNA sequence data, and there has long been recognition that a robust molecular phylogeny of this ancient group of vertebrates—with relatively few phylogenetically informative morphological characters—will require the use of a wider range of genes, particularly nuclear genes (e.g., Lang *et al.* 2009; Potter *et al.* 2015; Docker and Hume 2019). Hughes *et al.* (2025) performed this long awaited phylogenomic analysis to assess phylogenetic relationships of lampreys, and estimated divergence time and diversification rates among lamprey clades. They examined 355 exons among 81 specimens representing 36 recognized and one undescribed (*Lethenteron* sp. "N") extant lamprey species. The latter has recently been identified as *Lethenteron mitsukurii* (Hatta, 1901) by Sakai *et al.* (2025). To assess phylogenetic relationships, Hughes *et al.* (2025) estimated a maximum likelihood tree using concatenated exon sequences, and a multi-species coalescence tree using one gene tree per specimen. In agreement with previous studies using mt DNA (Docker *et al.* 1999; Lang *et al.* 2009; Brownstein and Near 2023; Carim *et al.* 2023), the authors observed a strongly supported clade representing species of: 1) *Lampetra* Bonnaterre, 1788 from Eurasia (and possibly eastern North America; see discussion below); 2) *Lampetra* from western North America; and 3) *Eudontomyzon* Regan, 1911 (Figure 1). Because the presence of *Eudontomyzon* rendered *Lampetra* polyphyletic, Hughes *et al.* (2025) recommended reassigning all members of *Eudontomyzon* to *Lampetra*.

A previously published study by Carim *et al.* (2023) encountered the same non-monophyletic patterns in mitochondrial phylogenies at two genes using a larger suite of specimens, particularly from western North America. In that study, a *cyt b* maximum likelihood tree was generated from a 988-base pair segment comprising 428 sequences, and a *COI* maximum likelihood tree was generated from a 585-base pair segment comprising 393 sequences; both datasets represented over 500 specimens of Petromyzontidae. In a subsequent publication (Carim *et al.* 2024), the authors concluded that the preferred approach to resolving polyphyly in *Lampetra* was to assign the western North American species to a new genus, *Occidentis* Carim *et al.*, 2024, while retaining *Eudontomyzon* as a recognized taxon (Figure 2). This paper focuses on these alternative interpretations of the phylogenetic relationships within *Lampetra sensu lato*.

Recognition of the genus *Occidentis*

Either approach recommended by Carim *et al.* (2024) or Hughes *et al.* (2025) would satisfy the criterion of monophyly for the genus *Lampetra.* We favor recognizing *Lampetra*, *Occidentis*, and *Eudontomyzon* for three reasons. First, *Lampetra* of the Eurasian and eastern North American lineage are geographically isolated from *Occidentis* of western North America (Figure 3)—occidens translating from Latin to "westerly" or "of the west". Members of *Lampetra* are found in river basins that drain to the Atlantic Ocean, Caspian Sea, Adriatic Sea, and Black Sea. In contrast, *Occidentis* is found exclusively in river basins of western North America that drain to the Pacific Ocean. Second, the minimum pairwise divergences among *Lampetra*, *Occidentis*, and *Eudontomyzon* exceed the minimum values typically observed among fish genera (Table 1;

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see Ward 2009). Third, retaining *Eudontomyzon* and promoting *Occidentis* recognizes taxonomic diversity of lampreys, and in the case of the former, retains a long-standing taxonomic entity (Regan 1911). Note that *Lampetra aepyptera* (Abbott, 1860) may also warrant placement in a distinct genus based on genetic differentiation and its distinct geographic distribution (i.e., with resurrection of the genus *Okkelbergia* Creaser & Hubbs, 1922; see Lang *et al.* 2009; Carim *et al.* 2023; Carim *et al.* 2024). Further discussion of this point, however, is beyond the scope of the present paper. *Occidentis* is recognized in both FishBase (https://www.fishbase.org/) and Eschemeyer's Catalog of Fishes (https://www.calacademy.org/scientists/projects/eschmeyers-catalog-of-fishes).

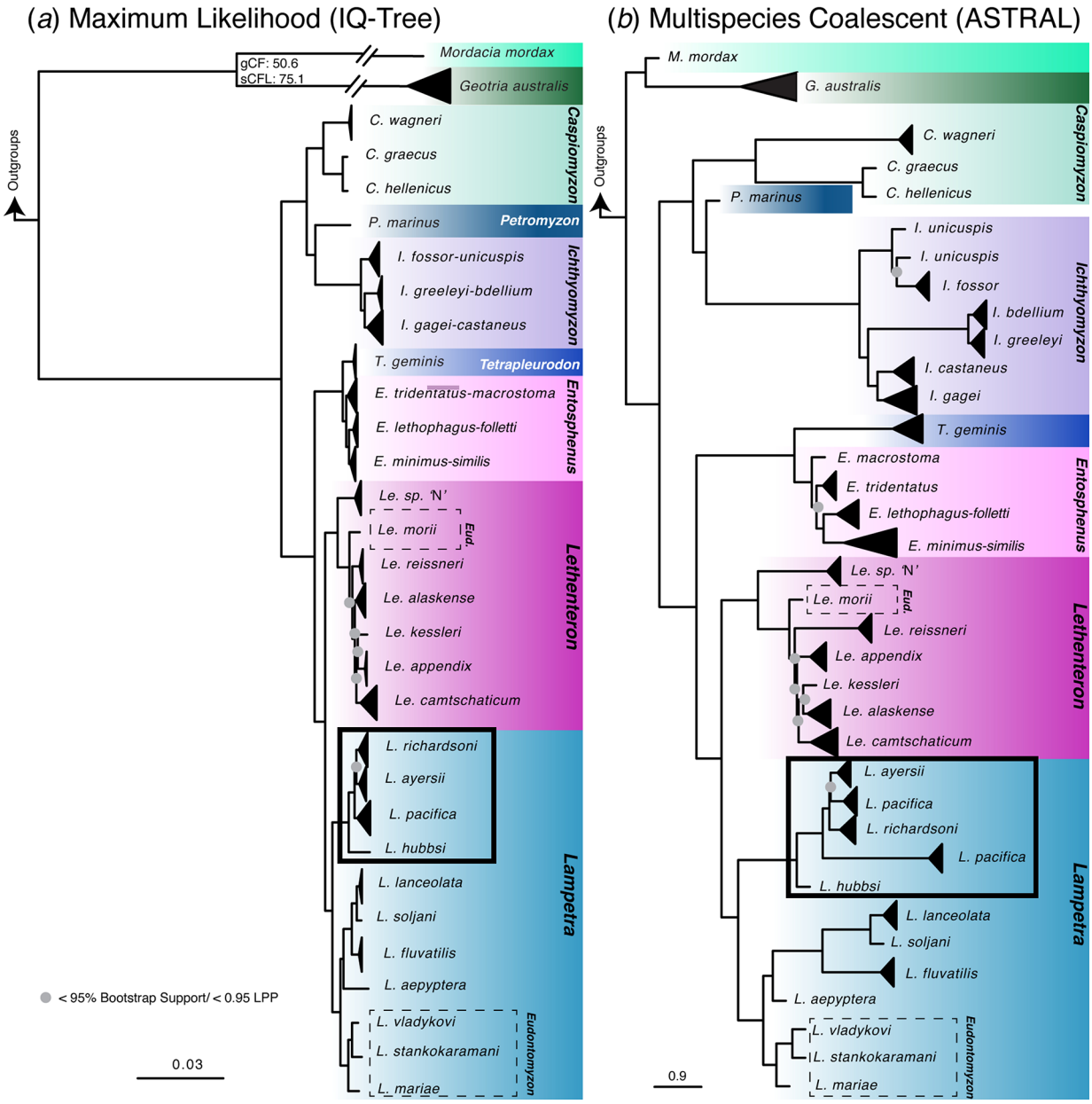

FIGURE 1. Maximum likelihood tree (a) and multispecies coalescent tree (b) of Petromyzontiformes modified from Hughes *et al.* (2025) by the addition of black boxes surrounding species now classified under the genus *Occidentis*. Taxa surrounded by dashed boxes indicate species classified as *Eudontomyzon*. Nodes with grey dots indicate < 95% ultrafast bootstrap support (a) and < .95 local posterior probability (b), and those without grey dots indicate > 95% ultrafast bootstrap support and > .95 local posterior probability, respectively. Note that *L. ayresii* is misspelled.

TABLE 1. Minimum pairwise genetic distance at the *cyt b* (above diagonal) and *COI* (below diagonal) genes among genera of Petromyzontidae, expressed as a percent. Reproduced from Carim *et al.* (2024). Comparisons among lineages of *Lampetra sensu lato* are shown in bold.

	Caspiomyzon	*Petromyzon*	*Ichthyomyzon*	*Lethenteron* sp. S	*Entosphenus*	*Tetrapleurodon*	*Lethenteron + Eudontomyzon morii*	*Occidentis*	*Eudontomyzon*	*Lampetra aepyptera*	*Lampetra + Lethenteron ninae*
Caspiomyzon	--	11.80	15.50	14.00	12.70	13.10	13.60	12.80	13.70	14.20	13.90
Petromyzon	12.48	--	12.40	13.38	12.30	12.90	12.29	12.29	12.40	12.77	12.90
Ichthyomyzon	9.74	11.28	--	15.00	15.30	15.10	14.50	14.50	15.90	16.20	16.20
Lethenteron sp. S	11.28	12.99	12.65	--	11.20	11.10	9.98	9.12	9.10	10.22	9.10
Entosphenus	11.28	13.50	11.62	8.72	--	3.40	8.60	7.40	8.20	9.00	8.50
Tetrapleurodon	13.16	14.36	12.99	10.77	3.08	--	9.50	8.60	9.10	10.20	9.40
Lethenteron + Eudontomyzon morii	13.50	14.87	13.68	10.26	9.06	9.92	--	6.33	6.10	6.08	6.10
Occidentis	11.62	14.53	13.33	9.57	7.69	9.40	7.69	--	**5.80**	**6.93**	**6.30**
Eudontomyzon	11.11	14.53	11.28	9.23	7.52	9.40	7.52	**6.84**	--	**4.10**	**3.40**
Lampetra aepyptera	11.62	13.85	11.80	9.74	8.03	9.40	7.35	**6.50**	**3.42**	--	**3.80**
Lampetra + Lethenteron ninae	11.45	13.68	11.45	8.55	7.86	9.23	6.67	**7.01**	**3.42**	**3.93**	--

Species diversity and relationships among lineages of *Occidentis*

Patterns among members of *Occidentis* observed in Hughes *et al.* (2025) also differed from previous studies. These differences may be explained by variation in the number and location of origin for specimens in each dataset. Hughes *et al.* (2025) examined 10 specimens of *Occidentis* obtained from six localities. Studies examining mt DNA sequences from a broader geographic range of *Occidentis* (e.g., Boguski *et al.* 2012; Auringer *et al.* 2023; Carim *et al.* 2023; Carim *et al.* 2024) have shown considerable genetic diversity not captured by the four nominal species and limited geographic sampling included in Hughes *et al.* (2025). For example, Carim *et al.* (2024) performed a species delimitation analysis using 192 *cyt b* sequences representing 305 specimens from 103 localities spanning the geographic range of *Occidentis*. Results of this analysis reaffirmed the validity of *O. pacifica* (Vladykov, 1973)*, O. hubbsi* (Vladykov & Kott, 1976), and *O. ayresii* (Günther, 1870), and identified as many as seven undescribed candidate species of *Occidentis* distributed across Oregon and California, USA. Note that work by Carim *et al.* (2023) and Carim *et al.* (2024) resolved the polyphyletic relationship between *O. richardsoni* (Vladykov & Follett, 1965) and *O. ayresii* by synonymizing the two, recognizing the resident, non-parasitic western brook lamprey as a life history variant of *O. ayresii*. Additionally, results of Carim *et al.* (2023) suggest that *O. pacifica* may be almost entirely restricted to a single river subbasin (Clackamas River, OR, USA; see also Reid *et al.* 2011). Specimens identified as *O. pacifica* in Hughes *et al.* (2025) were obtained from outside this river basin and therefore likely represent an undescribed species or a diverged lineage belonging to the *O. ayresii* species complex. Although more information is needed, this error may explain the inconsistent relationships among specimens of *Occidentis* observed in the various analyses by Hughes *et al.* (2025; see Figure 1). Despite the greater diversity within *Occidentis*, all studies still resolved this genus as unambiguously monophyletic and distinct from all other lampreys, regardless of the sample size or genes examined.

Considerations for the non-monophyly of *Eudontomyzon*

The reassignment of *Eudontomyzon* to *Lampetra* proposed by Hughes *et al.* (2025) may be warranted, pending additional information. *Eudontomyzon danfordi* Regan, 1911, the type species of the genus, was not included in the genomic analysis by Hughes *et al.* (2025), although they include it in a tree comprising a mixture of genomic and mt DNA. Because a type

species is the nominal species that is the name-bearing type of a nominal genus (ICZN 1999), it must be included in any analysis that aims to resolve phylogenetic relationships.

Additionally, the assertion that *Eudontomyzon morii* (Berg, 1931) should be placed within *Lethenteron* Creaser & Hubbs, 1922 overlooked sufficient context for the single specimen analyzed. The specimen analyzed by Hughes *et al.* (2025) was included in previous phylogenetic studies focused on various regions of the mt DNA (Lang *et al.* 2009; Li 2014; White 2014), which similarly classified this specimen as a distinct lineage of *Lethenteron*. This specimen was a metamorphosing individual identified as a member of *Eudontomyzon* based on the presence of developing exolateral teeth (Lang *et al.* 2009, see also Berg 1931). While this is one diagnostic character of *Eudontomyzon*, it is also sometimes observed in *Lethenteron* species (Naseka and Renaud 2020). Although the reclassification of *Eudontomyzon morii* to *Lethenteron* may be warranted based on both phylogenetic and geographic distributions (see Lang *et al.* 2009), sampling of adult specimens (with fully developed dentition) is needed to confirm classification of this lineage (Lang *et al.* 2009; Docker and Hume 2019).

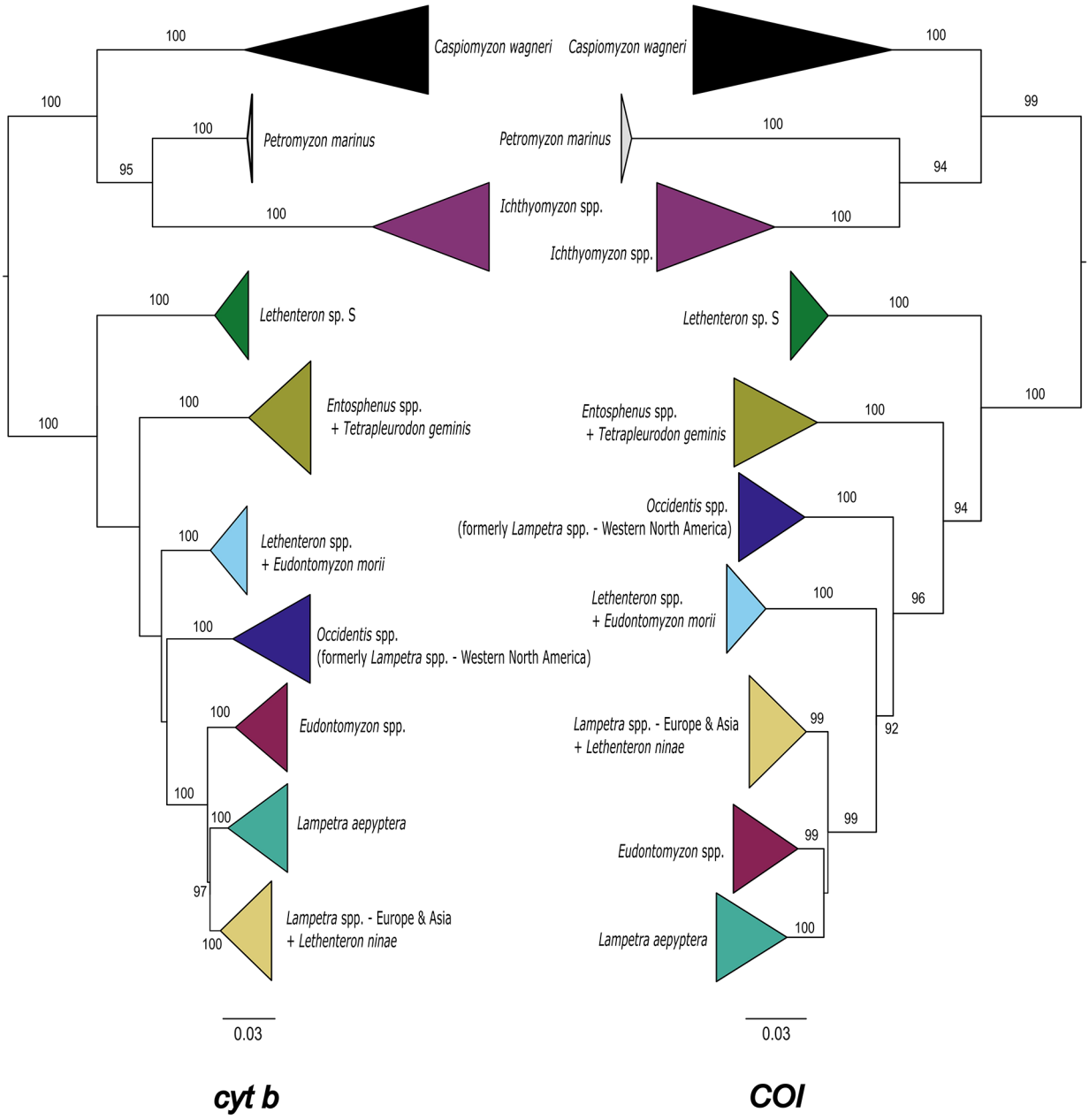

FIGURE 2. Maximum likelihood trees of Petromyzontidae at *cyt b* and *COI* reproduced from Carim *et al.* (2023). Bootstrap values are shown for branches with > 85% support.

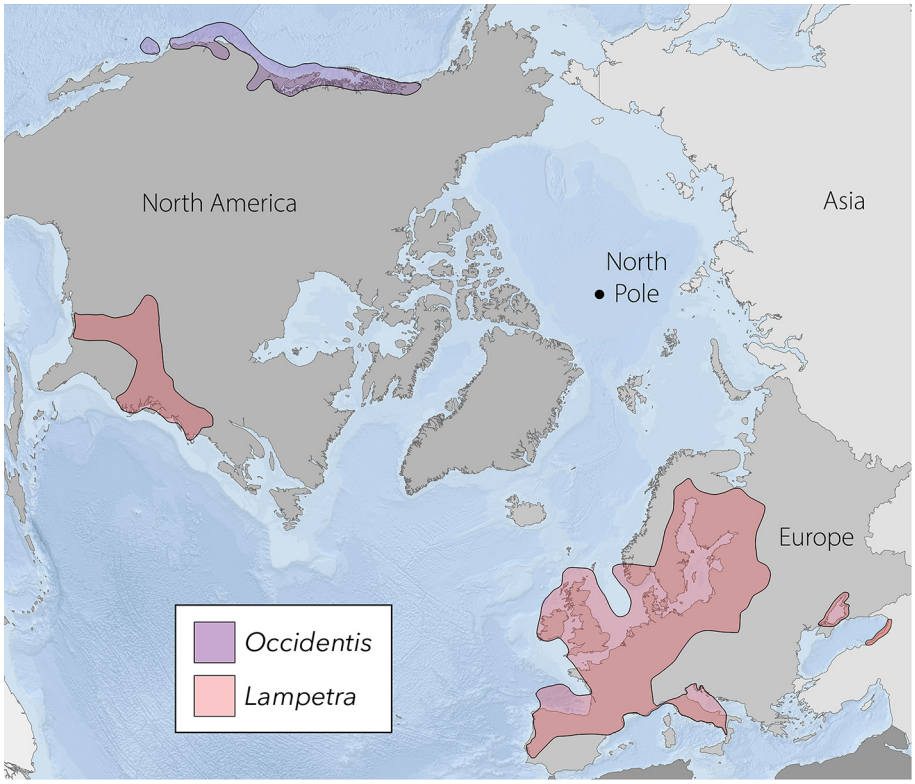

FIGURE 3. Geographic distribution of *Lampetra sensu lato* in western North America (now *Occidentis*), eastern North America and Eurasia updated from Potter *et al.* (2015).

Next Steps

There is still work to be done to resolve the relationship among Eurasian *Lampetra*, *Lethenteron*, and *Eudontomyzon*, with comprehensive sampling of vouchered specimens. The recognition of *Occidentis* for western North American lampreys, formerly classified as *Lampetra*, is an important step in clarifying these relationships. The inclusion of the two newly described Japanese species of *Lethenteron* (Sakai *et al.* 2025) into a phylogenomic analysis should be the aim of future efforts. In particular, the position of *Lethenteron hattai* Iwata, Sakai & Goto, 2025 in Sakai *et al.* 2025 (formerly recognized as *Lethenteron* sp. "S") as sister to an *Entosphenus-Lampetra-Lethenteron* clade, as determined by Yamazaki *et al.* (2006) based on the mt DNA *COI* gene, is perplexing and requires resolution.

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