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Seven-locus molecular phylogeny of Myctophiformes (Teleostei; Scopelomorpha) highlights the utility of the order for studies of deep-sea evolution

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ABSTRACT

Fishes of the order Myctophiformes (Teleostei; Scopelomorpha) comprise over half of all deep-sea biomass, and are a critical component of marine ecosystems worldwide. Members of the family Myctophidae, within Myctophiformes, form the majority of species diversity within the order (~250 species, 33 genera, 2 subfamilies), and are further known for their diverse bioluminescent traits, comprised of distinct cranial, postcranial, and caudal luminous systems that is perhaps the most elaborate among all vertebrates. These features make myctophids particularly compelling from both economic and scientific perspectives, yet no studies have sampled these fishes at a density appropriate for addressing any questions requiring a phylogenetic hypothesis as input. This study therefore presents a seven-locus molecular phylogeny of the order, sampling over 50% of all nominal myctophid species. This taxon sampling triples the representation of the next most comprehensive analysis, and reveals several new and well-supported hypotheses of relationships, in addition to supporting traditional hypotheses based on combined morphological data. This analysis shows that the slendertailed myctophids *Gonichthys*, *Centrobranchus*, *Loweina*, and *Tarletonbeania* are rendered non-monophyletic by a polyphyletic *Myctophum*; the enigmatic, monotypic genus *Notolychnus valdiviae* is nested within tribe Lampanyctini; the genus *Diaphus* is divided into at least two clades, with the suborbital (So) group recovered as monophyletic with strong support; and the genera *Lampanyctus* and *Nannobrachium* are recovered as non-monophyletic. These molecular results highlight the potential of myctophids as a premier model system for the application of modern comparative methods to studies of deep-sea evolution.

1. Introduction

Lanternfishes (family Myctophidae) are a midwater (mesopelagic) vertebrate group with several compelling features that make them amenable to species-dense molecular phylogenetic analysis and which also highlight their utility as a crucial system for understanding deep-sea evolutionary processes using modern analytical techniques. First, myctophid fishes are extremely abundant. They comprise over half of all deep-sea biomass (Gjøsaeter and Kawaguchi, 1980), and have been identified as a major contributor to the deep-scattering layer implicated in "false bottom" readings by bioacoustic equipment (Backus et al., 1968; Linkowski, 1983). The abundance of these fishes has also been noted by fisheries scientists as providing a potential "underexploited" or "virgin" resource for a variety of human uses (Valinassab et al., 2007; Vipin et al., 2012); as a source of crude protein qualitatively similar to that used for agricultural fishmeal (Haque et al., 1981); as a source of anti-oxidative health products (Chai et al., 2012); or as a source of cosmetic wax (Noguchi, 2004). Moreover, myctophid fishes play a critical role in many ecosystems as secondary consumers, between zooplankton and charismatic faunas such as squid and king penguin (Cherel et al., 2010; Kozlov, 1995). This trophic position suggests, therefore, that myctophids may have a high betweenness centrality (Freeman, 1977, 1979) in ecological food webs, and argues that their possible exploitation for human use may significantly destabilize epipelagic and deep-sea ecosystem interactions that are not yet fully understood (Catul et al., 2011; Devine et al., 2006; Pauly and Palomares, 2005; Roberts, 2002). The precarious position of lanternfishes as a highly noticeable and monetizable deep-sea group therefore places very practical demands on generating a hypothesis of their evolutionary relationships. This study, then, presents the first multilocus phylogenetic

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analysis of these fishes and is over 50% complete at the species level, a feature unique among phylogenetic analyses of deep-sea vertebrate organisms.

However, the resolution of debate on lanternfish relationships is not simply a taxonomic conundrum, although solving it would allow for policy recommendation, but is in fact a critical step toward understanding the evolution of development, bioluminescence, and communication in deep-sea vertebrates. Whereas both myctophid larvae and adults present many general problems with character conceptualization, polarity, and homology (Paxton et al., 1984) owing in part to their extreme fragility and small size, the main difficulty of lanternfish systematics stems from their most compelling character system—bioluminescence—which is variable even at the species level. Although some deep-sea fishes have evolved mechanisms for utilizing and perceiving several wavelengths of light invisible to their prey (Kenaley, 2010), lanternfishes exhibit three fundamentally different elaborations of luminous tissues: body photophores, caudal luminous organs, and cranial luminous complexes. The first two of these systems, photophores and caudal luminous organs, are especially charismatic examples of deep-sea bioluminescence. Analyzing these features in a phylogenetic context stands to critically expand our understanding of the evolution of these systems in the deep-sea environment and to bring much-needed attention to the study of deep-sea evolutionary biology.

Lanternfish body photophores, unlike those in nearly all other deep-sea fishes which retain serial rows of downward-facing structures to aid in counterillumination, are instead arranged in a combination of both lateral and ventral modular clusters first named by Lütken (1892) and standardized in later revisions (e.g. Bolin, 1939; Fraser-Brunner, 1949; Paxton, 1972). The relative positional arrangement of the photophores within these postcranial clusters, especially in the lateral complexes, is taxonomically informative and has been suggested to play a role in species recognition, coordinated shoaling, and size-assortative group formation during diel migration. Although some support for these roles is provided by the observation that lanternfish photophores exhibit significant dioptric modifications to focus light (Kier, 1967; Lawry, 1973), none of these proposed explanatory variables has been tested with character data, despite the fact that methods exist to test the hypotheses (e.g. Hadfield, 2010; Ives and Garland, 2010; Klingenberg and Marugán-Lobón, 2013; Martins and Hansen, 1997). Furthermore, the evolutionary origin and polarity of these clusters remain unclear, and both a "vertical drift" hypothesis (Fraser-Brunner, 1949; Ray, 1950) and a "loss/elaboration" hypothesis (Moser and Ahlstrom, 1972; Wisner, 1976) have been postulated to explain the patterns observed in lanternfish body photophores.

Lanternfishes also have caudal luminous organs, known as "stern-chasers" (Bolin, 1961), which exhibit compelling patterns of sexual dimorphism and monomorphism among genera and between subfamilies, with species of Myctophinae exhibiting predominantly dimorphic organs and species of Lampanyctinae exhibiting predominantly monomorphic ones (Herring, 2007). Some support for a signaling and/or reproductive role for these organs has been suggested by the observations that stern-chasers differ significantly from photophores in the structure and arrangement of their photogenic tissue (Anctil and Case, 1977; Barnes and Case, 1974; Case et al., 1977; Christophe and Baguet, 1982), in their innervation (Anctil and Case, 1977), and in the and duration and intensity of light emitted (Anctil, 1972; Barnes and Case, 1974). These features suggest lanternfishes may also be an exceptional system for studying links between phenotypic traits and patterns of species diversity (Van Valen, 1971; Vrba, 1980) in the deep-sea environment, especially since the abundance and species richness of lanternfishes makes them amenable to modern techniques for analyzing trait-dependence (FitzJohn, 2010, 2012; FitzJohn et al., 2009; Goldberg and Igić, 2012; Magnuson-Ford and Otto, 2012) in ways that smaller teleost groups are not (Chakrabarty et al., 2011).

What is understood about myctophid biology is predominantly taxonomic and zoogeographic in scope (e.g. Clarke, 1973; Hartmann and Clarke, 1975; Hulley, 1992; Hulley and Krefft, 1985; Koubbi et al., 2011; McGinnis, 1982; Nafpaktitis et al., 1977; Paxton, 1967), including detailed notes on their larval development widely regarded as some of the most disparate transformation trajectories (both within and among species) in vertebrates (Ahlstrom et al., 1976; Moser and Ahlstrom, 1970, 1972, 1974; Moser et al., 1984). However, the specific intrarelationships of these fishes are far from resolved. The first two lanternfish species, representing what would come to be recognized as the two general morphotypes of the eventual subfamilies (Paxton, 1972), were described in the same year. The first species, *Myctophum punctatum* Rafinesque, 1810, was named from the Greek *Mykter* ("nose") and *ophis* ("serpent") for the smooth, rounded cranial profile and large orbits characterizing members of the subfamily Myctophinae. The second species, *Lampanyctus crocodilus* (Risso, 1810), was named by Bonaparte (1840) from the Greek *Lampas* ("torch") and *nycte* ("night"). Many members of the subfamily Lampanyctinae are found at deeper depths than members of Myctophinae, but are also notable for possessing both longer jaws and more flaccid body types. Although descriptions and revisions of the currently valid genera (Bolin, 1939; Bonaparte, 1840; Brauer, 1904, 1906; Eigenmann and Eigenmann, 1890; Fowler, 1904, 1925; Fraser-Brunner, 1949; Gatti, 1904; Gistel, 1850; Goode and Bean, 1896; Günther, 1864, 1873, 1876, 1887; Hubbs and Wisner, 1964; Hulley, 1981; Lönnberg, 1905; Nafpaktitis and Paxton, 1978; Paxton, 1972; Wisner, 1963b) have remained relatively stable since the early 1980s, with 33 genera and approximately 250 species currently recognized (Nelson, 2006), the higher-order relationships among lanternfishes have been the subject of much debate (summarized in Fig. 1). Analyses based on adult osteology (Paxton, 1972), larval morphology (Ahlstrom et al., 1976; Moser and Ahlstrom, 1970, 1972), total morphological evidence (Paxton et al., 1984; Stiassny, 1996), and even some molecular data (Yamaguchi, 1999) have failed to provide intergeneric hypotheses with any resampling support. Although Poulsen et al. (2013) presented a seminal mitogenomic perspective on myctophiform fishes based on 41 ingroup species and observed that several significant gene rearrangements support many traditional higher-order myctophid classifications based on morphological evidence, they noted that their sampling is far from ideal, that the placement of some taxa was questionable, and that several critical nodes received low support. Therefore, the relationships of the lanternfish genera remain a significant outstanding problem in teleostean systematics (Stiassny, 1996), and the analysis in this study contributes significantly to resolving this problem by nearly tripling the ingroup coverage of previous studies.

2. Materials and methods

2.1. Outgroup selection

Outgroup taxa can have a significant effect on the structure of the ingroup phylogeny (Sanderson and Shaffer, 2002), and it is generally agreed that outgroup sampling should begin as close to the ingroup taxa as possible (Smith, 1994). Although outgroup selection in higher-level euteleost phylogenetic analyses is difficult due to the lack of phylogenetic resolution, because of the overlap of four nuclear protein-coding markers (*glyt*, *myh6*, *tbr1*, and *zic1*) between the present study and that of Near et al. (2012), the taxa from five orders recovered in that analysis as closest to

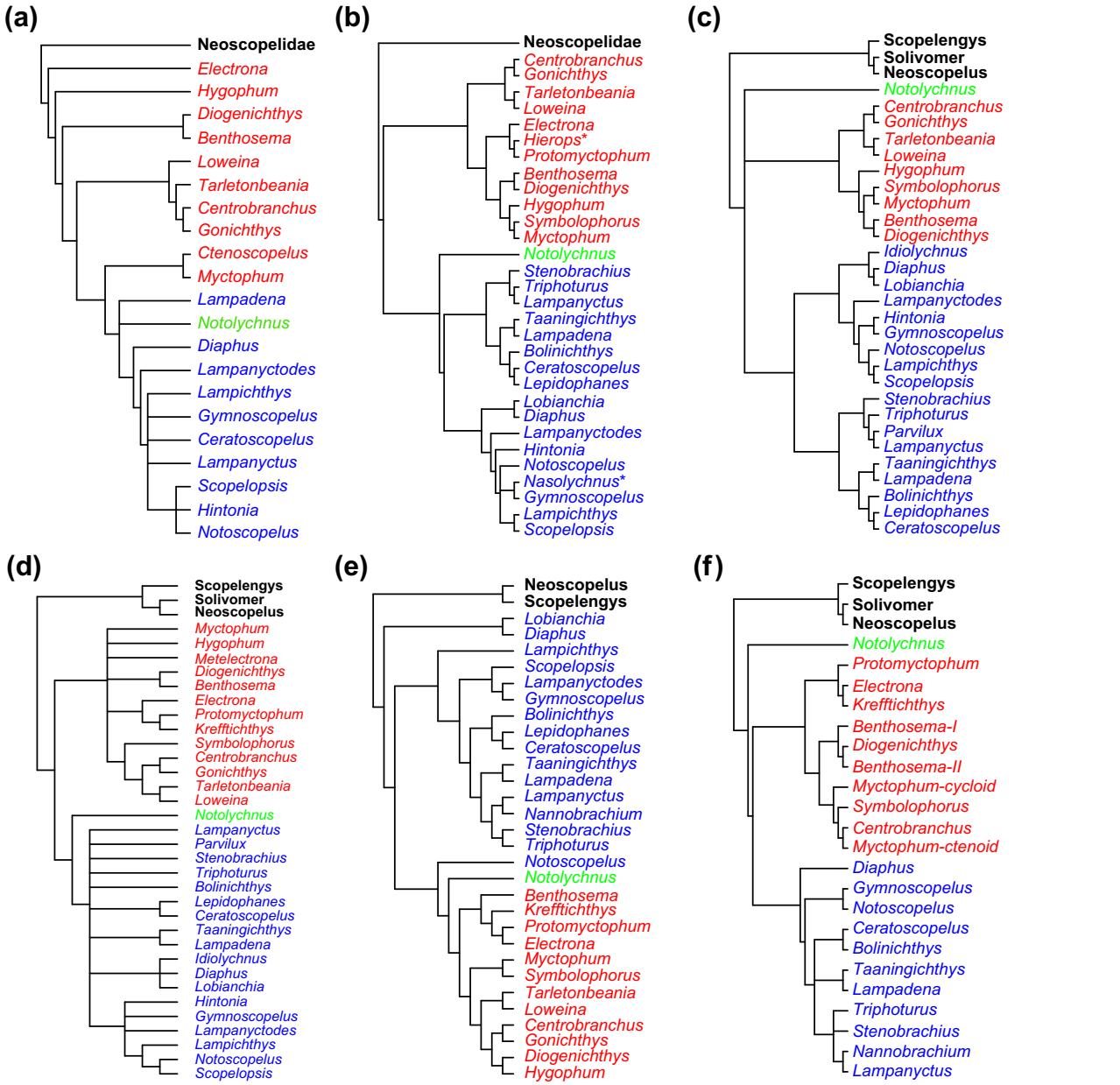

Fig. 1. Previous hypotheses of myctophiform intrarelationships. Only studies of novel datasets spanning the order Myctophiformes *sensu* Rosen (1973) are included, for brevity (but see Bolin (1939), Moser and Ahlstrom (1972), Ahlstrom et al. (1976) and Yamaguchi (2000) for subfamily analyses and reanalyses of existing datasets). Neoscopelid genera are shown in bold, and root the trees shown. Members of the currently recognized myctophid subfamilies Myctophinae and Lampanyctinae are shown in red and blue, respectively, and the enigmatic genus *Notolychnus* (a lampanyctine) is shown in green. (a) Hypothesis of Fraser-Brunner (1949), redrawn from an unrooted, network-like diagram based on holistic interpretation. (b) Hypothesis of Paxton (1972), based on examination of 78 characters of osteology, luminous structure, and meristic data. (c) Hypothesis of Paxton et al. (1984), based on combined analysis of 59 osteological, photophore, and larval morphological characters. (d) Hypothesis of Stiassny (1996), from a strict consensus of parsimony trees obtained from a phylogenetic analysis of the Paxton et al. (1984) dataset plus four new characters. (e) Unpublished topology from Yamaguchi (1999, Fig. 2-10), based on complete mitochondrial 16S sequences. (f) Hypothesis of Poulsen et al. (2013), based on analyses of mitogenomic gene order and sequences. Incongruities between results represented in their Figs. 4 and 5 are redrawn here as polytomies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Myctophiformes (Aulopiformes, Ateleopodiformes, Osmeriformes, Polymixiiformes, and Percopsiformes) were selected as outgroups for the present study. Lampriformes, an order recovered as sister to Myctophiformes in several mitogenomic studies (Miya et al., 2003; Poulsen et al., 2013) was not included in this analysis due to the conflicting position of this order between mitogenomic and nuclear gene analyses and the low resampling support observed in the mitogenomic analyses. Four additional taxa were added to the aulopiform outgroup to increase family-level coverage (Table 1).

2.2. Ingroup taxon and genetic marker sampling

Emphasis was placed on comprehensive tissue sampling at the species level, where possible, within the family Myctophidae. Sampling was drawn from fieldwork trawling aboard the vessel *Oscar Elton Sette* off the Kona Coast of Hawai'i (SE1104, 2011) and the seamounts off the coast of the island of Tutuila, America Samoa (SE1201, 2012), in collaboration with the National Oceanographic and Atmospheric Administration (NOAA) Pacific Islands Fisheries Science Center (PIFSC) and the American Samoa Division of Marine

Table 1
Taxon and molecular markers.

Taxon	Tissue/Specimen Voucher[a]	*bmp4*	*COI*	*glyt*	*histone H3*	*myh6*	*tbr1*	*zic1*
Outgroup								
Alepisaurus ferox				JX190305.1		JX190451.1	JX191178.1	JX191299.1
Amblyopsis rosae						HQ729506.1	HQ729564.1	HQ729593.1
Amblyopsis spelaea						JX459185.1	JX459112.1	JX459138.1
Anotopterus pharao				JX190306.1		JX190452.1		
Aphredoderus gibbosus						JX459184.1	JX459106.1	JX459137.1
Aphredoderus sayanus				JX190317.1		JX459181.1	JX459103.1	JX459134.1
Aplochiton taeniatus				JX190292.1		JX190435.1	JX191167.1	
Ateleopus japonicus				JX190303.1		JX190449.1		JX191297.1
Bathypterois atricolor				JX190307.1		JX190453.1	JX191179.1	JX191300.1
Benthalbella infans				JX190308.1		JX190454.1	JX191180.1	JX191301.1
Brachygalaxias bullocki				JX190293.1		JX190436.1	JX191168.1	
Chlorophthalmus albatrossis	AMNH 240657			KJ555497		KJ555849	KJ555961	KJ556153
Chlorophthalmus nigromarginatus	AMNH 242624			KJ555498		KJ555850	KJ555962	KJ556154
Chologaster cornuta						HQ729510.1	HQ729568.1	HQ729597.1
Forbesichthys agassizii						JX459190.1	JX459108.1	JX459143.1
Forbesichthys papilliferus						JX459188.1	JX459110.1	JX459141.1
Galaxias maculatus				JX190294.1		JX190437.1	JX191169.1	JX191286.1
Galaxiella nigrostriata				JX190295.1		JX190438.1		JX191287.1
Ijimaia loppei				JX190304.1		JX190450.1		JX191298.1
Lestidiops jayakari	AMNH 240651					KJ555891	KJ556066	
Neochanna burrowsius				JX190296.1		JX190439.1	JX191170.1	
Percopsis omiscomaycus				JX188681.1		JX459178.1	JX459100.1	JX189014.1
Percopsis transmontana						JX459179.1	JX459101.1	JX459132.1
Polymixia japonica				JX188676.1		JX189626.1	JX189164.1	JX189010.1
Polymixia lowei			AY662744.1			FJ918889.1	JX189163.1	JX189009.1
Scopelarchoides nicholsi	AMNH 261297			KJ555644		KJ555927	KJ556112	KJ556304
Speoplatyrhinus poulsoni						HQ729511.1	HQ729569.1	HQ729598.1
Synodus foetens				EU002057.1		EU001918.1	EU001998.1	EU001882.1
Typhlichthys eigenmanni						JX459191.1	JX459111.1	JX459146.1
Typhlichthys subterraneus						JN592144.1	JN592103.1	JX459144.1
Ingroup								
Benthosema fibulatum	AMS I.36455-005		KJ555324	KJ555478		KJ555838	KJ555942	KJ556129
Benthosema fibulatumS82	AMNH 261093		KJ555325	KJ555479	KJ555663	KJ555839	KJ555943	KJ556130
Benthosema glaciale	KUIT3734 / MCZ158723	KJ555211		KJ555480	KJ555664	KJ555840	KJ555944	KJ556131
Benthosema panamense	SIO 07-184	KJ555212	KJ555326	KJ555481	KJ555665	KJ555841	KJ555945	KJ556132
Benthosema pterotum3	AMNH 261306		KJ555327	KJ555482	KJ555666	KJ555842	KJ555946	KJ556133
Benthosema suborbitale	AMNH 261233	KJ555213		KJ555483	KJ555667	KJ555843		KJ556134
Bolinichthys distofax2	AMNH 261234	KJ555214		KJ555484	KJ555668		KJ555947	KJ556135
Bolinichthys indicus	MCZ 165773	KJ555215		KJ555485	KJ555669			KJ556136
Bolinichthys longipes1	SIO 06-101	KJ555216	KJ555328	KJ555486	KJ555670		KJ555948	KJ556137
Bolinichthys longipes2	AMNH 261213	KJ555217	KJ555329		KJ555671			KJ556138
Bolinichthys photothorax	AMNH 261214	KJ555218		KJ555487	KJ555672		KJ555949	KJ556139
Bolinichthys supralateralis1	NMVA 25111-028	KJ555219	KJ555330	KJ555488	KJ555673		KJ555950	KJ556140
Centrobranchus andreae1	AMNH 261293		KJ555331	KJ555489	KJ555674	KJ555844	KJ555951	KJ556141
Centrobranchus andreae2	AMNH 261298		KJ555332	KJ555490	KJ555675	KJ555845	KJ555952	KJ556142
Centrobranchus andreae3	AMNH 261298		KJ555333	KJ555491	KJ555676		KJ555953	KJ556143
Centrobranchus cf. *brevirostrisS60*	AMNH 261206		KJ555334		KJ555677	KJ555846	KJ555954	KJ556144
Centrobranchus choerocephalus	UW 111709	KJ555220	KJ555335	KJ555492	KJ555678	KJ555847	KJ555955	KJ556145
Centrobranchus nigroocellatus	MCZ 165495		KJ555336	KJ555493	KJ555679	KJ555848	KJ555956	KJ556146
Ceratoscopelus maderensis	KUIT 1066 / KUI 27065	KJ555221	KJ555337		KJ555680			KJ556147
Ceratoscopelus townsendi	SIO 09-075	KJ555222	KJ555338		KJ555681		KJ555957	KJ556148
Ceratoscopelus warmingii form 1S88	AMNH 261119	KJ555226	KJ555342		KJ555685		KJ555960	KJ556152
Ceratoscopelus warmingii form 4S72	AMNH 261148	KJ555225	KJ555341	KJ555496	KJ555684		KJ555959	KJ556151
Ceratoscopelus warmingii form A	AMNH 261216	KJ555223	KJ555339	KJ555494	KJ555682		KJ555958	KJ556149
Ceratoscopelus warmingii form B	AMNH 261217	KJ555224	KJ555340	KJ555495	KJ555683			KJ556150
Diaphus adenomus	NMVA 25120-002	KJ555227	KJ555343	KJ555499	KJ555686		KJ555963	KJ556155
Diaphus aliciaeS107	AMNH 261197	KJ555228	KJ555344	KJ555500	KJ555687		KJ555964	KJ556156
Diaphus anderseni10-169	SIO 10-169		KJ555345	KJ555501	KJ555688		KJ555965	KJ556157
Diaphus anderseni10-170	SIO 10-170		KJ555346	KJ555502	KJ555689		KJ555966	KJ556158
Diaphus antonbruuniS65	AMNH 261089	KJ555229	KJ555347	KJ555503	KJ555690		KJ555967	KJ556159
Diaphus brachycephalusS75	AMNH 261149	KJ555230	KJ555348		KJ555691		KJ555968	KJ556160
Diaphus chrysorhynchusT2	AMNH 261308						KJ555970	KJ556162
Diaphus chrysorhynchusT3	AMNH 261308			KJ555505	KJ555693		KJ555971	KJ556163
Diaphus chrysorhynchusT4	AMNH 261308	KJ555232			KJ555694		KJ555972	KJ556164
Diaphus chrysorhynchusT7	AMNH 261308	KJ555233		KJ555506			KJ555973	KJ556165
Diaphus effulgens	KUIT 3609 / MCZ 159080	KJ555234	KJ555350	KJ555507	KJ555695		KJ555974	KJ556166
Diaphus fragilisS32	AMNH 261137		KJ555351	KJ555508	KJ555696		KJ555975	KJ556167
Diaphus fragilisS57	AMNH 261137		KJ555352	KJ555509	KJ555697		KJ555976	KJ556168
Diaphus fulgens	SIO 06-291	KJ555235	KJ555353	KJ555510	KJ555698		KJ555977	KJ556169
Diaphus garmaniS80	AMNH 261151		KJ555354	KJ555511	KJ555699		KJ555978	KJ556170
Diaphus lobatusS95	AMNH 261210	KJ555236	KJ555355	KJ555512	KJ555700		KJ555979	KJ556171
Diaphus malayanusS35	AMNH 261138	KJ555237	KJ555356	KJ555513	KJ555701		KJ555980	KJ556172

(*continued on next page*)

Table 1 (*continued*)

Taxon	Tissue/Specimen Voucher[a]	*bmp4*	*COI*	*glyt*	*histone H3*	*myh6*	*tbr1*	*zic1*
Diaphus meadi	NMVA 25104-021		KJ555357	KJ555514	KJ555702		KJ555981	KJ556173
Diaphus metopoclampus	NMVA 25104-020	KJ555238	KJ555358	KJ555515	KJ555703		KJ555982	KJ556174
Diaphus cf. *mollisK13*	AMNH 261262	KJ555231	KJ555349	KJ555504	KJ555692		KJ555969	KJ556161
Diaphus mollis	NMVA 25104-019	KJ555239	KJ555359	KJ555516			KJ555983	KJ556175
Diaphus mollisS79	AMNH 261152	KJ555240	KJ555360	KJ555517	KJ555704		KJ555984	KJ556176
Diaphus nielseniT6	AMNH 261309	KJ555241		KJ555518	KJ555705		KJ555985	KJ556177
Diaphus parriS44	AMNH 261153	KJ555242	KJ555361	KJ555519	KJ555706		KJ555986	KJ556178
Diaphus parriS47	AMNH 261153	KJ555243	KJ555362	KJ555520	KJ555707		KJ555987	KJ556179
Diaphus parriS70	AMNH 261153	KJ555244	KJ555363	KJ555521	KJ555708		KJ555988	KJ556180
Diaphus perspicillatus	NMVA 25111-022			KJ555522	KJ555709		KJ555989	KJ556181
Diaphus perspicillatusS87	AMNH 261124		KJ555364	KJ555523	KJ555710		KJ555990	KJ556182
Diaphus perspicillatusS89	AMNH 261124		KJ555365	KJ555524	KJ555711		KJ555991	KJ556183
Diaphus phillipsiS46	AMNH 261154	KJ555245		KJ555525	KJ555712		KJ555992	KJ556184
Diaphus regani89002	AMS I.45489-002			KJ555526	KJ555713		KJ555993	KJ556185
Diaphus richardsoniS58	AMNH 261207	KJ555246	KJ555366				KJ555994	KJ556186
Diaphus schmidtiK15	AMNH 261264	KJ555247	KJ555367	KJ555527	KJ555714		KJ555995	KJ556187
Diaphus signatus	AMNH 239371	KJ555248	KJ555368	KJ555528	KJ555715		KJ555996	KJ556188
Diaphus sp. K12	AMNH 261261	KJ555249		KJ555529			KJ555997	KJ556189
Diaphus sp. S20	AMNH 261198	KJ555250	KJ555369	KJ555530	KJ555716		KJ555998	KJ556190
Diaphus sp. S61	AMNH 261125	KJ555251	KJ555370	KJ555531	KJ555717		KJ555999	KJ556191
Diaphus sp. S106	AMNH 33211	KJ555252	KJ555371	KJ555532	KJ555718		KJ556000	KJ556192
Diaphus splendidus	SIO 02-047	KJ555253	KJ555372	KJ555533	KJ555719		KJ556001	KJ556193
Diaphus splendidusS43	AMNH 261101	KJ555254	KJ555373	KJ555534	KJ555720		KJ556002	KJ556194
Diaphus suborbitalisS52	AMNH 261159			KJ555535	KJ555721		KJ556003	KJ556195
Diaphus suborbitalisS54	AMNH 261159			KJ555536	KJ555722		KJ556004	KJ556196
Diaphus termophilus	AMS I.28744-003	KJ555255		KJ555537	KJ555723		KJ556005	KJ556197
Diaphus theta1	UW 118842	KJ555256	KJ555374	KJ555538	KJ555724		KJ556006	KJ556198
Diaphus theta2	KUIT 2135 / KUI 27971	KJ555257		KJ555539	KJ555725		KJ556007	KJ556199
Diaphus thiollieriK1	AMNH 261256		KJ555375	KJ555540	KJ555726		KJ556008	KJ556200
Diaphus thiollieriK2	AMNH 261256		KJ555376	KJ555541			KJ556009	KJ556201
Diaphus umbroculusT8	AMNH 261313	KJ555258		KJ555542	KJ555727		KJ556010	KJ556202
Diaphus watasei1	AMNH 242864	KJ555259	KJ555377	KJ555543	KJ555728		KJ556011	KJ556203
Diaphus watasei2	AMNH 240616	KJ555260	KJ555378	KJ555544	KJ555729		KJ556012	KJ556204
Diaphus whitleyi	AMS I.45474-006	KJ555261	KJ555379	KJ555545	KJ555730		KJ556013	KJ556205
Diogenichthys atlanticus	SIO 09-075		KJ555380		KJ555731	KJ555851	KJ556014	
Diogenichthys atlanticusA13	AMNH 261303		KJ555381		KJ555732	KJ555852	KJ556015	
Diogenichthys cf. *panurgus*	AMS I.45493-004		KJ555382			KJ555853	KJ556016	
Diogenichthys laternatus	SIO 06-291		KJ555383		KJ555733	KJ555854		
Electrona antarctica1	AMS I.36252-002	KJ555262		KJ555546	KJ555734	KJ555855	KJ556017	KJ556206
Electrona antarctica2	uncatalogued			KJ555547		KJ555856	KJ556018	KJ556207
Electrona carlsbergi371	CSIRO H 6333-03		KJ555384	KJ555548	KJ555735	KJ555857	KJ556019	KJ556208
Electrona paucirastra4978	CSIRO H 6863-10		KJ555385	KJ555549		KJ555858	KJ556020	KJ556209
Electrona paucirastra4980	CSIRO H 6882-01		KJ555386	KJ555550	KJ555736	KJ555859	KJ556021	KJ556210
Electrona risso	NMVA25104-036		KJ555387	KJ555551	KJ555737	KJ555860	KJ556022	KJ556211
Electrona risso3794	CSIRO H 6855-02		KJ555388	KJ555552	KJ555738	KJ555861	KJ556023	KJ556212
Electrona risso3810	CSIRO H 6856-03		KJ555389	KJ555553		KJ555862	KJ556024	KJ556213
Gonichthys cocco	MCZ 165707	KJ555263	KJ555390	KJ555554	KJ555739	KJ555863	KJ556025	KJ556214
Gonichthys tenuiculus	UW 111573		KJ555391		KJ555740	KJ555864	KJ556026	KJ556215
Gymnoscopelus bolini	uncatalogued	KJ555264	KJ555392	KJ555555	KJ555741	KJ555865	KJ556027	KJ556216
Gymnoscopelus braueri1	AMS I.36251-001	KJ555265		KJ555556	KJ555742	KJ555866	KJ556028	KJ556217
Gymnoscopelus braueri2	uncatalogued	KJ555266	KJ555393	KJ555557	KJ555743	KJ555867		KJ556218
Gymnoscopelus hintonoides	uncatalogued	KJ555267	KJ555394	KJ555558		KJ555868	KJ556029	KJ556219
Gymnoscopelus nicholsi1	AMS I.36247-001	KJ555268		KJ555559	KJ555744	KJ555869	KJ556030	KJ556220
Gymnoscopelus nicholsi2	uncatalogued		KJ555395	KJ555560		KJ555870	KJ556031	KJ556221
Gymnoscopelus piabilis	uncatalogued	KJ555269	KJ555396	KJ555561	KJ555745	KJ555871	KJ556032	KJ556222
Hygophum atratum1	UW 111595	KJ555270	KJ555397	KJ555562	KJ555746	KJ555872	KJ556033	KJ556223
Hygophum hanseni55	AMNH 261181	KJ555271	KJ555398	KJ555563	KJ555747	KJ555873	KJ556034	KJ556224
Hygophum hygomii	uncatalogued	KJ555272	KJ555399	KJ555564	KJ555748	KJ555874	KJ556035	KJ556225
Hygophum proximum1	UW 111673	KJ555273	KJ555400	KJ555565	KJ555749	KJ555875	KJ556036	KJ556226
Hygophum proximum2	AMNH 261218	KJ555274	KJ555401	KJ555566	KJ555750	KJ555876	KJ556037	KJ556227
Hygophum reinhardtii	AMNH 261219	KJ555275	KJ555402	KJ555567	KJ555751	KJ555877	KJ556038	KJ556228
Krefftichthys anderssoni	uncatalogued		KJ555403	KJ555568		KJ555878	KJ556039	KJ556229
Krefftichthys anderssoni386	CSIRO H 6337-11	KJ555276	KJ555404	KJ555569	KJ555752	KJ555879	KJ556040	KJ556230
Lampadena luminosa94001	AMS I.45494-001	KJ555277		KJ555570	KJ555753	KJ555880		KJ556231
Lampadena luminosaS22	AMNH 261203		KJ555405	KJ555571	KJ555754		KJ556041	KJ556232
Lampadena luminosaS23	AMNH 261203		KJ555406	KJ555572	KJ555755	KJ555881	KJ556042	KJ556233
Lampadena speculigera	KUIT 5278 / MCZ 161560	KJ555278		KJ555573	KJ555756	KJ555882	KJ556043	KJ556234
Lampadena urophaos atlantica	SIO 09-318	KJ555279	KJ555407	KJ555574	KJ555757	KJ555883	KJ556044	KJ556235
Lampadena urophaos urophaos1	AMNH 261300		KJ555408	KJ555575	KJ555758	KJ555884	KJ556045	KJ556236
Lampadena urophaos urophaos2	AMNH 261300		KJ555409	KJ555576	KJ555759	KJ555885	KJ556046	KJ556237
Lampadena urophaos urophaos3	AMNH 261300		KJ555410	KJ555577	KJ555760	KJ555886	KJ556047	KJ556238
Lampadena urophaos urophaos4	AMNH 261300			KJ555578	KJ555761	KJ555887	KJ556048	KJ556239
Lampanyctodes hectoris	CSIRO H 6975-01	KJ555280		KJ555579	KJ555762	KJ555888	KJ556049	

Table 1 (*continued*)

Taxon	Tissue/Specimen Voucher[a]	*bmp4*	*COI*	*glyt*	*histone H3*	*myh6*	*tbr1*	*zic1*
Lampanyctus alatus	AMS I.45490-005			KJ555580	KJ555763		KJ556050	KJ556240
Lampanyctus festivus06-094	SIO 06-094			KJ555581	KJ555764		KJ556051	KJ556241
Lampanyctus festivus06-095	SIO 06-095			KJ555582	KJ555765		KJ556052	KJ556242
Lampanyctus hubbsi	SIO 06-293	KJ555281	KJ555411	KJ555583	KJ555766		KJ556053	KJ556243
Lampanyctus intricarius	NMVA 25111-014		KJ555412	KJ555584	KJ555767		KJ556054	KJ556244
Lampanyctus jordani	UW 117617	KJ555282	KJ555413		KJ555768		KJ556055	KJ556245
Lampanyctus macdonaldi	KUIT 7446 / MCZ 164404	KJ555283	KJ555414	KJ555585	KJ555769		KJ556056	KJ556246
Lampanyctus parvicauda	UW 111675			KJ555586	KJ555770		KJ556057	KJ556247
Lampanyctus pusillus	KUIT 267 / KUI 26890	KJ555284	KJ555415	KJ555587	KJ555771		KJ556058	KJ556248
Lampanyctus tenuiformis	SIO 05-080	KJ555285		KJ555588	KJ555772		KJ556059	KJ556249
Lampanyctus turneriS81	AMNH 261160	KJ555286	KJ555416	KJ555589	KJ555773		KJ556060	KJ556250
Lampanyctus vadulus94004	AMS I.45494-004			KJ555590	KJ555774		KJ556061	KJ556251
Lampichthys procerus3823	CSIRO H 6857-03	KJ555287		KJ555591	KJ555775	KJ555889	KJ556062	KJ556252
Lampichthys procerus3825	CSIRO H 6857-04	KJ555288		KJ555592	KJ555776	KJ555890	KJ556063	KJ556253
Lepidophanes guentheriKU	KUIT 3796 / KUI 28493	KJ555289	KJ555417	KJ555593	KJ555777		KJ556064	KJ556254
Lepidophanes guentheriMCZ	MCZ 165730	KJ555290	KJ555418	KJ555594	KJ555778		KJ556065	KJ556255
Lobianchia dofleini	NMVA 25104-039	KJ555291	KJ555419	KJ555595	KJ555779		KJ556067	KJ556256
Lobianchia gemellarii	KUIT 265 / KUI 26901	KJ555292	KJ555420	KJ555596	KJ555780		KJ556068	KJ556257
Loweina rara10-171	SIO 10-171		KJ555421	KJ555597	KJ555781	KJ555892	KJ556069	KJ556258
Metelectrona ventralis3775	CSIRO H 6853-02	KJ555293	KJ555422	KJ555598	KJ555782	KJ555893	KJ556070	KJ556259
Metelectrona ventralis3788	CSIRO H 6854-01		KJ555423	KJ555599	KJ555783	KJ555894		
Metelectrona ventralis3964	CSIRO H 6875-01	KJ555294	KJ555424	KJ555600	KJ555784	KJ555895	KJ556071	KJ556260
Myctophum affine	MCZ165770	KJ555295	KJ555425	KJ555601	KJ555785	KJ555896	KJ556072	KJ556261
Myctophum asperum	AMNH 240603	KJ555296	KJ555426	KJ555602	KJ555786	KJ555897	KJ556073	KJ556262
Myctophum aurolaternatum	UW 111625	KJ555297	KJ555427	KJ555603	KJ555787	KJ555898	KJ556074	KJ556263
Myctophum brachygnathum	UW 111558	KJ555298	KJ555428	KJ555604	KJ555788	KJ555899	KJ556075	KJ556264
Myctophum lychnobium	UW 111723	KJ555299	KJ555429	KJ555605	KJ555789	KJ555900	KJ556076	KJ556265
Myctophum nitidulum	UW 111635		KJ555430	KJ555606			KJ556077	KJ556266
Myctophum obtusirostre	UW 114331	KJ555300	KJ555431	KJ555607	KJ555790	KJ555901	KJ556078	KJ556267
Myctophum orientaleS25	AMNH 261099	KJ555301	KJ555432	KJ555608	KJ555791	KJ555902	KJ556079	KJ556268
Myctophum phengodes	AMS I.41889-001	KJ555302	KJ555433	KJ555609	KJ555792	KJ555903		KJ556269
Myctophum punctatum	KUIT 3802 / KUI 28499	KJ555303	KJ555434	KJ555610	KJ555793	KJ555904	KJ556080	KJ556270
Myctophum selenops1	AMNH 261299		KJ555435	KJ555611	KJ555794	KJ555905	KJ556081	KJ556271
Myctophum selenops2	AMNH 261299		KJ555436	KJ555612	KJ555795	KJ555906	KJ556082	KJ556272
Myctophum selenops3	AMNH 261299		KJ555437	KJ555613	KJ555796	KJ555907	KJ556083	KJ556273
Myctophum spinosumS27	AMNH 261116		KJ555438	KJ555614	KJ555797	KJ555908	KJ556084	KJ556274
Myctophum spinosumS30	AMNH 261096		KJ555439	KJ555615	KJ555798	KJ555909	KJ556085	KJ556275
Nannobrachium achirus	uncatalogued		KJ555440	KJ555616	KJ555799		KJ556086	KJ556276
Nannobrachium atrum	AMS I.28740-004		KJ555441	KJ555617	KJ555800		KJ556087	KJ556277
Nannobrachium bristori10-169	SIO 10-169		KJ555442	KJ555618	KJ555801		KJ556088	KJ556278
Nannobrachium fernae10-165	SIO 10-165		KJ555443	KJ555619	KJ555802		KJ556089	KJ556279
Nannobrachium hawaiiensis10-169 1	SIO 10-169			KJ555620	KJ555803		KJ556090	KJ556280
Nannobrachium hawaiiensis10-169 2	SIO 10-169			KJ555621	KJ555804		KJ556091	KJ556281
Nannobrachium lineatum	KUIT 3634 / MCZ 159035	KJ555304	KJ555444	KJ555623	KJ555806		KJ556093	KJ556283
Nannobrachium regale	SIO 08-031	KJ555305	KJ555445		KJ555807		KJ556094	KJ556284
Nannobrachium ritteri	KUIT 2371 / KUI 27975	KJ555306		KJ555624	KJ555808		KJ556095	KJ556285
Neoscopelus macrolepidotus	KUIT 3297 / MCZ uncatalogued					EU001917.1	EU001997.1	EU001881.1
Neoscopelus microchir1	AMNH 239376		KJ555446	KJ555625	KJ555809	KJ555910	KJ556096	KJ556286
Neoscopelus microchir2	AMNH 239306		KJ555447	KJ555626	KJ555810	KJ555911	KJ556097	KJ556287
Neoscopelus porosus	AMNH 240619		KJ555448	KJ555627	KJ555811	KJ555912	KJ556098	KJ556288
Notolychnus valdiviae	SIO 06-2932	KJ555307	KJ555449	KJ555628	KJ555812	KJ555913		KJ556289
Notolychnus valdiviae83001	AMS I.45483-001	KJ555308		KJ555629	KJ555813	KJ555914		KJ556290
Notoscopelus caudispinosus	KUIT 5307	KJ555309	KJ555450	KJ555630		KJ555915	KJ556099	KJ556291
Notoscopelus resplendens	NMVA 25104-037	KJ555310	KJ555451	KJ555631	KJ555814	KJ555916	KJ556100	KJ556292
Parvilux ingens	SIO 08-145		KJ555452	KJ555632	KJ555815		KJ556101	KJ556293
Protomyctophum andreashevi360	CSIRO H 6388-03		KJ555453	KJ555633	KJ555816	KJ555917	KJ556102	KJ556294
Protomyctophum andreashevi362	CSIRO H 6352-01		KJ555454	KJ555634		KJ555918	KJ556103	KJ556295
Protomyctophum bolini349	CSIRO H 6338-01		KJ555455	KJ555635	KJ555817	KJ555919	KJ556104	KJ556296
Protomyctophum bolini353	uncatalogued		KJ555456	KJ555636				
Protomyctophum crockeri	SIO 08-031	KJ555311	KJ555457	KJ555637	KJ555818	KJ555920	KJ556105	KJ556297
Protomyctophum gemmatum366	CSIRO H 6338-04		KJ555458	KJ555638		KJ555921	KJ556106	KJ556298
Protomyctophum gemmatum3911	CSIRO H 6863-05		KJ555459	KJ555639		KJ555922	KJ556107	KJ556299
Protomyctophum parallelum367	CSIRO H 6337-03			KJ555640	KJ555819	KJ555923	KJ556108	KJ556300
Protomyctophum parallelum369	CSIRO H 6337-04			KJ555641		KJ555924	KJ556109	KJ556301
Protomyctophum thompsoni1	UW 118841	KJ555312	KJ555460	KJ555642		KJ555925	KJ556110	KJ556302
Protomyctophum thompsoni2	KUIT 2133 / KUI 27969			KJ555643	KJ555820	KJ555926	KJ556111	KJ556303
Scopelengys tristis1	KUIT 3240 / KUI 28210		KJ555461	KJ555645	KJ555821	KJ555928	KJ556113	KJ556305
Scopelengys tristis2	uncatalogued		KJ555462	KJ555646		KJ555929	KJ556114	KJ556306
Scopelopsis multipunctatus1	AMS I.28740-002	KJ555313	KJ555463	KJ555647	KJ555822	KJ555930	KJ556115	KJ556307
Scopelopsis multipunctatus2	NMVA 25104-025	KJ555314		KJ555648	KJ555823	KJ555931	KJ556116	KJ556308
Solivomer arenidens	NSMT-DNA-19792		KJ555464	KJ555649	KJ555824	KJ555932	KJ556117	KJ556309
Stenobrachius leucopsarus	KUIT 461 / KUI 28125	KJ555315	KJ555465	KJ555650	KJ555825			KJ556310

(*continued on next page*)

Table 1 (*continued*)

Taxon	Tissue/Specimen Voucher[a]	*bmp4*	*COI*	*glyt*	*histone H3*	*myh6*	*tbr1*	*zic1*
Symbolophorus californiensis1	AMNH 259818		KJ555466	KJ555651	KJ555826	KJ555933	KJ556118	KJ556311
Symbolophorus californiensis2	AMNH 259819		KJ555467	KJ555652	KJ555827	KJ555934	KJ556119	KJ556312
Symbolophorus evermanni	UW 111614	KJ555316	KJ555468	KJ555653	KJ555828	KJ555935	KJ556120	
Symbolophorus reversus	UW 114349	KJ555317	KJ555469	KJ555654	KJ555829	KJ555936	KJ556121	
Symbolophorus rufinus	UW 111555	KJ555318	KJ555470	KJ555655	KJ555830	KJ555937	KJ556122	
Taaningichthys bathyphilus	uncatalogued	KJ555319	KJ555471	KJ555656	KJ555831	KJ555938	KJ556123	KJ556313
Taaningichthys minimus	AMNH 261302		KJ555472	KJ555657	KJ555832	KJ555939	KJ556124	KJ556314
Tarletonbeania crenularis1	UW 112165	KJ555320	KJ555473	KJ555658	KJ555833	KJ555940	KJ556125	KJ556315
Tarletonbeania crenularis2	KUIT 2209 / KUI 27938	KJ555321	KJ555474	KJ555659	KJ555834	KJ555941	KJ556126	KJ556316
Triphoturus mexicanus	AMS I.35018-003	KJ555322	KJ555475	KJ555660	KJ555835		KJ556127	KJ556317
Triphoturus nigrescens	AMS I.45492-018		KJ555476	KJ555661	KJ555836			KJ556318
Triphoturus oculeum	SIO 06-286	KJ55532	KJ555477	KJ555662	KJ555837		KJ556128	KJ556319

[a] Voucher specimen and tissue accession numbers shown for specimens from which sequence data was generated in this study.

and Wildlife Resources (DMWR). All specimens obtained during fieldwork were accessioned into the Ichthyology collection at the American Museum of Natural History. Tissue samples were also obtained from the collections of the Scripps Institution of Oceanography (SIO); the Museum of Comparative Zoology (MCZ); the American Museum of Natural History (AMNH); the Muséum National d'Histoire Naturelle (MNHN); the National Museum of Victoria, Melbourne, Australia (NMVM); the Australian Museum, Sydney, Australia (AMS); the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Hobart, Tasmania; the Biodiversity Institute at the University of Kansas (KUI, KUIT); the Burke Museum of the University of Washington (UW); the National Museum of Marine Biology and Aquarium Research, Taiwan; and the National Museum of Nature and Science, Tokyo (NSMT). Ingroup sampling within the order Myctophiformes included all three neoscopelid genera (*Neoscopelus*, *Scopelengys*, *Solivomer*) and five of the six nominal species in the family, excluding *Scopelengys clarkei* Butler and Ahlstrom, 1976. Ingroup sampling within the family Myctophidae included 31 of the 33 nominal myctophid genera (Herring, 2007; Nelson, 2006), excluding the rare monotypic taxa *Idiolychnus urolampus* (Nafpaktitis and Paxton, 1978) and *Hintonia candens* Fraser-Brunner, 1949, and featured 50% or greater coverage at the species level within all genera except *Lampadena*, *Lampanyctus*, *Nannobrachium*, and *Diaphus*, for which representatives of the five cranial photophore groups (Supraorbital [Suo], Suborbital [So], Antorbital [Ant], Dorsonasal–Ventronasal group I [Dn–Vn I], and Dorsonasal–Ventronasal group II [Dn–Vn II]) were included at differing levels of sampling completeness. Where possible, several individuals were included for a given species as both a check on possible gene paralogy, and as a check on species identification, given the fragile nature of many of the diagnostic characters of these fishes.

Seven protein-coding markers—six nuclear and one mitochondrial—were selected for use in this analysis. Marker selection was based on a combination of two factors: marker length and informativeness (Supplemental Table S1) and marker biological function (Supplemental Text 1). Emphasis was placed, during marker selection and preliminary PCR amplification, on incorporating genes with different biological functions.

2.3. Marker amplification and sequencing

Total genomic DNA was extracted from tissues (muscle or fin clips) from specimens either preserved in 95% EtOH or frozen at −80 °C, using a Qiagen DNEasy Tissue Extraction Kit (Qiagen Inc, Valencia, CA), following the manufacturer's protocol. Polymerase Chain Reaction (PCR) reactions for each sample were performed in 25 μL volumes, each containing one illustra PuReTaq Ready-To-Go PCR bead (GE Healthcare), 21 μL of molecular-biology-grade water, 1 μL of 10 μM forward and 1 μL reverse primer, and between 1 μL and 5 μL of genomic template DNA. In general, nested PCR following the procedure of Li et al. (2007) was used (see Table 2 for thermocycler profiles and primer sequences). For reactions in which a larger template volume was used, the volume of molecular-biology-grade water was adjusted downward. Due to the occasional presence of double bands, *bmp4* PCR products were cleaned by gel extraction using a QiaQuick Gel Extraction kit (Qiagen Inc., Valencia, CA). Full volumes of *bmp4* PCR products were run on a 1.3% quick-melting agarose gel in 1× Tris–Acetate-EDTA. For each sample, all bands conforming to the expected length of *bmp4* for the primers used (between 500 bp and 700 bp) were excised and gel extracted using the manufacturer's protocol. Final elutions of *bmp4* product were carried out into 30 μL molecular-biology-grade water and sequenced directly. For the other six markers, double-stranded PCR products were purified using Agencourt AMPure XP (Beckman Coulter Inc., Indianapolis, IN) by transferring 10 μL of PCR product into 18 μL Ampure XL, following the manufacturer's recommended ratio of product to beads. Each mixture was incubated for 5 min at room temperature (RT), and then pelleted on a magnet. Pellets were washed with three cycles of 200 μL 70% EtOH, dried for 25 min, and resuspended in 40 μL molecular-biology-grade water before sequencing. Sequencing of forward and reverse strands for each amplified product was carried out separately. Each reaction was performed in an 8 μL total volume, containing 1 μL of 3.2 μM primer, 1.0 μL of BigDye® Terminator v3.1 (Life Technologies, Carlsbad, CA), 1 μL of BigDye® Terminator v3.1 5× Sequencing Buffer, and 5 μL of cleaned PCR product. Sequencing reactions consisted of a 2:00 min initial denaturation at 94 °C, followed by 35 cycles of denaturation at 94 °C for 0:30 min, annealing at 50 °C for 1:00 min, and extension at 60 °C for 4:00. Sequencing reaction products were cleaned by adding 10 μL of AgenCourt® CleanSEQ® (Life Technologies, Carlsbad, CA) and 37.5 μL 85% EtOH to the sequencing reaction and mixing. Reaction mixtures were pelleted and washed twice with 100 μL 85% EtOH, dried at RT for 10 min and resuspended in 40 μL 0.5 mM EDTA prior to sequencing. Sequences were generated on an Applied Biosystems® 3730xl DNA Analyzer (Life Technologies, Carlsbad, CA) at the AMNH Molecular Systematics Laboratories. Forward and reverse sequences for each reaction were assembled and edited using Geneious Pro v5.1.7 (Biomatters, 2010).

2.4. Sequence alignment, partition selection, and phylogenetic analysis

The resulting sequences were trimmed to exclude primer regions and examined for appropriateness using BLASTx (Altschul

Table 2
PCR protocols.

Marker	Source	Primer	Sequence	Thermocycler profile
H3	Colgan et al. (1998)	H3a-L	ATGGCTCGTACCAAGCAGACVGC	94 °C/3:00; [94 °C/0:45; 52–50 °C/0:45; 72 °C/0:45] × 35; 72 °C/6:00
	Colgan et al. (1998)	H3b-H	ATATCCTTRGGCATRATRGTGAC	
glyt	Li et al. (2007)	Glyt_F559	GGACTGTCMAAGATGACCACMT	95 °C/3:00; [98 °C/0:20; 57 °C/0:45; 72 °C/0:45] × 25
	Li et al. (2007)	Glyt_R1562	CCCAAGAGGTTCTTGTTRAAGAT	[98 °C/0:20; 55 °C/0:45; 72 °C/0:45] × 10; 72 °C/6:00
	Li et al. (2007)	Glyt_F577	ACATGGTACCAGTATGGCTTTGT	
	Li et al. (2007)	Glyt_R1464	GTAAGGCATATASGTGTTCTCTCC	
	This study	glyt-mycto-F	GGGAATGAGATCCGACAGTTT	
	This study	glyt-mycto-R	CATGGGATCTGCCAGGAGAC	
myh6	Li et al. (2007)	myh6_F459	CATMTTYTCCATCTCAGATAATGC	95 °C/3:00; [98 °C/0:20; 57 °C/0:45; 72 °C/0:45] × 25
	Li et al. (2007)	myh6_R1325	ATTCTCACCACCATCCAGTTGAA	[98 °C/0:20; 55 °C/0:45; 72 °C/0:45] × 10; 72 °C/6:00
	Li et al. (2007)	myh6_F507	GGAGAATCARTCKGTGCTCATCA	
	Li et al. (2007)	myh6_R1322	CTCACCACCATCCAGTTGAACAT	
	This study	myh6F-mycto	ACACCAAGCGAGTCATCCA	
	This study	myh6R-mycto	TCCGAGGGAGTAGTAGACTTGA	
COI	Folmer et al. (1994)	LCO1490	GGTCAACAAATCATAAAGATATTGG	95 °C/3:00; [94 °C/1:00; 45 °C/0:45; 72 °C/1:15] × 35; 72 °C/6:00
	Folmer et al. (1994)	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	
bmp4	Smith et al. (2008)	Bmp4-2Fa	TCTYATYTCAGAGCACATGGAGAGG	95 °C/1:30; [95 °C/0:30; 57–55 °C/1:00; 72 °C/1:30] × 35; 72 °C/5:00
	Smith et al. (2008)	Bmp4-2R	ATCGCTGAAGTCCACGTAC	
	This study	bmp4myctoF	AGCACATGGAGAGGCAGT	
	This study	bmp4myctoR	GTACAGTGCGTGGCGTCT	
tbr1	Li et al. (2007)	tbr1_F1	TGTCTACACAGGCTGCGACAT	95 °C/3:00; [98 °C/0:20; 55 °C/0:45; 72 °C/0:45] × 25
	Li et al. (2007)	tbr1_R820	GATGTCCTTRGWGCAGTTTTT	[98 °C/0:20; 53 °C/0:45; 72 °C/0:45] × 10; 72 °C/6:00
	Li et al. (2007)	tbr1_F86	GCCATGMCTGGYTCTTTCCT	
	Li et al. (2007)	tbr1_R811	GGAGCAGTTTTTCTCRCATTC	
zic1	Li et al. (2007)	zic1_F9	GGACGCAGGACCGCARTAYC	95 °C/3:00; [98 °C/0:20; 55 °C/0:45; 72 °C/0:45] × 25
	Li et al. (2007)	zic1_R967	CTGTGTGTGTCCTTTTGTGRATYTT	[98 °C/0:20; 53 °C/0:45; 72 °C/0:45] × 10; 72 °C/6:00
	Li et al. (2007)	zic1_F16	GGACCGCAGTATCCCACYMT	
	Li et al. (2007)	zic1_R963	GTGTGTCCTTTTGTGAATTTTYAGRT	

et al., 1990) and the genetic code corresponding to the marker (Standard, or VertMito for *co1*). Sequences having |*E*-value| larger than 90 were kept. All sequences were checked for stop codons and for miscalled amino acids by examining translation alignments of the nucleotide data, generated in Geneious Pro v5.1.7 (Biomatters, 2010), against the sequence chromatograms. Polymorphism was retained using the IUPAC designation assigned by Geneious. Final sequence alignments were conducted in Geneious using the Translation Align feature, with MAFFT v7017 (Katoh et al., 2005) as the underlying sequence alignment algorithm, using the appropriate genetic code (Standard, or VertMito for *co1*). Individual sequence alignments were concatenated into a full alignment in SequenceMatrix (Vaidya et al., 2011).

Both model selection and partition selection was carried out using PartitionFinder (Lanfear et al., 2012), beginning from an initial gene × codon position partitioning scheme that resulted in 21 *a priori* partitions. Because the number of possible character partitions scales according to Bell numbers (Bell, 1934) by the number of columns in the dataset (Huelsenbeck et al., 2004; Li et al., 2008), an exhaustive examination of nucleotide character sets was not possible given the size of this dataset, and the PartitionFinder greedy algorithm was employed to search for an optimal scheme, with a number of partitions between gene x codon and one, and to fit nucleotide models to each of these partitions, under the assumption of independent model parameters and branch lengths for each partition. Partition selection and model selection in the intermediate steps of the algorithm was accomplished using the Schwarz ("Bayesian") information criterion (Schwarz, 1978). Because of the well-documented tendency of the penalty term of the Schwarz criterion to select models of lower complexity than other information criteria variants used in statistical phylogenetics (Alfaro and Huelsenbeck, 2006), the final selection of the partitioning scheme and models over the set of schemes and models produced during greedy search was accomplished using the Akaike information criterion (Akaike, 1974).

2.5. Phylogenetic inference

Model-based analyses were conducted using maximum likelihood (ML) and Bayesian methods on a personal-use six-core Pentium i7 3930 K desktop computer with 16 GB RAM, or on the CIPRES cluster (Miller et al., 2010). Likelihood analyses for the heuristically optimal phylogenetic tree were conducted in multithreaded GARLI 2.0 (Zwickl, 2006) using 50 independent search replicates. Starting trees were built using stepwise addition under likelihood, with 50 attachment sites evaluated per taxon. Each independent search used four individuals per generation, holding over 1 per generation, with a selection intensity of 0.5 and no hold-over penalty. Selection strength parameters establishing the relative weights of topology rearrangements (default 1.0), branch lengths (default 0.2), and model parameter estimates (default 0.05) were decreased to 0.01, 0.002, and 0.002, respectively.

Branch swapping in GARLI was conducted using a combination of subtree pruning and regrafting (SPR) and nearest-neighbor interchange (NNI), as GARLI does not implement tree bisection and reconnection (TBR). Stringency of floating point optimization for branch lengths and model parameters during swapping was graded using five incrementally increasing optimization precisions, from 0.5 to 0.01.

Termination conditions for each run were set according to when the run exceeded 5,000,000 generations, or to when the run had proceeded 5000 generations without a change in tree topology. The output of the analysis was logged to the terminal every ten generations, and the output was saved to file every 100 generations.

Bootstrapping was conducted in GARLI by modifying the above parameters to resample proportion 1.0 of the data, running 100 replicates, searching on each replicate twice, and stopping each replicate after 2500 generations without a topological improvement. All other configuration values remained the same. Bootstrap output was mapped onto the heuristically optimal ML tree using

the SumTrees command (*sumtrees.py boot.tre – target = best.tre – output = mapped.tre*) in the DendroPy python package (Sukumaran and Holder, 2010).

Bayesian analysis was conducted in MrBayes 3.2.1 (Ronquist et al., 2012) on the CIPRES cluster. Analysis was run for 40 million generations using two runs, each with four chains. To avoid discrepancies in model specification that would occur by approximating PartitionFinder-selected models using the limited fixed model set available in MrBayes, each PartitionFinder partition was assigned *nst = mixed* to use reversible jump MCMC to sample over all 203 submodels of GTR (Huelsenbeck et al., 2004) and provide a distribution of model support in each partition from the posterior. As in the ML analysis, separate model parameters and branch lengths were estimated for each partition.

Preliminary analyses of 40 and 50 million generations occasionally placed a clade of outgroup taxa within the ingroup, suggesting that either nonconvergence or support for multiple trees within the data was potentially confounding the MCMCMC procedure (Mossel and Vigoda, 2005, 2006). This result was not observed in any permutation of ML analysis. Because of this observation, and because the goal of the analysis was an examination of relationships within the monophyletic ingroup (Johnson, 1992; Rosen, 1973; Stiassny, 1986, 1996), the topology prior was constrained to recover the ingroup myctophiform taxa as monophyletic. The first fifty percent of the run was discarded as burn-in, and the observation of the between-chains RF distance falling within the RF distances reported for each chain using the Var command in AWTY (Nylander et al., 2008) was used to assess 'effective' convergence of the analysis in sampling the topology. Both the 50% majority consensus tree and the *maximum a posteriori* (MAP) tree topology (Rannala and Yang, 1996) were reported and examined for differences.

3. Results

3.1. Model and partition selection and model support

PartitionFinder selected a scheme with three named model partitions. The model for the first partition, TN93/TrN (Tamura and Nei, 1993), was recovered by MrBayes as the highest posterior probability model in the posterior distribution for the partition (Table 3). The named models assigned to the second (TVM) (Posada, 2003) and third (TIM) (Posada, 2003) partitions were not recovered in their corresponding posterior distributions. The complexity of the highest-ranking models receiving support in the second partition was the same as for the named model identified by PartitionFinder. The complexity of the highest-ranking models receiving support in the third partition was lower than for the named model identified by PartitionFinder. The shape of model support for each partition varied substantially. The first partition exhibited strong support for the named model, and the remaining support was spread across unnamed GTR submodels. The second partition assigned more support to unnamed submodels broadly resembling TVM, with the GTR model (Tavaré, 1986) falling within the distribution. The third partition assigned largely uniform support to a set including unnamed GTR submodels, HKY85 (Hasegawa et al., 1985), and K3P/K81 (Kimura, 1981).

3.2. Phylogeny of myctophiform fishes

GARLI (LL = −73910.3233) and MrBayes (arithmetic mean LL = −74257.29) recovered topologies that were identical for genus-level relationships, and the MAP tree was the same as the 50% majority-rule consensus tree. The phylogeny is presented in Fig. 2, and discussed in the following sections.

3.2.1. Phylogeny of Neoscopelidae

Within Myctophiformes, the family Neoscopelidae appears as a grade into a monophyletic Myctophidae, with *Solivomer arenidens* sister to the remaining taxa, and a monophyletic *Neoscopelus* most closely allied with Myctophidae. Each split within the neoscopelid fishes was supported by very high resampling support in both likelihood and Bayesian analysis (Fig. S1).

3.2.2. Phylogeny of Myctophidae: Electronini

The family Myctophidae was recovered as monophyletic with very strong support (bootstrap proportion [BP] = 1.0; clade posterior [CP] = 1.0). Within Myctophidae, the subfamily Myctophinae was also recovered with strong support (BP = 1.0; CP = 1.0). Within Myctophinae, the tribe Electronini Wisner, 1963b, comprised of the genera *Metelectrona*, *Electrona*, *Protomyctophum*, and *Krefftichthys*, was recovered as monophyletic with strong support (BP = 1.0; CP = 1.0). Within Electronini (Fig. 3), *Metelectrona ventralis* was recovered as sister to the remaining taxa, whereas *Electrona* was recovered as polyphyletic, with a clade comprised of *E. antarctica*, *E. carlsbergi*, and *E. risso*, and a clade comprised of *E. paucistrastra*. However, the intrarelationships within and among *Electrona* and *Metelectrona* were poorly supported, with bootstrap proportion and clade posterior support values no higher than 70%.

Table 3
Summary of Bayesian posterior model supports.

Partition	Model	Posterior probability	PartitionFinder model in set?	Model name
1	[121131]	0.566	Yes	TN93
1	[121134]	0.073	Yes	Unnamed
1	[123343]	0.066	Yes	Unnamed
1	[123141]	0.064	Yes	Unnamed
1	[123143]	0.06	Yes	TIM3
1	[121341]	0.053	Yes	Unnamed
2	[123453]	0.277	No	Unnamed
2	[123456]	0.147	No	GTR
2	[123454]	0.129	No	Unnamed
2	[123343]	0.098	No	Unnamed
2	[121345]	0.082	No	Unnamed
2	[121341]	0.076	No	Unnamed
2	[123451]	0.06	No	Unnamed
3	[121321]	0.173	No	Unnamed
3	[121121]	0.171	No	HKY85
3	[123323]	0.141	No	Unnamed
3	[123321]	0.097	No	K3P

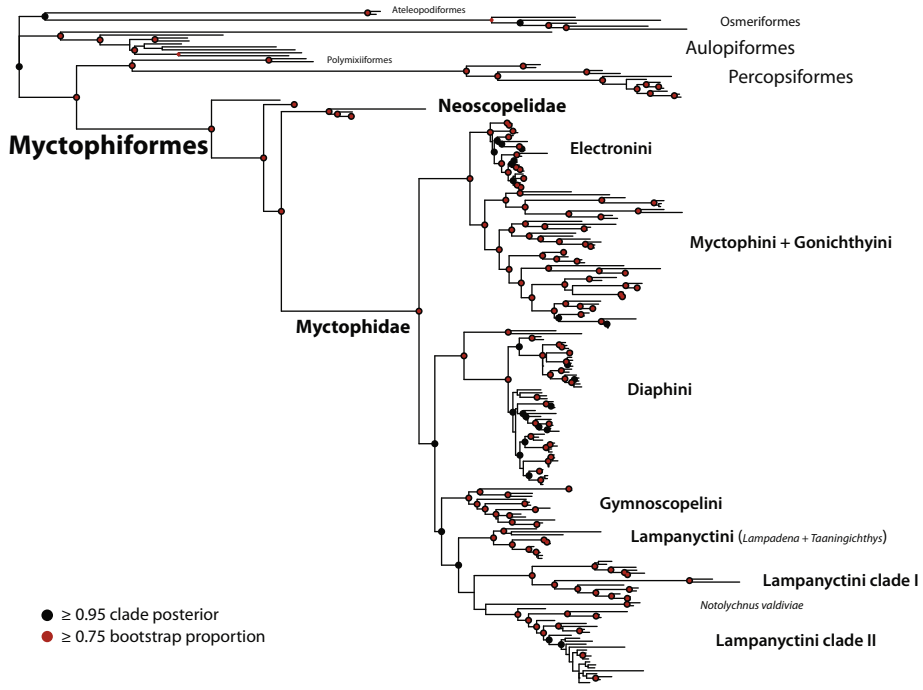

Fig. 2. Phylogenetic hypothesis of myctophiform intrarelationships from the present analysis based on seven protein-coding genes (*H3*, *glyt*, *myh6*, *co1*, *bmp4*, *tbr1*, *zic1*), with tribal relationships *sensu* Paxton (1972) shown. Tree topology shown is the 50% majority-rule consensus tree from MrBayes3.2.1, with clade posterior values and bootstrap proportions from an analysis in GARLI2.0 mapped onto the nodes. The majority-rule consensus topology had the same structure as the maximum *a posteriori* tree.

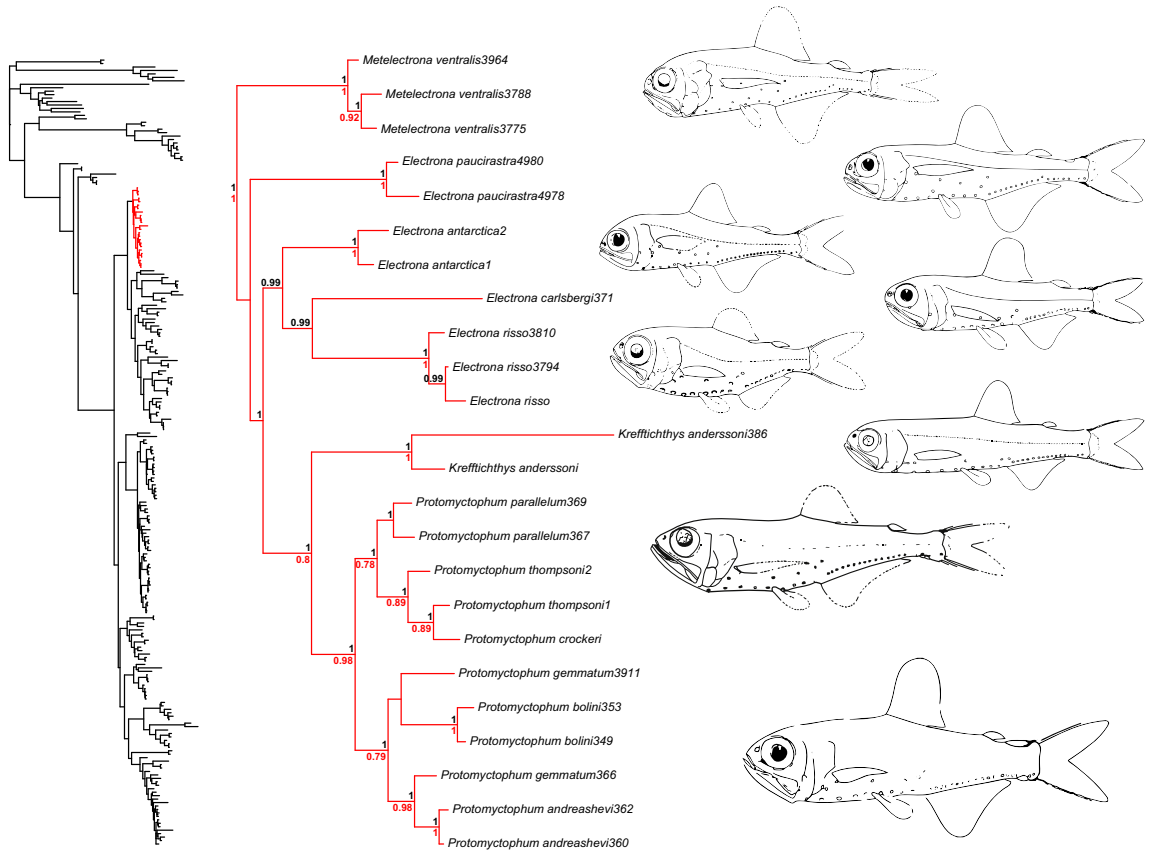

Fig. 3. Phylogeny of tribe Electronini Wisner, 1963b (right), with clade position highlighted in total tree (left). Numerical support values provided for clarification, with clade posteriors above the edge and bootstrap proportions below the edge. Numbers lower than those for the legend of Fig. 2 not shown. Generic status of *Metelectrona* and *Krefftichthys* is supported. Polyphyly of *Electrona* is implied. Monophyly of *Protomyctophum*, with subgenera *Hierops* and *Protomyctophum*, is supported. All images adapted from Hulley (1986), Becker (1983), Zahuranec (2000), and Hubbs and Wisner (1964).

The traditional sister-taxon affinity of the monotypic *Krefftichthys anderssoni* with the genus *Protomyctophum* was recovered, with moderate support (BP = 0.8; CP = 1.0). Within *Protomyctophum*, recovered as monophyletic (BP = 0.98; CP = 1.0), there was moderate support for the subgenera *Hierops*, represented in this analysis by *P. parallelum*, *P. thompsoni*, and *P. crockeri* (BP = 0.78; CP = 1.0) and *Protomyctophum*, represented by *P. gemmatum*, *P. andreashevi*, and *P. bolini* (BP = 0.79; CP = 1.0). Branch lengths within the tribe Electronini were markedly short.

3.2.3. Phylogeny of Myctophidae: Myctophini and Gonichthyini

A clade containing the remaining myctophine genera (*Benthosema*, *Diogenichthys*, *Myctophum*, *Hygophum*, *Symbolophorus*, *Gonichthys*, *Loweina*, *Tarletonbeania*, and *Centrobranchus*) was recovered with strong support (BP = 1.0; CP = 1.0). However, the tribes Myctophini Fowler, 1925, containing the genera *Benthosema*, *Diogenichthys*, *Myctophum*, *Hygophum*, and *Symbolophorus*, and Gonichthyini Paxton, 1972, containing the genera *Gonichthys*, *Centrobranchus*, *Loweina*, and *Tarletonbeania*, were not recovered as monophyletic (Fig. 4).

The non-monophyly of Myctophini and Gonichthyini resulted from the subdivision of the genus *Myctophum* Rafinesque, 1810 into three groups. A first group, *Myctophum sensu stricto*, recovered with strong support (BP = 0.93; CP = 1.0) contained the type species *M. punctatum* Rafinesque, 1810, as well as *M. aurolaternatum*, *M. nitidulum*, and *M. affine*, and was recovered within the traditional Myctophini genera. A second group, *Myctophum sensu Ctenoscopelus* Fraser-Brunner, 1949, containing the enigmatic species *Myctophum phengodes*, was recovered with strong support as basal to the gonichthyine sister taxa *Loweina* and *Tarletonbeania* (BP = 0.95; CP = 1.0). A third group, *Myctophum sensu Dasyscopelus* Günther, 1864, containing the species *M. asperum*, *M. brachygnathum*, *M. lychnobium*, *M. spinosum*, *M. selenops*, *M. orientale*, and *M. obtusirostre*, was recovered with strong support (BP = 1.0; CP = 1.0) as sister to a clade containing the gonichthyine genera *Gonichthys* and *Centrobranchus* (BP = 0.94; CP = 1.0).

Within the clade comprising the genera of Myctophini and Gonichthyini, a clade comprised of the sister genera *Benthosema* and *Diogenichthys* was recovered as sister to the remaining taxa, with strong support (BP = 0.98; CP = 1.0). *Benthosema* was recovered as paraphyletic, with a clade comprised of the species *B. glaciale* and *B. suborbitale* (BP = 0.95; CP = 1.0) sister to a clade comprising the remaining *Benthosema* (*B. fibulatum*, *B. panamense*, *B. pterotum*). This latter clade formed a monophyletic grouping (BP = 1.0; CP = 1.0) sister to a monophyletic *Diogenichthys* (BP = 1.0; CP = 1.0), with strong support (BP = 0.98; CP = 1.0).

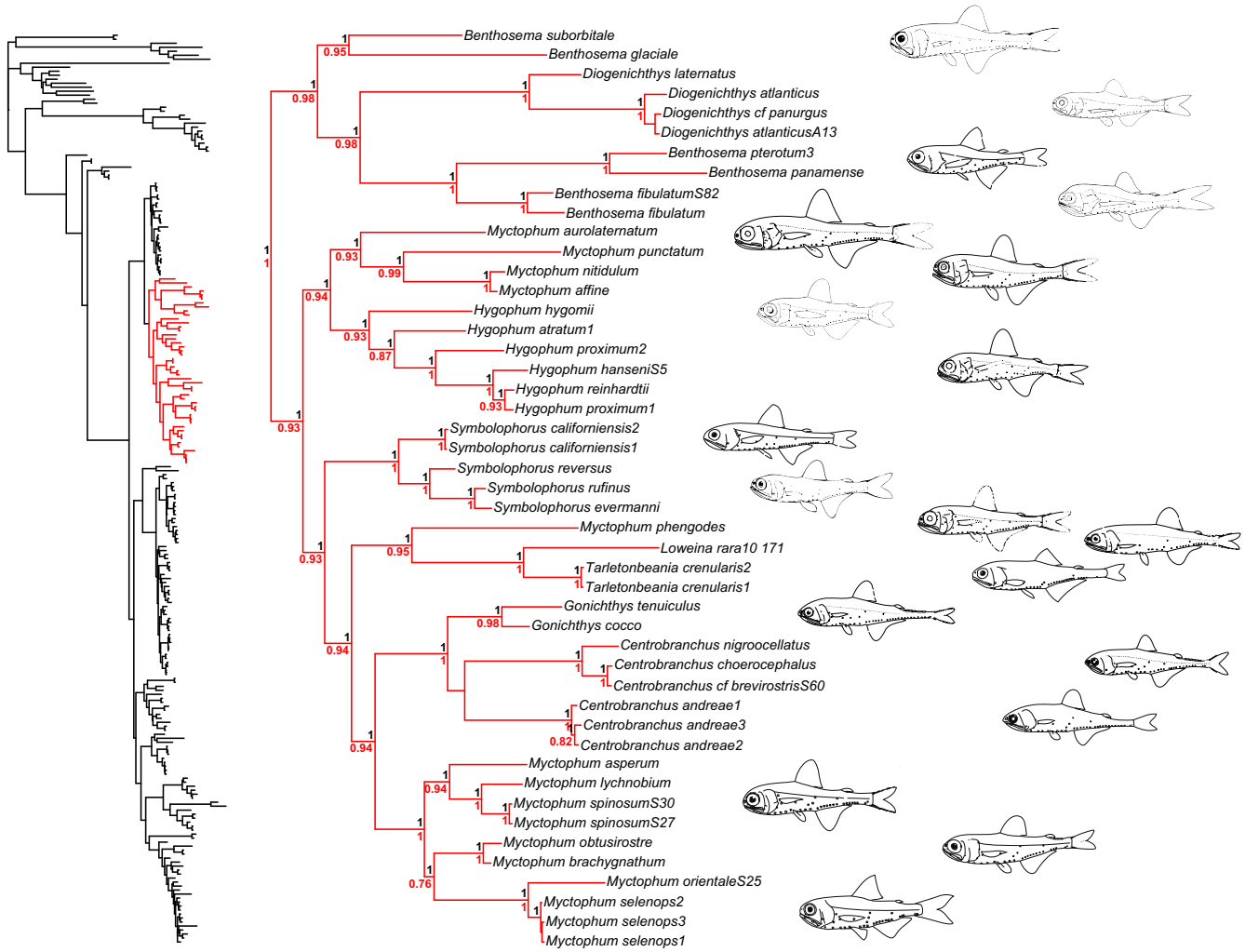

Fig. 4. Phylogeny of tribes Myctophini and Gonichthyini *sensu* Paxton, 1972 (right), with clade position highlighted in total tree (left) Numerical support values provided for clarification, with clade posteriors above the edge and bootstrap proportions below the edge. Numbers lower than those for the legend of Fig. 2 not shown. *Benthosema* is recovered as a grade. Monophyly of the two tribes is not recovered due to the polyphyly of *Myctophum*, which is recovered as three groups. *Myctophum* Rafinesque, 1810 *sensu stricto* ("cycloid" *Myctophum* of Poulsen et al. (2013)) is recovered sister to *Hygophum*. *Myctophum sensu Ctenoscopelus phengodes* Fraser-Brunner, 1949 is recovered at the base of *Loweina* + *Tarletonbeania*. *Myctophum sensu Dasyscopelus* Günther, 1864 ("ctenoid" *Myctophum* of Poulsen et al. (2013)) is recovered sister to *Gonichthys* + *Centrobranchus*. All images adapted from Hulley (1986), Becker (1983), Zahuranec (2000), and Hubbs and Wisner (1964).

Sister to the *Benthosema* + *Diogenichthys* assemblage was a clade comprised of *Myctophum s. str.* and a monophyletic *Hygophum* (BP = 0.93; CP = 1.0), recovered with strong support (BP = 0.94; CP = 1.0). Within *Myctophum s. str.*, the sister-taxon relationship of *M. affine* and *M. nitidulum* was supported (BP = 1.0; CP = 1.0). Within *Hygophum*, *H. hygomii* was recovered as sister to the remaining *Hygophum* sampled (*H. atratum*, *H. hanseni*, *H. proximum*, and *H. reinhardtii*), forming a well-supported clade (BP = 0.87; CP = 1.0).

Sister to the clade of *Myctophum s. str.* + *Hygophum* was a monophyletic *Symbolophorus* (BP = 1.0; CP = 1.0), with support for divisions into the "*S. boops*/*californiensis*" and "*S. evermanni*" (BP = 1.0; CP = 1.0) groups recognized by Gago (1993) and Wisner (1976).

The remaining clade, comprised of myctophine and gonichthyine taxa, was recovered with strong support (BP = 0.94; CP = 1.0). Within this clade was the well-supported monophyletic assemblage of *Myctophum s. Ctenoscopelus* + *Loweina* + *Tarletonbeania* (BP = 0.95; CP = 1.0). Sister to this assemblage was a clade (BP = 0.94; CP = 1.0) containing reciprocally monophyletic clades of *Gonichthys* + *Centrobranchus* (BP = 1.0; CP = 1.0) and *Myctophum s. Dasyscopelus* (BP = 1.0; CP = 1.0). Whereas support for a monophyletic *Gonichthys* was high (BP = 0.98; CP = 1.0), support for a monophyletic *Centrobranchus* was moderate (BP = 0.57; CP = 0.91), with subdivisions into a *C. andreae* group (BP = 1.0; CP = 1.0) and a *C. nigroocellatus* group (BP = 1.0; CP = 1.0). Within the clade of *Myctophum s. Dasyscopelus*, three lineages were recovered with strong support. First, an "*M. asperum* group," containing the species *M. asperum*, *M. lychnobium*, and *M. spinosum* (BP = 0.94; CP = 1.0), was recovered as basal within the clade. Second, a clade containing *M. brachygnathum* and *M. obtusirostre* (BP = 1.0; CP = 1.0) was recovered. Third, an "*M. orientale* group," containing the deep-bodied *M. selenops* and *M. orientale*, was recovered (BP = 1.0; CP = 1.0). The intrarelationships among these three lineages were not well resolved.

3.2.4. Phylogeny of Myctophidae: subfamily Lampanyctinae

The myctophid subfamily Lampanyctinae Paxton, 1972 was recovered as monophyletic, albeit with incongruent levels of support between the two inference methods (BP = 0.49; CP = 1.0).

3.2.5. Phylogeny of Myctophidae: tribe Diaphini

Within Lampanyctinae, the tribe Diaphini Paxton, 1972, containing the genera *Lobianchia* and *Diaphus*, was recovered as monophyletic with strong support (BP = 1.0; CP = 1.0) and also recovered as sister to a monophyletic grouping of the remaining lampanyctine tribes (BP = 0.41; CP = 0.98). Within Diaphini (Fig. 5), the genera *Lobianchia* (BP = 1.0; CP = 1.0) and *Diaphus* (BP = 1.0; CP = 1.0) were recovered as reciprocally monophyletic. The genus *Diaphus* Eigenmann and Eigenmann, 1890 was subdivided into a clade of *Diaphus sensu stricto* (BP = 0.79; CP = 1.0), containing the type species of the genus, *Diaphus theta*, sister to other *Diaphus* of the

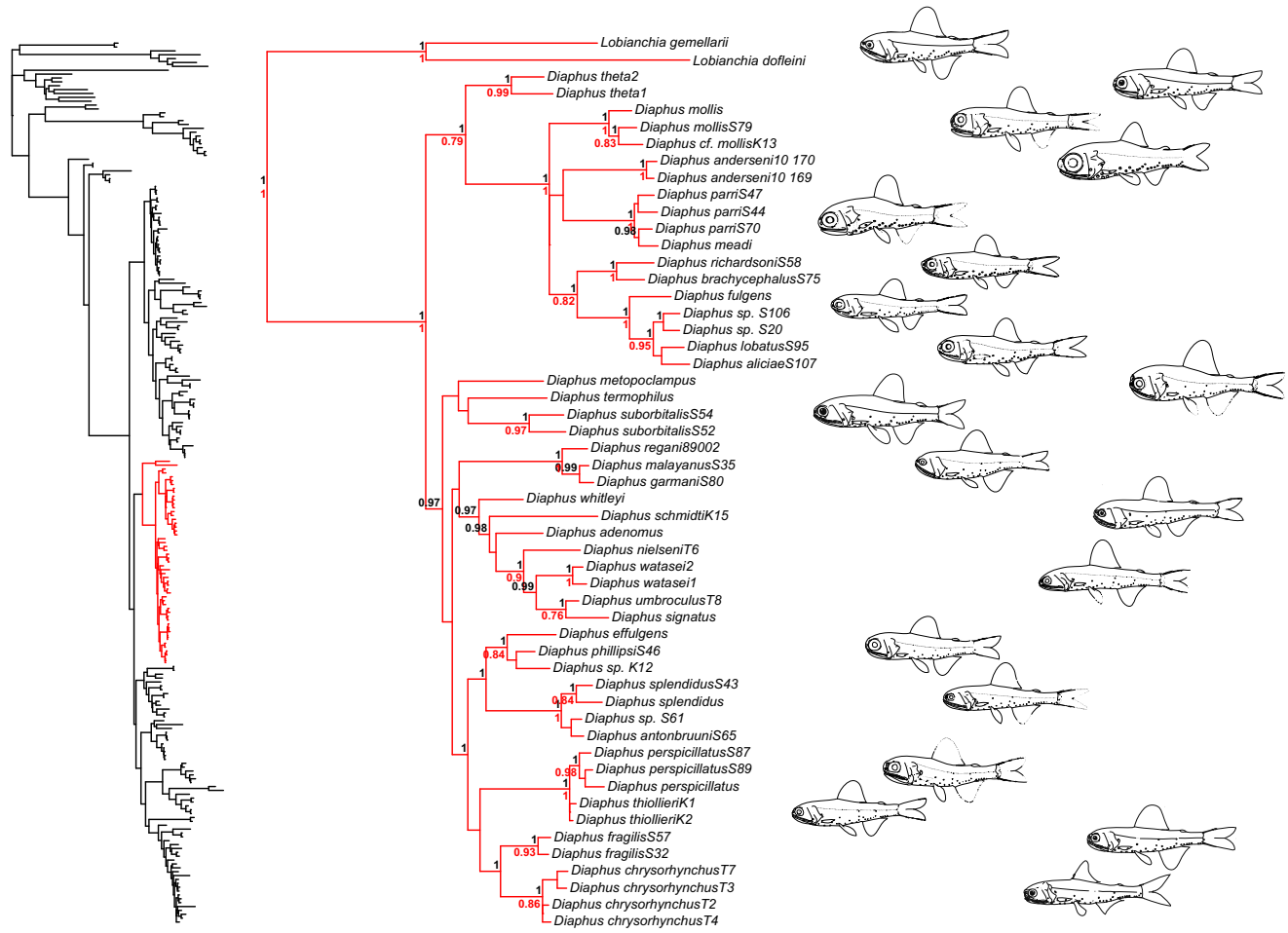

Fig. 5. Phylogeny of tribe Diaphini Paxton, 1972 (right), with clade position highlighted in total tree (left). Numerical support values provided for clarification, with clade posteriors above the edge and bootstrap proportions below the edge. Numbers lower than those for the legend of Fig. 2 not shown. Monophyly of *Diaphus* is supported, and monophyly of the suborbital (So) *Diaphus* recovered with strong support. Some structure within the second *Diaphus* clade suggests the components of the headlight complex may not be homologous. All images adapted from Hulley (1986) Becker (1983), Zahuranec (2000), and Hubbs and Wisner (1964).

So-photophore group (Fraser-Brunner, 1949; Kawaguchi and Shimizu, 1978; Nafpaktitis, 1968, 1978). This clade of So-*Diaphus* was reciprocally monophyletic with a clade containing the remaining *Diaphus* (BP = 0.41; CP = 0.97).

Within this second *Diaphus* clade, resampling supports and tree topologies differed somewhat between the two analyses (Fig. 5). A clade of dorsonasal–ventronasal-I (Dn–Vn-I) taxa (*D. termophilus*, *D. suborbitalis*) was recovered, with poor support (BP = 0.21; CP = 0.52), and an antorbital (Ant) species, *D. metopoclampus*, was recovered with low support as sister to the Dn–Vn-I clade (CP = 0.59). The two remaining clades (clade A and clade B) contained predominantly Dn–Vn-II species. Clade A (BP = 0.27; CP = 0.57) contained predominantly Dn–Vn-II species, as well as the supraorbital (Suo) species *D. adenomus* and the Ant species *D. watasei*. Clade B (BP = 0.39; CP = 1.0) contained predominantly Ant species, with a clade of Dn–Vn-II species (BP = 1.0; CP = 1.0) nested sister to a clade containing *D. effulgens*, *D. phillipsi*, and *D. sp.* (BP = 0.84; CP = 1.0). Support for the sister-taxon relationship of these clades was moderate (BP = 0.65; CP = 1.0).

3.2.6. Phylogeny of Myctophidae: tribe Gymnoscopelini

The tribe Gymnoscopelini Paxton, 1972 was recovered as monophyletic (Fig. 6), with strong support (BP = 0.87; CP = 1.0). Within the tribe, a clade composed of *Notoscopelus* + *Scopelopsis multipunctatus* (BP = 0.99; CP = 1.0) was found sister to a clade containing *Lampanyctodes hectoris* + *Lampichthys procerus* + *Gymnoscopelus* spp. (BP = 0.92; CP = 1.0). Within the monophyletic genus *Gymnoscopelus* (BP = 1.0; CP = 1.0), no support was observed for the subgenera *Nasolychnus*, represented in this analysis by *G. hintonoides* and *G. piabilis*, and *Gymnoscopelus*, represented in this analysis by *G. bolini*, *G. braueri*, and *G. nicholsi*.

3.2.7. Phylogeny of Myctophidae: tribe Notolychnini

The tribe Notolychnini Paxton, 1972, containing the monotypic genus *Notolychnus valdiviae*, was recovered as monophyletic (BP = 1.0; CP = 1.0) and nested within the tribe Lampanyctini Paxton, 1972, sister to a clade containing *Stenobrachius*, *Triphoturus*, *Parvilux*, *Lampanyctus*, and *Nannobrachium*, albeit with moderate to low support (BP = 0.45; CP = 0.76). An alternate position in the ML analysis ($\Delta LL \sim 2$) placed *Notolychnus valdiviae* as sister to the rest of Lampanyctini, though still nested within the subfamily Lampanyctinae.

3.2.8. Phylogeny of Myctophidae: tribe Lampanyctini

The tribe Lampanyctini Paxton, 1972, exclusive of *Notolychnus valdiviae*, was recovered, with moderate to low support (BP = 0.52; CP = 0.77). At the base of this clade (Fig. 7) was a clade containing *Lampadena* and *Taaningichthys* (BP = 1.0; CP = 1.0). *Lampadena* was recovered as paraphyletic, with a clade comprised of *L. speculigera* + *L. urophaos urophaos* + *L. u. atlantica* (BP = 1.0; CP = 1.0) sister to a clade composed of *L. speculigera* + *Taaningichthys bathyphilus* + *T. minimus* (BP = 0.86; CP = 1.0). Sister to this clade, two further reciprocally monophyletic clades were recovered. The first clade, composed of the monophyletic genera

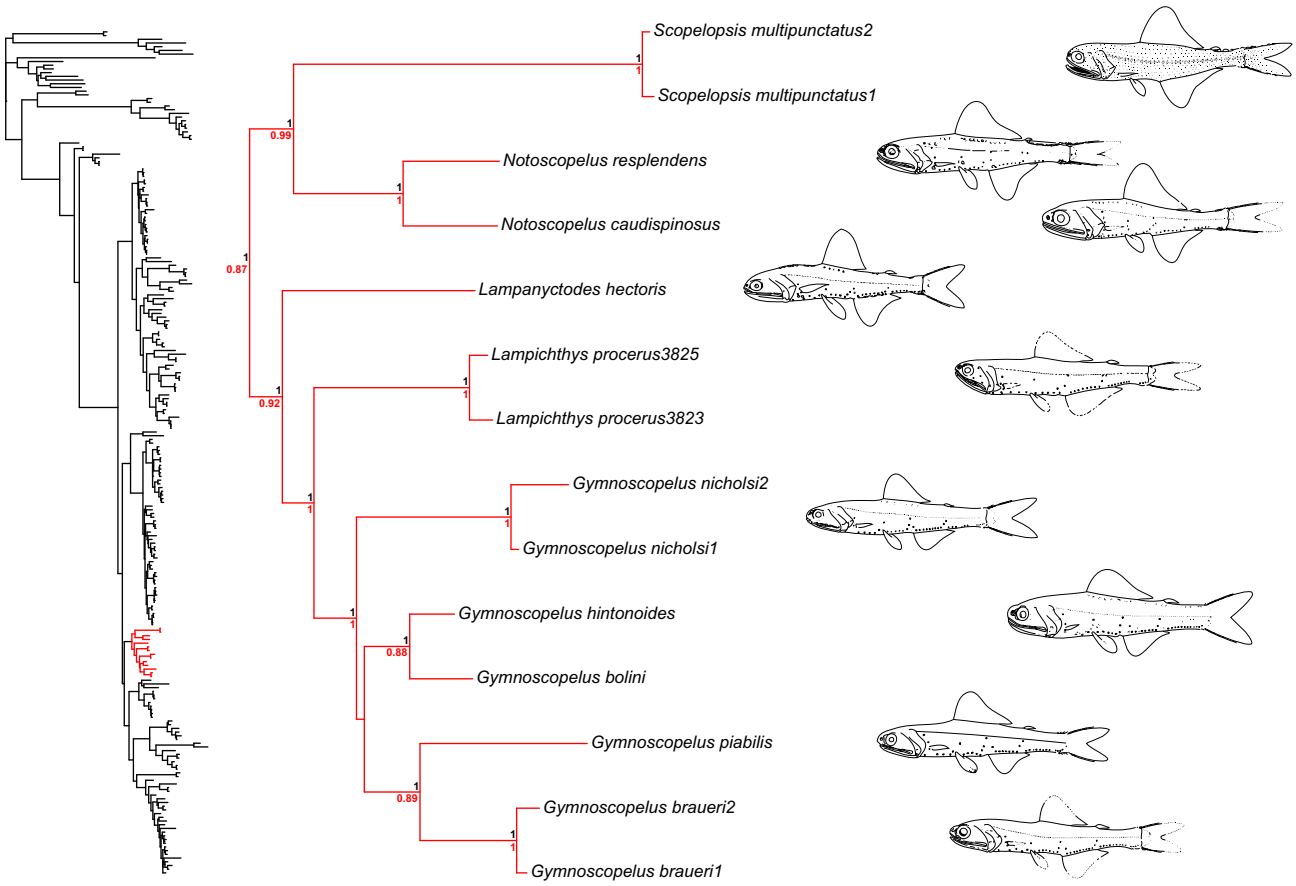

Fig. 6. Phylogeny of Gymnoscopelini Paxton, 1972 (right), with clade position highlighted in total tree (left). Numerical support values provided for clarification, with clade posteriors above the edge and bootstrap proportions below the edge. Numbers lower than those for the legend of Fig. 2 not shown. A clade of *Notoscopelus* + *Scopelopsis* sister to the remaining gymnoscopeline fishes is recovered with high support. All images adapted from Hulley (1986), Becker (1983), Zahuranec (2000), and Hubbs and Wisner (1964).

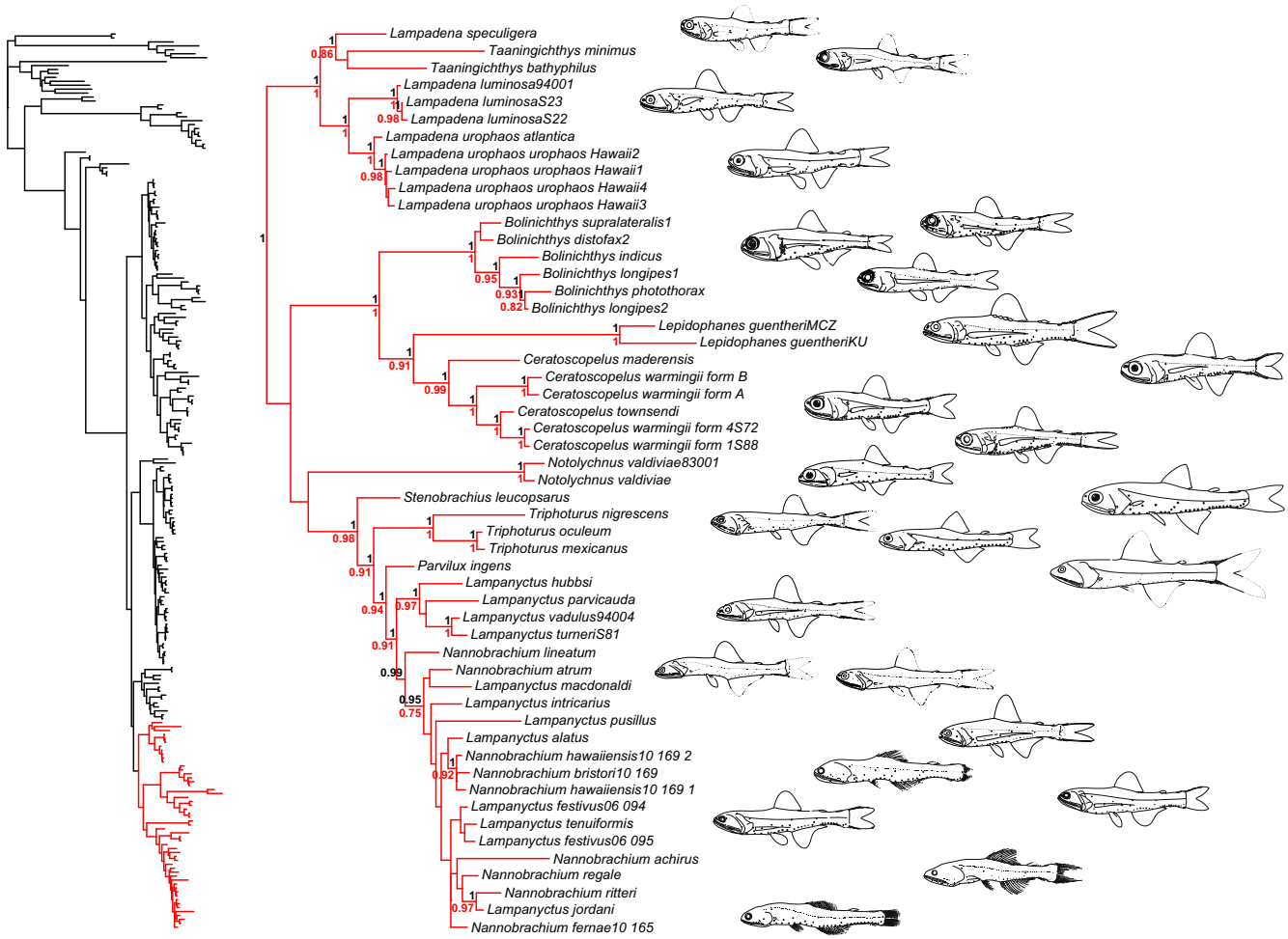

Fig. 7. Phylogeny of Lampanyctini Paxton, 1972 (right), with clade position highlighted in total tree (left). Numerical support values provided for clarification, with clade posteriors above the edge and bootstrap proportions below the edge. Numbers lower than those for the legend of Fig. 2 not shown. The clade is recovered with three main lines: *Lampadena* + *Taaningichthys*, *Bolinichthys* + *Lepidophanes* + *Ceratoscopelus* (subclade I), and *Stenobrachius* + *Triphoturus* + *Parvilux* + *Lampanyctus*/*Nannobrachium* (subclade II). The tribe is not recovered as monophyletic, due to the inclusion of *Notolychnus valdiviae*. Relationships within subclades generally follow those proposed by Paxton et al. (1984). All images adapted from Hulley (1986), Becker (1983), Zahuranec (2000), and Hubbs and Wisner (1964).

Bolinichthys (BP = 1.0; CP = 1.0), *Lepidophanes* (BP = 1.0; CP = 1.0), and *Ceratoscopelus* (BP = 0.99; CP = 1.0), was recovered with high support (BP = 1.0; CP = 1.0). Two clades were observed in *Bolinichthys*: *B. distofax* + *B. supralateralis* (BP = 0.58; CP = 0.7) and *B. indicus* + *B. longipes* + *B. photothorax* (BP = 0.95; CP = 1.0) A sister-group relationship for *Ceratoscopelus* + *Lepidophanes* was strongly supported (BP = 0.91; CP = 1.0). The cosmopolitan genus *Ceratoscopelus* was divided into three clades: *C. maderensis*, the Hawai'ian *C. warmingii* forms A and B (BP = 1.0; CP = 1.0), and a *C. townsendi* + American Samoan *C. warmingii* forms 1 and 4 (BP = 1.0; CP = 1.0). The *C. warmingii*/*C. townsendi* clade was recovered as monophyletic (BP = 1.0; CP = 1.0).

The second clade was comprised of a pectinate structure of the genera *Notolychnus, Stenobrachius, Triphoturus, Parvilux, Lampanyctus, and Nannobrachium*. The clade containing *Stenobrachius, Triphoturus* (BP = 1.0; CP = 1.0), *Parvilux, Lampanyctus, and Nannobrachium* was recovered with strong support (BP = 0.98; CP = 1.0). Additionally, each nested group in the pectinate structure was recovered with strong support (BP = 0.98, 0.91, 0.94, 0.91; CP = 1.0, 1.0, 1.0, 1.0). A clade comprising representatives of the genera *Lampanyctus and Nannobrachium* was recovered as monophyletic (BP = 0.91; CP = 1.0). Neither genus was itself recovered as monophyletic.

4. Discussion

Given the large number of results from this analysis, the following discussion is divided into sections, in which the higher taxonomic implications are first discussed, followed by tribal and generic placements, as follows: phylogeny of Neoscopelidae, phylogeny of Myctophidae, position of Notolychnini, phylogeny of Myctophinae, and phylogeny of Lampanyctinae.

4.1. Phylogeny of Neoscopelidae

The appearance of blackchins as a grade within Myctophiformes *sensu* Rosen (1973), with high resampling support for each split regardless of either the support or phylogenetic inference method, is an unusual result that is contradicted by two cranial morphological synapomorphies summarized in Stiassny (1996). The further results of a basal *Solivomer arenidens* and a monophyletic *Neoscopelus* + Myctophidae also appear outlandish, considering three further cranial synapomorphies have been cited favoring a *Neoscopelus* + *Solivomer* relationship (Stiassny, 1996).

Furthermore, the observed sister relationship of *Neoscopelus* and Myctophidae suggests a single origin of photophores in these fishes. Although exhibiting some positional similarity, especially

near the cleithrum, the photophores of *Neoscopelus* and myctophid fishes appear to be different structures, with *Neoscopelus* photophores lacking both a lentiform scale and a proliferated reflecting layer (Kier, 1967). Putative non-homology of the photophores in these fishes based on differences in innervation patterns has been described for the photophores of the pectoral girdle (Denton and Stiassny, 2010), and Kenaley (2010) also hypothesized non-homology of different cranial photophores in loosejaw dragonfishes by observing differences in innervation to the structures (Herrick, 1909).

However, despite this evidence, several points must be noted regarding neoscopelid fishes that have not been raised elsewhere. First, no anatomical revision of Neoscopelidae has yet been undertaken. The absence of non-cranial synapomorphies for the family, while noted elsewhere (Stiassny, 1996, p. 406), remains striking. Second, *Solivomer arenidens*, found sister to the other taxa in this analysis, exhibits a range most closely approximating the Tethys/Paratethys area of origin for the order Myctophiformes, and numerous "stem" myctophoid fishes have been described from continental Europe and Australia (Prokofiev, 2006; Uyeno and Matsui, 1993). Lastly, a recent mitogenomic analysis of myctophiform fishes (Poulsen et al., 2013) exhibited discrepancies in support values for neoscopelid monophyly between bootstrap and clade posterior values, as well as low support for the *Neoscopelus* + *Solivomer* relationship. Although the result observed in the present analysis may be an artifact of outgroup selection and completeness, the neoscopelid fishes warrant further study, especially in comparison to fossil myctophoid fishes.

4.2. Phylogeny of Myctophidae

The degree of support observed in this study for the monophyly of the family Myctophidae by both analytical methods is uncontroversial and is corroborated by morphological characters (Moser and Ahlstrom, 1970, 1972, 1974; Moser et al., 1984; Paxton, 1972; Paxton et al., 1984; Stiassny, 1996). The subfamily Myctophinae Fowler, 1925 is similarly recovered with uncontroversial support values and species composition. By contrast, the subfamily Lampanyctinae Paxton, 1972 is here recovered with strongly divergent support values, and as containing the enigmatic monotypic *Notolychnus valdiviae* of tribe Notolychnini Paxton, 1972. This latter result is the first non-marginal placement of the taxon. These results warrant significant discussion and are elaborated below.

The differences in support for the monophyly of Lampanyctinae observed between bootstrap values (BP = 0.49) and clade posteriors (CP = 1.0) are likely attributable to the well-documented tendency of clade posteriors to overestimate support (Erixon et al., 2003; Simmons et al., 2004), although the exact underlying factors responsible for inflated estimates are nuanced, determined by combinations of factors like the relationship between taxon and character sampling, the shape of priors (Yang and Rannala, 2005), convergence of MCMCMC (Mossel and Vigoda, 2006), Bayesian long branch artifacts (Kolaczkowski and Thornton, 2009), and heterogeneity of the evolutionary process (Pagel and Meade, 2004, 2008). This last point bears mention in the context of Lampanytinae, because although clade posterior estimates appeared uniformly higher than bootstrap proportions across all clades, discrepancies between bootstrap and clade posterior estimates were higher within Lampanyctinae than within Myctophinae, especially for the higher-level groupings within Lampanyctinae, including the basal position of Diaphini and *Diaphus* clade B. The support discrepancy is potentially explainable by a heterogeneous evolutionary process acting within Lampanyctinae. A heterogeneous process would decrease the fit of a single set of evolutionary models selected by information criteria, and so reduce resampling support under frequentist methods such as ML. An rj-MCMC method, such as the one employed for the Bayesian analysis, would to some degree account for heterogeneity by sampling over the space of models to generate a distribution of model posterior support.

4.3. Position of Notolychnini

The position of the tribe Notolychnini, inferred as sister to the Lampanyctini clade containing *Stenobrachius*, *Triphoturus*, *Parvilux*, *Lampanyctus*, and *Nannobrachium*, is unique among phylogenetic hypotheses of myctophid relationships, but is strongly supported by the hypothesis of Bolin (1946), and the acknowledgement of Fraser-Brunner (1949), who observed similarity in the elevated positions of the PLO, VLO, uppermost SAO, Pol, and Prc photophores, and hypothesized an affinity of *Notolychnus* with *Lampanyctus*, *Stenobrachius*, and *Triphoturus*. Additional support for the placement of *Notolychnus* observed in the present study is provided by the gross morphology of the supracaudal organ, which is similar to the unusual structure observed in *Lampadena* and *Taaningichthys* (Bolin, 1946; Brauer, 1908).

In presenting an ingroup position for *Notolychnus*, the present study strongly disagrees with previous results, which have favored different marginal positions for *Notolychnus*: as sister to the remaining lampanyctine taxa (Paxton, 1972; Stiassny, 1996); as sister to the myctophine taxa (Yamaguchi, 2000, reanalyzing the dataset of Paxton et al. (1984)); as sister to the rest of Myctophidae, based on mitogenomic data (Poulsen et al., 2013); or in an unresolved trichotomy (Paxton et al., 1984). The hypothesized position of *Notolychnus* as sister to the other lampanyctine taxa based on morphological data is quite possibly a conceptual artifact of character individuation (Rieppel and Kearney, 2007), a potential problem noted in part by Paxton et al. (1984) in discussing character polarity among myctophid taxa. The position of *Notolychnus* observed in these studies may also be a higher-order artifact of missing character information (Kearney, 2002; Kearney and Clark, 2003; Nixon and Davis, 1991; Wiens, 2003). In the previous morphological studies of Myctophidae, *Notolychnus* has been coded as '?' for the following characters: extrascapulars from fusion/from loss; larval eyes round/narrow; PO4 level/raised; and CO5 keel or ridge absent/present (Paxton et al., 1984). Both the number of extrascapulars and larval eye morphology are critical characters for diagnosing Lampanyctinae, and so the absence or ambiguity in *Notolychnus* of states associated with these characters is likely to significantly influence the position of the taxon.

The difference in position of *Notolychnus* observed between this study and the study of Poulsen et al., also based on molecular data, is striking, even though neither analysis placed the genus with confidence. The discrepancy in the position of *Notolychnus* between the two analyses is likely due to a combination of taxon and character sampling. Individual mitochondrial markers, while easy to amplify relative to nuclear markers, are inherited as a single locus (Rubinoff and Holland, 2005 for summary) that is functionally coupled to metabolism. A mitogenomic analysis, while providing legitimate character synapomorphies in the form of gene rearrangements, is a phylogeny of metabolic systems. The sister-taxon position of *Notolychnus* to Myctophidae observed by Poulsen et al. is therefore not surprising given that the growth features of the genus suggest significant metabolic shifts. The observation by Poulsen et al. of an independent origin of a second tRNA-Met gene in *Notolychnus* further supports the concept of the metabolic autapomorphy of the genus.

4.3.1. Phylogeny of Myctophinae: Electronini *Wisner, 1963b*

The strong resampling support observed for the subfamily Myctophinae is in accordance with previous morphological analyses based on adult and larval morphology, and is not discussed

further. However, the strongly-supported monophyly observed in this study for the tribe Electronini disagrees with some previous morphological analyses (Paxton, 1972; Paxton et al., 1984), and there has been some debate over the status of the tribe. Wisner (1963b) erected the tribe to include the genera *Protomyctophum*, *Hierops*, *Metelectrona*, and *Electrona*, with the characters, "PLO and PVO photophores located below, or but very little above the lower edge of the pectoral base, large eyes, and by relatively blunt, non-projecting snouts, and entirely terminal mouths" (p. 28). Paxton (1972), in noting some imprecision with these terms especially related to the PLO and subterminal mouth, grouped Electronini within the larger tribe Myctophini, citing the absence of unique osteological synapomorphies to define a tribe. However, the result of the present analysis is in accordance with that of Poulsen et al., who noted the presence of a large (>200 bp) intergenic spacer, between ND1 and tRNA-Ile, in the three electronin mitogenomes sampled in their analysis. Moreover, the present analysis significantly expands on the result of Poulsen et al. by providing the first molecular evidence for finer-scale resolution within this difficult tribe.

The electronin relationships recovered in this study closely follow the features of larval morphology, which reiterate four major trends. First, the generic status of *Metelectrona* Wisner, 1963b is confirmed by strong resampling support. Wisner erected the genus based largely on the apparent presence of two Pol photophores subdividing the linear AO series, a feature otherwise unique in electronin fishes, and noted the similarity of this feature uniting *Metelectrona* and *Hygophum*. Larvae of *Metelectrona* are distinguishable from those of *Electrona* based on their more laterally compressed body profile, on the absence of an anus/anal fin interspace, on a unique pigmentation pattern, on the square shape of the scleral envelope of the eye, and on the development of the PO5 photophore before transformation (Moser and Ahlstrom, 1974). The results of the present analysis strongly corroborate distinction at the generic level based on these features.

Second, the apparent polyphyly of *Electrona* into clades containing *E. antarctica* + *E. risso* + *E. carlsbergi* and *E. paucirastra* (plus, it is assumed, *E. subaspera*), albeit with low resampling support, is a result also largely consistent with several characters of larval and adult morphology. Although *Electrona* larvae share a gestalt of body form, larvae of *E. antarctica*, *E. risso*, and *E. carlsbergi* possess choroid tissue below the eye, whereas larvae of *E. paucirastra* and *E. subaspera* do not, and the eye is more rounded than in the other *Electrona* larvae (Moser and Ahlstrom, 1974). Fraser-Brunner (1949) observed an 'incipient' Pol photophore and an elevated fifth PO photophore (also observed in *E. paucirastra*) in *E. subaspera*, and also noted a line from SAO2-3 passing through or directly ahead of the last VO in *E. subaspera* and *E. paucirastra*, and well ahead of the last VO in the other *Electrona*, as distinguishing the species from the three other *Electrona*, and recommended the designation of a subgenus (*Elampa*) for *E. subaspera*. Later authors have dismissed the suggestion based largely on the variability of the Pol position in other electronin taxa, and some general controversy exists regarding the homology of Pol-like photophores (Fraser-Brunner, 1949, pp. 1025–1027).

Third, the well-supported sister-group relationship inferred for *Krefftichthys* and *Protomyctophum* agrees with traditional assumptions, as the monotypic *Krefftichthys* was erected from *Protomyctophum anderssoni* Lönnberg, 1905 based on a suite of distinguishing characters, including the horizontal arrangement of the PVO/PLO photophore complex, the presence of only two SAO photophores, and the unique anatomy of the supracaudal organ (Hulley, 1981). Larval characters, including apparently autapomorphic teardrop-shaped choroid tissue and the very long gut (Moser and Ahlstrom, 1974), provide further evidence of the generic status of *Krefftichthys*. However, the affinity of *Krefftichthys* and *Protomyctophum* observed in the present study is supported by the position in both genera of the PLO over the first PVO photophore (Paxton et al., 1984), a feature observed in adults, and not by larval morphology. This fact reiterates the complexities associated with myctophid development, and underlines the importance of these fishes as a system for studying the evolution of deep-sea vertebrates.

Fourth, the subdivision of the genus *Protomyctophum* into two clades, with moderate support, presents the first multilocus molecular evidence in favor of the subgenera *Hierops* and *Protomyctophum*, recognized traditionally on the basis of both larval morphology and adult phenotype (Fraser-Brunner, 1949; Paxton, 1972). Larvae of the two subgenera are distinguished based on eye width (narrower in *Hierops*), and based on adult phenotype (eyes displaced upward to become "semi-telescopic," and supracaudal organs always bordered by heavy black pigment in *Hierops*). Revision of *Protomyctophum* is therefore warranted.

Lastly, the possible relationship between the markedly short branch lengths observed for the Electronini subclade, previously observed by Gordeeva (2013) in the *co1* gene on a smaller sample of species, and the seeming canalization of adult morphology to resemble a form hypothesized to be close to ancestral must be discussed. Electronin myctophids are almost exclusively Southern Ocean fishes (with the exceptions of *E. risso*, *P. arcticum*, *P. crockeri*, and the rare *P. beckeri*), which exhibit some variation of a Broadly Antarctic distribution, *sensu* Hulley (1998). Several factors may explain what might be inferred as a shift in evolutionary tempo within Electronini. First, strong environmental constraints on electronin fishes living near the circumpolar Antarctic current may favor selection on features resulting in decreased evolutionary rates. Such constraints may be related to the smaller body sizes of electronin fishes compared to many gymnoscopeline fishes, including *Gymnoscopelus*, *Lampichthys*, and *Hintonia*, which have a similar Southern Ocean distribution, but which exhibit much larger body sizes. Second, the observed branch lengths may be an artifact of locus sampling, and the seven markers used in the present analysis may simply represent regions with low molecular evolutionary rates in these fishes.

4.3.2. Phylogeny of Myctophidae: Myctophini and Gonichthyini sensu Paxton, 1972

The relationships among members of these tribes in the present analysis differ in several critical ways from those in traditional hypotheses. The non-monophyly of the tribes Myctophini and Gonichthyini *sensu* Paxton (1972) in the present analysis—based on the strongly-supported polyphyly of the genus *Myctophum*—is an unusual result given the cohesion among members of this putative genus in adult gross morphology, and so is discussed first.

The genus *Myctophum* Rafinesque, 1810 has been traditionally defined based on adult phenotypic traits, including nine osteological characters and seven photophore characters (Paxton, 1972). However, many synoptic keys (Kawaguchi and Aioi, 1972) have noted the difficulty in distinguishing among members of the genus, given overlapping meristic counts among geographic variants, and there has been some historical disagreement regarding the condition of body scales, although a "cycloid" and "ctenoid" (more accurately, 'spinoid,' *sensu* Roberts (1993)) group have been proposed (Kawaguchi and Aioi, 1972). By contrast, larval studies have observed two generally different morphotypes in *Myctophum* larvae, based on the timing of larval photophore development (Moser and Ahlstrom, 1974), with one group (*M. aurolaternatum*, *M. nitidulum*, *M. punctatum*, and *M. affine*) developing only the second branchiostegal photophore, and the other group (*M. asperum*, *M. obtusirostre*, *M. lychnobium*, *M. spinosum*, and *M. selenops*, among those examined) additionally developing the dorsonasal as larvae. These two larval groups reiterate the strongly supported relationships

observed in the present study. Poulsen et al. further note a unique gene rearrangement in *Myctophum* of the "cycloid" species group (*M. nitidulum*, *M. affine*, and *M. punctatum*) involving ND6, tRNA-Glu, and cytb. This arrangement is not observed in *Myctophum* of the 'spinoid' species group. These results strongly corroborate the distinctness of a *Myctophum sensu stricto* (referred to as such for containing the type for the genus).

The strong support observed in the present analysis for the affinity of *Myctophum s. str.* and *Hygophum* is a result reported for the first time, and cannot yet be corroborated by mitogenomic evidence, as the study by Poulsen et al. did not include samples from the latter genus. Traditionally, *Hygophum* has been assumed to be sister to the rest of Myctophini Paxton, 1972, and an affinity of *Myctophum* and *Symbolophorus* has instead been favored based on similarities in shape of the larval pectoral fin (Paxton et al., 1984). Analysis of character polarity in *Hygophum* larvae (Yamaguchi et al., 2000) implying the second morph type as ancestral does not establish any larval characters uniting *Myctophum s. str.* and *Hygophum*, because conical choroid tissue is also shared with larval *Symbolophorus*.

The strong support observed in this analysis for *Myctophum sensu Dasyscopelus* Günther, 1864 was intimated by Poulsen et al., who observed *M. asperum* and *M. orientale* to retain a mitogenomic gene order in common with the slendertail myctophids (*Gonichthys*, *Centrobranchus*, *Loweina*, *Tarletonbeania*), and with *Symbolophorus*. Some morphological support uniting *Myctophum s. Dasyscopelus* with gonichthyine myctophids is suggested by the tooth morphology of the third pharyngobranchial of *Myctophum asperum* and *Gonichthys* (Paxton, 1972, p. 26), although other of these *Myctophum* (e.g. *M. lychnobium*) do not exhibit this character, and further examination of other *Myctophum s. Dasyscopelus* species is needed. Additional support separating these two *Myctophum* groups is provided by larval characters. However, the present analysis goes much further in corroborating structure within this clade, recovering three further groups. The "*M. asperum*" group, noted by Becker and Borodulina (1971, 1978) and Tsarin (1993) to contain at least *M. asperum*, *M. fissunovi*, *M. ovcharovi*, and *M. lunatum*, based on adult characters, is here observed to contain also *M. spinosum* and *M. lychnobium*, an unusual result given the specializations observed in *M. lychnobium* and *M. spinosum* larvae, although the scales of these six species are the most distinctively spinoid in the nominal genus. As no information is apparently available on larvae of *M. ovcharovi*, *M. lunatum*, or *M. fissunovi* (Paxton, pers comm), more data is needed to assess this observed hypothesis. A grouping of *M. brachygnathum* and *M. obtusirostre*, also observed here, agrees with traditional assumptions based on meristic counts. A last grouping, the "*M. orientale*" group, is also in agreement with both larval characters and the characteristic deep body depth observed in these species.

The strongly-supported relationship of the *Myctophum s. Dasyscopelus* + *Gonichthys*/*Centrobranchus* clade, implied for the first time by this study, is an important result that suggests resolution of a longstanding debate between relationships implied by larval (Moser and Ahlstrom, 1970) and adult (Paxton, 1972) morphology, and is discussed alongside the relationship of *Myctophum sensu Ctenoscopelus* + *Loweina*/*Tarletonbeania*. Larvae of the two slendertail myctophid groups (*Gonichthys* + *Centrobranchus* [*G* + *C*], and *Loweina* + *Tarletonbeania* [*L* + *T*]) are distinguishable as two groups based on numerous characters of the eye, and on the basis of these differences Moser and Ahlstrom (1970, p. 139) suggested that the two generic pairs were not closely related to one another, citing larvae of L + T as perhaps the most specialized of all myctophid larvae, "being so divergent as to give no clue of their affinities within the subfamily Myctophinae" (Moser and Ahlstrom, 1974, p. 403). However, on the basis of adult morphology, Paxton (1972) erected the tribe Gonichthyini based on several distinctive characters including the presence in slendertails of spinous procurrent caudal rays, a subterminal mouth, and a PLO in line with or only slightly above the dorsal insertion of the pectoral fin. The results of the present analysis corroborate the hypothesis of Moser and Ahlstrom that the slendertail phenotype is instead a result of convergence, likely based on the ecological constraints imposed by a pelagic trophic niche.

Whereas the relationship between G + C and *Myctophum s. Dasyscopelus* observed in the present study is supported by the robust head, by the morphology and orientation of the choroid tissue mass shared by the larvae of these fishes, and by the somewhat more elongate caudal peduncle in both G + C and *Myctophum s. Dasyscopelus* adults, compared with L + T, the strongly-supported relationship observed between L + T and *Myctophum s. Ctenoscopelus* is somewhat of a mystery, and reiterates the history of uncertain taxonomic placement of *Myctophum phengodes* (Fraser-Brunner, 1949; Paxton, 1972). Larvae of *Myctophum phengodes* are superficially similar to those of *M. nitidulum* (Moser and Ahlstrom, 1974). However, adults of *Myctophum phengodes* are remarkable for having an extremely wide Prc1-2 interspace, a feature used frequently in synoptic keys of the genus to delimit this species early in the couplets (Kawaguchi and Aioi, 1972). Much more work remains to be done to understand the characters associated with this hypothesized clade, as significant developmental shifts in these taxa are apparent, given the Prc1-2 interspace of *M. phengodes* and the unique loss of Prc and SAO photophores in *Tarletonbeania* and *Loweina*, respectively.

The polyphyly of *Myctophum* observed in this study reiterates the intuition that the slendertail phenotype arose from a *Hygophum–Myctophum–Symbolophorus* stock (Paxton, 1972, p. 60), and, more specifically, from a symbolophoroid ancestor. The strongly-supported placement of *Symbolophorus* as sister to the complex assemblage discussed above reiterates the results of the cladistic analyses of Stiassny (1996) and Yamaguchi (2000), who found *Symbolophorus* sister to a slendertail clade. However, the present analysis lacks representatives of the *S. boops*/*barnardi* complex, and the exact species composition of the genus remains unclear; at least one new species remains to be described, and the genus is in need of revision (Gago and Ricord, 2005; Wisner, 1976).

4.3.3. Phylogeny of Myctophidae: Benthosema and Centrobranchus

Two species-level phylogenetic relationships within the subfamily Myctophinae also bear discussion, in light of the existing literature on the genera. First, the genus *Benthosema* Goode and Bean, 1896 is recovered in this analysis rather as a grade into the genus *Diogenichthys* Bolin, 1939, a result in agreement with the result of Poulsen et al. based on mitogenomic data, but based here on almost 90% species-level coverage. In addition to the fact that species in the genus exhibiting almost no cohesion in the anatomy of the caudal luminous organs, the split observed in this study between *B. suborbitale* + *B. glaciale* and *B. fibulatum* + *B. panamense* + *B. pterotum* reiterates a split observed in single-gene analyses by Zahuranec et al. (2012). Separation between these two groups is further supported by significant differences in both cranial and postcranial larval anatomy and in the timing of photophore development; these characters unite the latter three *Benthosema* with larvae of *Diogenichthys* (Moser and Ahlstrom, 1974). The taxonomic status of this assemblage, and the question of whether to split or merge classifications, remains an open problem.

Second, the split observed in this analysis of the genus *Centrobranchus* into two clades, a *C. andreae* group and a *C. nigroocellatus* group, reiterate the suggestion of Gago and Lavenberg (1992) to distinguish *C. andreae* from the rest of the genus. This suggestion is supported by the highly diagnostic anteriorly displaced SAO1 photophore in *C. andreae*, as the genus has otherwise few characters outside morphometric measurements and meristic counts to

distinguish among the other three species in the genus. Because of this fact there has been some debate on the validity of the other three species (Becker, 1983; Gago and Lavenberg, 1992). However, the resampling support in the present study separating the three species supports their distinctness.

4.3.4. Phylogeny of Myctophidae: tribe Diaphini Paxton, 1972

The position of a monophyletic tribe Diaphini observed in this study corroborates the results of Poulsen et al., who further observed a number of mitogenomic specializations in the diaphine taxa they studied, including a shifted tRNA-Gln/tRNA-Met order and the presence of a tRNA-Met pseudogene between tRNA-Gln and ND1. The position of Diaphini in Lampanyctinae potentially disagrees with adult morphology, which unites Diaphini and Gymnoscopelini Paxton, 1972 based on the presence of a keel or ridge on the fifth circumorbital (Paxton et al., 1984). This result, however, is likely a result of homoplasy, as stratigraphic evidence based on fossil otoliths (Brzobohaty and Nolf, 1995, 1996, 2000; Schwarzhans, 2013) suggests members of Diaphini to be much older than the gymnoscopeline fishes, for which an origin in conjunction with the opening of the Drake passage has been postulated (Hulley, 1998).

The resolution observed in this study within the genus *Diaphus* is the first phylogenetic data for the genus, and is a crucial result. Numerous studies (Fraser-Brunner, 1949; Kawaguchi and Shimizu, 1978; Nafpaktitis, 1968, 1978) have noted the taxonomic difficulty of the genus, as many of the characters diagnosing species are fragile and superficial features related to the headlight complex and body scales, and very little character information discriminates among *Diaphus* larvae (Flynn and Paxton, 2013; Moser and Ahlstrom, 1974). The results of the present analysis corroborate the uniqueness of the Suborbital (So) *Diaphus* clade, referred to below as *Diaphus* Eigenmann and Eigenmann, 1890 *sensu stricto*, recovered by both methods with high support. The uniqueness of this clade of *Diaphus* is apparent from the possession by members of this group of dorsonasal (Dn), ventronasal (Vn) and suborbital photophores, but is also corroborated by the slender and elongate morphology of their larvae, one of the only distinguishing differences in *Diaphus* larvae (Moser and Ahlstrom, 1974), which are themselves diagnosed relative to other lampanyctines based upon the accelerated development of postcranial photophores prior to transformation. Members of *Diaphus s. str.* are also unique among lampanyctine myctophids for their short-jawed cranial profile, a feature seemingly convergent with the subfamily Myctophinae. Given the support provided by this study, in combination with the diagnostic features for members of this clade, the possibility of splitting the assemblage into two genera, *Diaphus s. str.* and *Aethoprora* Goode and Bean, 1896 (not the later name *Pantophos* Jordan and Hubbs, 1925, by Fraser-Brunner (1949)), as suggested by Bolin (1959, p. 22), must again be considered.

The second clade recovered by this analysis is a somewhat heterogeneous assemblage of the remaining *Diaphus* species, comprised of members of the dorsonasal–ventronasal groups I and II (Dn–Vn-I and –II), the supraorbital (Suo), and antorbital (Ant) photophore groups traditionally recognized within the genus. Although support values within this group were generally low, this study lends some support for the uniqueness of the Dn–Vn-I species (*D. termophilus* and *D. suborbitalis*), observed at the base of this second *Diaphus* clade. Species in this group are unique in lacking a Vn-like photophore in the traditional position, instead possessing a photophore underneath or at the posterior margin of the eye. The phylogenetic structure of the remaining taxa suggests that the Suo, defining *D. adenomus*, is not an organ itself, but rather an elaboration of the Dn. Additionally, the observed results suggest the possible non-homology of the Ant and the fusiform Dn–Vn-II complex, as both complexes appear several times in the tree. The antorbital appears in a *D. thiollieri* group, a *D. effulgens* group, in *D. watasei*, and in *D. metopoclampus*, whereas the Dn–Vn-II complex appears in a *D. regani* group and a *D. antonbruuni* group. Surprisingly, no anatomical work has yet been conducted on the innervation of the cranial photophore complex of *Diaphus* species, and it is possible to consider a multiple-origin hypothesis of the Ant as arising through different budding events or duplication from a larger Dn organ. Similarly, the two origins of the Dn–Vn-II complex observed in this study may be regarded as potentially two separate convergence events of the Dn and Vn, as the gross morphology of the Dn–Vn complex in the *D. regani* group differs noticeably from the morphology of the complex in *D. antonbruuni* and *D. splendidus*, in the former being more closely fused, with the Dn oriented distinctly forward, a feature noted in Kawaguchi and Shimizu (1978, p. 98). Because coverage of the genus in this analysis is lower than 50% of the nominal species and represents uneven sampling within the different photophore groups, these results must be regarded as preliminary. However, the potential non-homology of several of the different cranial complexes reiterates the need for comprehensive study of this difficult genus.

4.3.5. Phylogeny of Myctophidae; tribe Gymnoscopelini Paxton, 1972

The monophyly of tribe Gymnoscopelini, corroborated in the present analysis, is strongly supported by morphological analysis (Yamaguchi, 2000), whereas Poulsen et al. did not observe a unique mitochondrial gene rearrangement to mirror the strength of morphological support. Gymnoscopeline myctophids have a much larger number of procurrent caudal rays (9–15) than all other myctophids (Paxton, 1972; Paxton et al., 1984) and, like members of tribe Electronini, are almost exclusively limited in geographic range to the Southern Hemisphere (excepting some species of *Notoscopelus*). An unusual feature of the tribe is its assemblage of putatively monotypic genera (*Lampichthys*, *Scopelopsis*, *Hintonia*, and *Lampanyctodes*), and an apparently complex gain/loss/elaboration pattern of several osteological (supramaxillary present, elaboration of the hypural flange, elaboration of the basibranchial plate behind the third hypobranchial) and luminous tissue (angle of Pol photophores, presence of secondary photophores and cheek photophores) characters has obscured relationships within the tribe (Paxton, 1972). The hypothesis in the present study differs from the traditional assumption based on morphological characters in recovering a strongly-supported relationship between *Notoscopelus* and *Scopelopsis*, whereas morphology has traditionally favored a sister-group relationship between *Lampichthys* and *Scopelopsis* based on the presence in both taxa of proliferated secondary photophores (Paxton et al., 1984). *Scopelopsis multipunctatus* Brauer, 1906 is unique among lanternfishes (except possibly *Taaningichthys paurolychnus* Davy, 1972, for which no complete larval series is known) in almost completely replacing a complement of primary body photophores with secondary photophores during larval transformation. The horizontal arrangement of pre-transformation Pol in *Scopelopsis* larvae (Moser and Ahlstrom, 1972) suggests the affinity of *Scopelopsis* and *Notoscopelus* observed in this study, but more work is needed to corroborate the present hypothesis of relationships, as representation of *Notoscopelus* in this study was limited, and the status of the subgenus *Pareiophus* Nafpaktitis, 1975 within *Notoscopelus* remains to be tested.

The strongly supported position of *Lampanyctodes hectoris* observed in this study is an unusual one, as the monotypic genus has been assumed to be basal within the tribe based on morphological analyses. The monotypic genus exhibits a single Pol photophore and a horizontal PVO photophore arrangement reminiscent of some Myctophinae, including *Benthosema* and *Diogenichthys*. These photophore arrangements may be ecologically correlated, as *Lampanyctodes* is a shelf-break/upper slope species (Hulley, 1981), similar to some *Benthosema*.

Monophyly of the genus *Gymnoscopelus* Günther, 1873 is strongly corroborated in the present analysis, but reciprocal monophyly of the subgenera *Nasolychnus* Smith, 1933 and *Gymnoscopelus* is not. Andriashev (1962) argued in favor of the subgenera based upon the difference between the subgenera in the strongly elevated PVO2 above the base of the pectoral fin. Paxton (1972) argued in favor of the subgenera, citing, among other points, that the PVO2 position corroborated an apparent trend within Gymnoscopelini and that similar features were accepted as distinguishing characters within Myctophinae (p. 73). The results of the present analysis suggest instead that the PVO2 position in some *Gymnoscopelus* species is homoplastic, and this hypothesis is supported by the great degree of developmental and adult phenotypic diversity seen within the tribe.

The hypothesis of relationships observed within Gymnoscopelini must be regarded as provisional, as the rare and exclusively Southern Ocean monotypic taxon *Hintonia candens* Fraser-Brunner, 1949 was not included in the analysis. The taxon exhibits an intermediate array of character states hypothesized to place it sister to *Gymnoscopelus* (Paxton et al., 1984), and although taxon sampling within this tribe in the present analysis was generally strong, the unusual number of monotypic genera in this tribe limits the strength of the observed hypotheses somewhat.

4.3.6. Phylogeny of Myctophidae: tribe Lampanyctini Paxton, 1972

The monophyly of Lampanyctini was not corroborated in the present analysis, as *Notolychnus valdiviae* (discussed earlier) was recovered within the tribe. Furthermore, higher-order intergeneric relationships recovered in this analysis differed somewhat from traditional morphological hypotheses in that a clade comprised of *Lampadena* + *Taaningichthys* was recovered as sister to the remaining taxa, with moderate to low support. Members of these two genera are among the deepest dwelling myctophid fishes, and morphological hypotheses have been at odds with regard to the affinities of these two genera. Paxton (1972), although observing that "certain [osteological] characters indicate that the *Taaningichthys–Lampadena* line is the most primitive of the tribe" (p. 67), placed the two genera as sister to the highly-derived genera *Bolinichthys*, *Lepidophanes*, and *Ceratoscopelus* (B–L–C). Moser and Ahlstrom (1972) and Ahlstrom et al. (1976), in analyses of larval characters, placed the two genera within tribe Gymnoscopelini, sister to *Lampanyctodes*, and then sister to B–L–C, and proposed restriction of Lampanyctini to those taxa exhibiting standard larval photophore development, in which only the second branchiostegal photophore develops before transformation. Paxton et al. (1984), in an analysis of combined larval and adult morphological characters, placed *Lampadena–Taaningichthys* as sister to B–L–C, based on the presence (except in *Lampadena*) of expanded larval photophore development beyond the second branchiostegal. Poulsen et al. reiterated this uncertain placement, observing some degree of topological incongruence in the placement of these genera based on gene order and on mitogenomic analyses.

The results of the current study present a somewhat different view, recovering the genus as a grade, with a paraphyletic grouping of *Lampadena urophaos urophaos* + *L. urophaos atlantica* + *L. luminosa*, and a monophyletic grouping of *L. speculigera* + *Taaningichthys* Davy, 1972. The inferred grouping of *L. urophaos urophaos* with *L. urophaos atlantica* and *L. luminosa* intimates possible molecular corroboration of the putative subgenus *Lychnophora* Fraser-Brunner, 1949, although this result is tentative. Although Paxton (1963) suggested that *L. luminosa* (representing subgenus *Lychnophora*) and *L. urophaos* were most closely related based on morphology, he cautioned that because the character state distribution of *L. urophaos* spanned both putative subgenera, the validity of the subgeneric divisions should be reassessed, and in a subsequent review of the genus by Nafpaktitis and Paxton (1968), the subgenus *Lychnophora* was not recognized (p. 27). However, this analysis noted similarities shared by *L. speculigera*, *L. dea*, *L. chavesi*, and *Taaningichthys*, including expanded neural arches of the anterior vertebrae, and the results of the present analysis grouping *L. speculigera* with *Taaningichthys* appear to be moving in that direction. The inferred split of *Lampadena* in the present study disagrees with the monophyletic *Lampadena* of Poulsen et al., who sampled a larger number of *Lampadena* species. However, given a single overlap in taxonomic coverage (*L. urophaos atlantica*) between these two studies, no conclusions can yet be drawn.

The intrageneric structure observed in the present analysis within the two Lampanyctini subclades (exclusive of *Notolychnus valdiviae*), recovers the hypotheses based on morphology. The B–L–C clade received nearly 100% resampling support at all splits, a result apparently reiterating the strength of morphological support for the clade. Members of the B–L–C clade exhibit unique forms of secondary luminous tissue at the medial and paired fin elements, most strongly elaborated in *Ceratoscopelus*, and a sister-taxon relationship for *Lepidophanes* and *Ceratoscopelus* is favored by the unique hook-like projections of strongly-fused procurrent caudal rays (Paxton, 1972).

Within this clade, a monophyletic *Bolinichthys* Paxton, 1972 was recovered, with some structure at the species level—a grouping of *B. supralateralis* + *B. distofax* and *B. longipes* + *B. indicus* + *B. photothorax*. This result corroborates the key couplets of Hulley and Duhamel (2009), who split the genus into two groups based on differences in the distance of the VLO from the lateral line, the presence of three evenly-spaced post-ocular photophores, the elevation of VO2 relative to the series, and the angle of VO2-5. The results of the present analysis suggest that these morphological characters are valid for diagnosing the very fragile members of this genus.

The present analysis represents the first genetic evidence for structure within *Ceratoscopelus* Günther, 1864, as Poulsen et al. analyzed only *C. maderensis* Lowe, 1839. The basal position of *C. maderensis* recovered in this analysis reiterates the assumption of its position in the genus based on morphological evidence and geographic range (Linkowski, 1997). Additionally, the position of *C. townsendi* as nested inside a clade of *C. warmingii* reiterates the longstanding debate on the *C. townsendi*/*warmingii* species complex (Badcock and Araújo, 1988; Gartner, 1998; Linkowski, 1997; Wisner, 1976). Traditional morphological diagnostics separate the N.E.-Pacific *C. townsendi* from the cosmopolitan *C. warmingii* based upon the presence in *C. townsendi* of a supraorbital luminous patch not present in *C. warmingii* (Wisner, 1976). By contrast, Badcock and Araújo (1988) argued that differences in larval development between the two species were not significant, and that variation in *C. warmingii* adult luminous structures were too broad to retain it as a valid species distinct from *C. townsendi*, arguing instead that the complex be synonymized under *C. townsendi* Eigenmann and Eigenmann, 1889, which would contain multiple geographically isolated populations, with separation (form A) or cohesion (form B) of infracaudal luminous tissue as a valid character distinguishing morphotypes. Gartner (1998) questioned the conclusion of Badcock and Araújo (1988) that morphological variation in the complex was primarily ecophenotypic in nature, and presented life history data on Gulf of Mexico and Atlantic populations showing differences in adult sexual size dimorphism and male lifespan, and suggested that these features implied at least incipient genetic differences. Linkowski (1997), in a review of life history data based on otolith microstructure from both Atlantic and Pacific populations, noted geographic differences in the correlation between somatic and otolith growth, and agreed with Gartner (1998) in suggesting that *C. warmingii* may instead contain several species. The results of the present analysis appear at least in part to corroborate the multiple-species hypothesis for

C. warmingii, based on the strong resampling support observed for unique geographic clades comprising specimens from Hawai'i and American Samoa.

Lastly, the present analysis recovered a strongly-supported Lampanyctini subclade comprised of *Stenobrachius*, *Triphoturus*, *Parvilux*, *Nannobrachium*, and *Lampanyctus*, a result corroborated by unique gene rearrangements in this subclade between cytb and the mitochondrial control region (Poulsen et al., 2013). Furthermore, the intergeneric relationships recovered in the present analysis are the same as those based on total morphological evidence (Paxton et al., 1984). Two results are worthy of note. First, *Parvilux* Hubbs and Wisner, 1964 was recovered as sister to the *Lampanyctus*/*Nannobrachium* complex with strong support. Paxton (1972) suggested synonymizing *Parvilux* with *Lampanyctus* based on holistic discussion of both adult characters and nomenclatural priority, but noted some adult characters recalled a transitionary form between *Stenobrachius* and *Triphoturus* (pp. 69–70). However, subsequent analyses observed *Parvilux* larvae to exhibit a rounded cranial shape closer to *Stenobrachius* and *Triphoturus* than to the distinctive rostral projection present in many *Lampanyctus* larvae (Moser and Ahlstrom, 1974), and also to lack trunk myoseptal pigmentation, a feature present in *Lampanyctus* larvae (Paxton et al., 1984). The results of the present analysis corroborate the generic status of *Parvilux*.

Second, the genera *Lampanyctus* and *Nannobrachium* were recovered as non-monophyletic. This result requires extended discussion. The *Lampanyctus*/*Nannobrachium* (*L–N*) complex has been the subject of much speculation, and is in many ways a more difficult group than the *Diaphus* complex due to the extreme fragility of *L–N* specimens (Nafpaktitis et al., 1977, p. 193) and the lack of consensus regarding valid characters defining different lineages within the complex. Fraser-Brunner (1949) distinguished several groups of *Lampanyctus* based on the presence or absence of cheek photophores, the length of the pectoral fin, and the position of the VLO photophore. Bolin (1959) suggested several major lineages to be present within the genus *Lampanyctus*, three of which were based on character combinations suggested by Fraser-Brunner: a lineage with moderate or long pectoral fins and cheek photophores present (*Lampanyctus sensu stricto*); a lineage with long pectoral fins and cheek photophores absent (*Lampanyctus*, with no subgeneric designation); and a lineage with short or no pectoral fins and cheek photophores absent (*Lampanyctus s. Nannobrachium* Günther, 1887). Paxton (1972) broadly reiterated the scheme of Bolin (1959), while further observing that many species possessing cheek photophores and long pectoral fins also exhibited additional secondary luminous tissue (p. 69). However, he cautioned that few unreversed characters diagnosed any sets of species. Moser et al. (1984) designated between three and six larval morphs within the complex. Olivar and Beckley (1997) designated three larval morphs, based on clusters derived from a dendrogram of 24 binary characters, with features in general agreement with the groupings by Moser et al., and observed that short-pelvic-finned forms did not form a clade. However, Zahuranec (2000), in a review of the genus *Nannobrachium*, argued for monophyly of the genus and designated 17 species in five species groups based on a suite of characters, including short/absent pelvic fins with a narrow fin base, squarish otoliths with smooth margins, flaccid body, "pinched" body profile with concave dorsal and ventral postcranial profiles, and atrophied swimbladder.

The results of the present analysis strongly contradict the monophyly of *Nannobrachium*, and suggest the validity of the genus should be revisited, as the definitive characters listed by Zahuranec are more likely a combination of ecomorphological and preservational artifacts. Although the results of the present analysis indicate some misidentification of species—reiterating the difficulty of identifying species in this complex—the strongly-supported monophyly of a clade containing *L. hubbsi*, *L. parvicauda*, *L. turneri*, and *L. vadulus*—all members of Bolin (1959)'s second *L–N* group—is a result mostly consistent with adult morphology. Wisner (1963a) noted that elevation of the second VO photophore directly over the first VO, and a strongly arched AOa photophore series defined *L. parvicauda*, *L. omostigma*, and *L. hubbsi*, and these photophore characters are also seen in *L. turneri*, but not in *L. vadulus*, which has an unelevated VO2 and an evenly arched AOa series. Paxton (1972, p. 70) noted *L. parvicauda*, *L. omostigma*, and *L. hubbsi* to be unique among the specimens of *Lampanyctus* he studied in lacking a strongly concave lateral shelf on the third circumorbital. Although osteological analysis of *L. vadulus* and *L. turneri* is outstanding, the results of the present analysis argue in favor of the distinctness of this *Lampanyctus* group, and suggest that future taxonomic revision of the *L–N* complex might make progress by starting there.

5. Conclusions

The results of this phylogenetic analysis of Myctophidae based on over 50% coverage at the species level presents a framework that is in large part congruent at multiple levels with previous morphological hypotheses based on larval transformation series, adult osteology, and photophore characters, with five novel results that highlight the extraordinary potential of myctophid fishes as a system for macroevolutionary and developmental analyses. First, polyphyly of *Myctophum* into three groups suggests complex convergence by *Gonichthys* + *Centrobranchus* and *Loweina* + *Tarletonbeania* onto the slendertail phenotype from a *Myctophum*- or *Symbolophorus*-like ancestor. Second, the inferred placement of *Notolychnus valdiviae* within Lampanyctini implies significant modification has occurred within this monotypic and enigmatic lineage. Third, phylogenetic structure observed within *Diaphus* reveals for the first time that some components of the conspicuous headlight complex may not be homologous. Fourth, apparent phylogenetic structure within different geographic isolates of *Ceratoscopelus townsendi*/*warmingii* highlights the potential of this complex as a model for studying deep-sea speciation. Finally, the lack of resolution within *Lampanyctus*/*Nannobrachium* reiterates the complexity of this group as an outstanding problem in systematics and taxonomy.

It is hoped that the results of the present analysis will form the backbone for a new research program on these fishes, as significant work remains, especially in assessing the homology of the photophore and luminous tissue complexes, and in genetically corroborating the assignment of larvae to their putative adult species.

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Appendix A. Supplementary data

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