

Myctophidae: Relationships

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THE family Myctophidae has usually been placed in the order Myctophiformes (Iniomi, Scopeliformes) since the work of Regan (1911a), who recognized two suborders, the Myctophoidea and Alepisauroidea (ateleopodids, given a third suborder, are currently placed elsewhere). The families Myctophidae and Neoscopelidae have long been considered close relatives; they were placed in one family until 1949 (Smith). Although Greenwood et al. (1966:371) relegated the order to a subordinal level within the Salmoniformes, they pointed out that myctophoids, and neoscopelids in particular, possess advanced characters that indicate they may be ancestral to the paracanthopterygian radiation. Paxton (1972:54–55) considered myctophids and neoscopelids most closely related to the Chlorophthalmidae, with that evolutionary line of the Myctophoidea arising from an aulopid-like ancestor. Moser and Ahlstrom (1970:141–142) described the larval similarities in the families Chlorophthalmidae, Neoscopelidae and Myctophidae.

FAMILY RELATIONSHIPS

Rosen (1973, 1982) split off the Myctophidae and Neoscopelidae as a restricted order Myctophiformes which he considered the primitive sister group of both the Paracanthopterygii and Acanthopterygii; the remaining myctophiform families were placed in a new order Aulopiformes. Matsuoka and Iwai (1983) found cartilage in the adipose fin of only the Myctophidae and

Neoscopelidae in the five 'iniomous' families they studied. Okiyama (1974b) studied the relationships of the suborder Myctophoidea (*sensu* Gosline et al., 1966) and based on larval peritoneal pigment spots and the relationship of abdominal to caudal vertebrae, three familial groups were recognized: Aulopidae-Synodontidae-Bathysauridae, Chlorophthalmidae-Ipnopidae and Neoscopelidae-Myctophidae. Sulak (1977) lumped the Ipnopidae and Bathypteroidae into the Chlorophthalmidae and the Harpadontidae and Bathysauridae into the Synodontidae, considering both groups arose from the Aulopidae; he did not consider the position of the Myctophidae. Schwarzhans (1978) considered myctophids and neoscopelids most closely related and distinct from Aulopiformes on the basis of otolith morphology.

In his excellent study of the Evermannellidae, Johnson (1982) presented a rigorous analysis of 51 characters involving mostly adult but some larval features. He concluded that neoscopelids and myctophids are most closely related to each other, sharing eight derived character states, but that they were the sister group of four families (Notosudidae, Scopelarchidae, Chlorophthalmidae and Ipnopidae) constituting a chlorophthalmoid group within the Myctophiformes. However, he noted only a single shared derived character in those six families, and it is shared with part of another line. Johnson (1982:95) placed the Aulopidae in a second line and all remaining families in the third

TABLE 63. CHARACTERS OF THE MYCTOPHIDAE. (0) = plesiomorphic state, (1) = apomorphic state, (2) = different or advanced apomorphic state, 1 = by outgroup comparison, 2 = raised photophore, 3 = generalized larva, * = discussed in text.

Characters
1. Jaws long (0), moderate (1), short (2)—*
2. Extrascapulars 2 (0), 1 from fusion (1), 1 from loss (2)—*
3. Cleithral shelf absent (0), present (1)—1.
4. Prc 3-9 (0?), 1-2 (1?)—*
5. Larval eyes round (0), narrow (1)—1, 3.
6. Dn present (0?), absent (1?)—*
7. Moderately or strongly hooked teeth in posterior dentary absent (0), present (1)—1.
8. Procurrent ventral rays 5-10 (0), 9-15 (1)—1.
9. Supramaxillary present (0), absent (1)—1, *
10. PO ₁ level (0), raised (1)—2.
11. Pubic plate narrow (0), wide (1)—1.
12. PO ₂ and PO ₃ level (0), raised (1)—2.
13. VO ₁ level (0), raised (1)—2.
14. PVO horizontal (0), angled (1), vertical (2)—2.
15. Caudal luminous organs present (0), absent (1)—*
16. AOa, level (0), raised (1)—2.
17. Pol angled (0), horizontal (1)—2, *
18. Enlarged teeth in dentary absent (0), present (1)—1.
19. Vertebrae 28-41 (0), 41-45, (1)—1, *
20. VO ₂ level (0), elevated (1)—2.
21. Enlarged dentigerous area on anterior premaxillary absent (0), present (1)—1.
22. Secondary photophores absent (0), present (1)—1.
23. Larval gut moderate (0), initially short (1), long (2)—3, *
24. Larval trunk myoseptal pigment absent (0), present (1)—1, 3.
25. Slightly hooked teeth in posterior dentary absent (0), present (1)—1.
26. Caudal luminous organs not sexually dimorphic (0), sexually dimorphic (1)—*
27. Larval photophores (except Br ₁) absent (0), present (1)—1, 3, *
28. Hyomandibular foramen behind anterior head (0), in anterior head (1)—1.
29. Accessory luminous tissue absent (0), present (1)—1.
30. Caudal luminous organs any other state (0), homogeneous and translucent (1)—*
31. Procurrent ventral rays without hooks (0), with hooks (1)—1.
32. Procurrent dorsal rays without hooks (0), with hooks (1)—1.
33. Crescent of white tissue on posterior iris absent (0), present (1)—1.
34. Pol 0 (0), 1 (1), 2-3 (2)—2, *
35. Dorsal process of opercular head of hyomandibula absent (0), present (1)—1.
36. SAOs weakly angled (0), strongly angled (1)—2, *
37. Larval eyes moderate (0), very large (1)—1, 3.
38. PLO level with PVO ₁ (0), above PVO ₁ (1)—2.
39. SAO 2, close to VO and AO series (0), 2-3 above VO and AO series (1)—2.
40. Larval pectoral fin moderate (0), large (1)—3, *
41. Mouth terminal (0), subterminal (1)—1.
42. Antorbital broad (0), thin (1)—1.
43. Larval fin fold small (0), extensive (1)—1, 3.
44. PLO below (0) opposite or proximate to upper pectoral base (1), far above upper pectoral base (2)—2.
45. Lower pharyngeal teeth conical (0), pegs or plates (1)—1.
46. Nasal trough-shaped (0), convex (1)—1.
47. Larval lower pectoral ray not elongate (0), elongate (1)—1, 3.
48. Gill rakers lathe-like (0), as tooth plates (1)—1.
49. Dorsal hypurals 4 (0), 3-2 (1), 1 (2)—1.
50. Coracoid fenestra present (0), absent (1)—1.
51. Double row of isthmus pigment in larvae absent (0), present (1)—1, 3.
52. Premaxillary teeth conical (0), flattened (1)—1.
53. Larval pectoral base fan-shaped (0), wing shaped (1)—1, 3.
54. Larval head pigment present (0), absent (1)—1, 3.

TABLE 63. CONTINUED.

- | |
|---|
| 55. Larval choroid tissue absent (0), present (1)—1, 3. |
| 56. Larval body width moderate (0), thin (1)—1, 3. |
| 57. Larval gut uniform (0), bipartite (1)—1, 3. |
| 58. Ossified distal pectoral radials 0 (0), 1-7 (1)—1. |
| 59. CO, keel or ridge absent (0), present (1)—1, *. |

group (the alepisauroids plus synodontoids) in his arrangement of the order. We do not have further evidence to present in favour of any of the above hypotheses (but do note the coiled gut of neoscopelid larvae resembles the condition found in higher groups).

GENERIC RELATIONSHIPS

Paxton (1972) analyzed features of the osteology and photophore patterns of the Myctophidae and presented a taxonomy outlining his views of evolutionary relationships that included two subfamilies (Myctophinae and Lampanyctinae), six tribes (Myctophini, Gonichthyini, Notolychnini, Lampanyctini, Diaphini and Gymnoscopelini), 28 genera and two subgenera. The Myctophinae was considered the more primitive of the subfamilies, while the monotypic Notolychnini was provisionally placed in the Lampanyctinae. In four papers Moser and Ahlstrom (1970, 1972, 1974; Ahlstrom et al., 1976) detailed the larval characteristics of all but two genera of Myctophidae and translated their findings into a picture of evolutionary relationships. The relationships proposed by Paxton and Moser and Ahlstrom were strikingly similar overall and in many details. The larval studies supported the recognition of two subfamilies composed of the same genera indicated by the adult analysis, highlighted the enigmatic features of *Notolychnus*, and recognized three additional tribes in the Lampanyctinae. Notable differences in the conclusions of the two studies included consideration of the Lampanyctinae as the most primitive subfamily by Moser and Ahlstrom, non-recognition of the tribe Gonichthyini (*Tarletonbeania*, *Loweina*, *Gonichthys*, *Centrobranchus*) as a monophyletic taxon in the larval study, inclusion of the genera *Taaningichthys*, *Lampadena*, *Bolinchthys*, *Lepidophanes* and *Ceratoscopelus* in the tribe Gymnoscopelini by Moser and Ahlstrom and the tribe Lampanyctini by Paxton, and recognition of the genera *Metelectrona* and *Parvilux* as valid genera on the basis of larval characters, which Paxton had synonymized with *Electrona* and *Lampanyctus* respectively on the basis of adult features. Neither study restricted characters to the derived state and the proposed phylogenies were based on overall similarities. The present work will attempt an analysis of derived character states and re-examine the proposed relationships within the family.

We have used as character states (Table 63) features of adult osteology and photophore patterns as described by Paxton (1972), and features of larvae as described by Moser and Ahlstrom (1970, 1972, 1974) and Ahlstrom et al. (1976) summarized in Moser et al. (this volume). The distribution of the character states among the genera (we have not considered subgenera in this analysis) is tabularized (Table 64). The criteria for determining apomorphic character states have been considered by many, including Marx and Rabb (1972) and Zehren (1979:153). We have used three criteria, the numbers of which are listed after each character in Table 63: (1) Outgroup com-

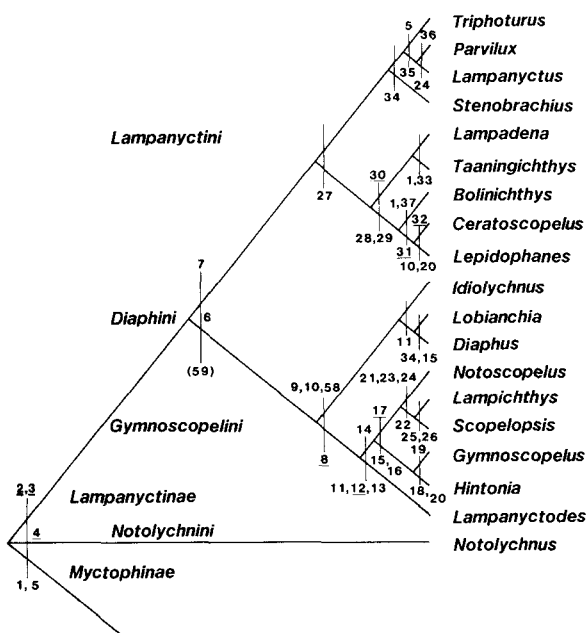


Fig. 125. Phylogenetic diagram of the Myctophidae, subfamily Lampanyctinae. Numbers refer to the apomorphic characters described in Table 63. Numbers in the middle of vertical lines (e.g., 4, 6) refer to characters for which the apomorphic state is unknown. Underlined numbers refer to apomorphic states unique to all members of a given lineage; bracketed numbers (e.g., 59) refer to apomorphic states that have secondarily reversed in at least one member of the lineage; non-bracketed, non-underlined numbers refer to character states found in all members of a given lineage but also by convergence in at least one other taxon in the family.

parison. All previous workers have considered the Myctophidae and Neoscopelidae as sister groups; we have taken the character state in the Neoscopelidae to be the plesiomorphic condition for the Myctophidae. Paxton (1972:57) described the parallel evolutionary trends in the neoscopelids and myctophids, with *Solivomer* similar to the Lampanyctinae and *Neoscopelus* similar to the Myctophinae. We have largely limited our analysis to those characters which display only one state in the Neoscopelidae. Where variation occurs within the family, the character is discussed individually below. (2) Linear photophores. We have considered a photophore elevated out of linear series to be apomorphic. One line of support for this decision occurs in the ontogeny of those myctophid species with a larval PLO photophore, which develops on the pectoral base (where it presumably has a different function from that of the adult) and moves dorsally during development (Ahlstrom et al., 1976:Fig. 4). Also the photophores of *Neoscopelus*, the only luminous neoscopelid genus, are largely linear. However there is some question of the homology of *Neoscopelus* and myctophid photophores. O'Day (1972:71) described the ultrastructure of myctophid photophores and "... confirm(s) Brauer's (1908) original recognition of the close resemblance of photogenic tissue in the Neoscopelidae to that found in the Myctophidae." However Herring and Morin (1978:318) considered photophores of *Neoscopelus* and the myctophids to be very different, on the basis

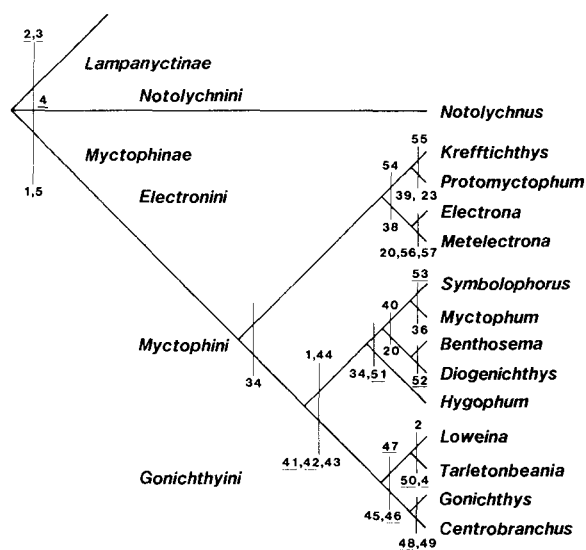


Fig. 126. Phylogenetic diagram of the Myctophidae, subfamily Myctophinae. Numbers are defined as in Fig. 125.

of Kuwabara's (1954) description of *Neoscopelus* compared to that of Brauer (1908). As ventral photophores have evolved independently at least one other time in the stomiiform fishes (Fink and Weitzman 1982:71), the potential for such evolution in deeper water fishes is high enough that one cannot consider their mere existence a case for homology. A study of the ultrastructure of *Neoscopelus* photophores would be of value. (3) Generalized larvae. The larvae of neoscopelids are highly specialized with a robust body, a large head and jaws with prominent teeth, a long gut that may be coiled and large pectoral fins. We do not think these features were present in the ancestors of the two families, and where they are present in the myctophids, consider they have evolved independently. We have used only one such feature, large pectoral fins (40, Table 63) in our analysis. We consider the generalized larva of the myctophid ancestor had the following characters, based on the distribution of larval features in myctophids and other teleosts: body moderately slender, gut slightly S-shaped, extending to about midbody, head moderate in size, eyes round or nearly so, without stalks or choroid tissue, small or moderate finfold and fins and Br_2 the only larval photophores present.

We have used a total of 59 characters, far fewer than the total described in the previous studies. For many we were unable to determine a derived state, as they displayed two or more states or were absent in the neoscopelids. In the osteological descriptions small shape differences or classifications of a continuum were often found in both families and were not included. A number of the characters utilized require comment or explanation: (1) Jaws are long in *Solivomer* and short in *Neoscopelus*, and following our ground rules should not be utilized. However, they appear to be of such fundamental importance, affecting many correlated characters and appearing to represent a major subfamilial difference (Paxton, 1972), that they are included here. Paxton (1972:58) considered short jaws to be primitive, primarily because they occurred in *Protomyctophum*, thought

TABLE 64. CHARACTER STATES IN THE GENERA OF MYCTOPHIDAE. The 59 characters are described in Table 1. 0 = plesiomorphic state, 1 = apomorphic state, 2 = different or advanced apomorphic state, 9 = unknown or both states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Krefflichthys</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Protomyctophum</i>	2	0	0	1	1	9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Electrona</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0
<i>Metelectrona</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
<i>Benthoema</i>	2	0	0	1	1	9	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	9	0	0	1	1
<i>Diogenichthys</i>	2	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
<i>Hygophum</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Myctophum</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	9	0	0	1	9
<i>Symbolophorus</i>	2	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	9	0	0	0	0	0	0	0	1	0
<i>Loweina</i>	1	2	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	1	0
<i>Tarletonbeania</i>	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0
<i>Gonichthys</i>	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Centrobranchus</i>	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Notolychnus</i>	0	9	0	1	9	0	0	0	1	9	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0
<i>Lobianchia</i>	0	1	1	0	9	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	1
<i>Diaphus</i>	9	1	1	0	0	0	0	0	1	1	1	0	1	1	1	9	0	9	0	1	0	0	0	0	0	0	1
<i>Idiolychnus</i>	0	1	1	0	9	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	9	9	0	1	9	
<i>Lampanyctodes</i>	0	1	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Gymnoscopelus</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	1
<i>Scopelopsis</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	9	0	1	0	0	1	1	1
<i>Lampichthys</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	0	0	0	1
<i>Notoscopelus</i>	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	1
<i>Hintonia</i>	0	1	1	0	9	0	0	1	9	0	0	0	0	2	1	0	9	1	0	1	0	1	9	9	1	0	9
<i>Lampadena</i>	0	1	1	0	0	1	1	0	1	9	0	0	0	2	0	0	0	1	0	0	1	0	0	0	0	0	1
<i>Taaningichthys</i>	1	1	1	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Ceratoscopelus</i>	1	1	1	0	0	1	1	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Lepidophanes</i>	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Bolinichthys</i>	2	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	1	9	0	0	0	0	1
<i>Triphoturus</i>	0	1	1	0	1	1	1	0	1	1	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Stenobranchius</i>	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Parvilux</i>	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lampanyctus</i>	0	1	1	0	0	1	1	0	1	1	0	0	0	2	0	0	0	0	0	9	0	9	0	1	0	0	0
<i>Solvomer</i>	0	1	0	9	9	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	9	9	0	0	9
<i>Neoscopelus</i>	2	1	0	9	0	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	0	0	0	0	0
<i>Scopelengys</i>	0	1	0	9	0	1	0	0	0	9	0	9	9	9	1	9	9	0	0	9	0	0	0	0	0	0	0

to represent the most primitive myctophid based on photophore pattern. However Myers (1958) has shown that short jaws have arisen from the long-jawed condition a number of times in teleost evolution, and discussed their adaptive advantages. We consider short jaws to be the apomorphic condition within both the Myctophidae and Neoscopelidae, and moderate jaws also to be derived from long jaws. (2) Extrascapulars are single in neoscopelids; therefore two extrascapulars in some myctophids should be the derived condition. However Paxton (1972:58) described how the neoscopelid extrascapular differs in position and shape from that of myctophids. Following Williston's Rule we consider a single extrascapular to be derived from the fusion of two elements, independently attained in each family. In *Loweina* the single condition has arisen through the loss of the dorsal extrascapular. (4) With no outgroup with similar photophores for comparison, we are unable to determine whether 1-2 or 3-9 Prcs is the apomorphic state. However the two character states follow subfamilial limits, and one of the states must be derived and definitive for its subfamily. (6) All myctophids have at least one of the orbital light organs, Dn and Vn, and most have both. We are not sure whether the presence or the absence of a Dn is apomorphic, but one of those states defines a major line within the Lampanyctinae. (9) Although the Neoscopelidae have a supramaxillary, Paxton (1972:62) considered the supramaxillary of some Myctophidae to be an independently derived feature,

due to a difference in shape and its required loss at least four times within the family if considered primitive. However, Johnson (1974b:205, 1982:79) has shown the presence of supra-maxilla(e) to be primitive in other myctophiforms (*sensu lato*); the absence of a supra-maxilla in myctophids is here considered a derived state through loss. (15) Although caudal luminous organs are not present in neoscopelids, they are present in all but three myctophid genera, where their loss is here considered derived. No other characters indicate that any of the three genera (*Diaphus*, *Gymnoscopelus*, *Hintonia*) are the most primitive in the family. (17) Two or three horizontal Pcls are in a linear position and should be considered the plesiomorphic condition. However in those genera with horizontal Pcls (*Notoscopelus*, *Lampichthys* and *Scopelopsis*) the photophores are high, close to the lateral line. We consider the primitive myctophid state to be one with low photophores with none or one Pol (character 34). We therefore consider the horizontal position of Pcls to be derived, while noting the state in *Hintonia* is intermediate between angled and horizontal. (19) Although Johnson (1982:76) considered a higher number of vertebrae (42-62) plesiomorphic for iniomous fishes, lower numbers of vertebrae in neoscopelids and almost all myctophids indicate the higher number in *Gymnoscopelus* is a secondary specialization in these families. (23) The larval gut of some neoscopelids is long and coiled, clearly a specialization foreshadowing the condition of

TABLE 64. EXTENDED.

28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	
1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	0
1	0	0	0	0	0	0	0	9	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	9	0	
1	0	0	0	0	0	9	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	
1	0	0	0	0	0	1	0	9	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	9	0	0	0	1	0
1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	9	9	9	1	0	
1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	9	2	9	0	0	0	9	0	0	0	0	0	1	0	0	9	0	
1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	0	9	0	
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	
1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	
0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	9	
1	0	0	0	0	0	9	0	0	0	1	1	1	0	0	0	2	0	0	0	0	9	0	0	0	0	1	9	0	0	1	1	
9	9	0	0	0	0	9	0	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	1	0	0	0	1	9	
1	0	0	0	0	0	2	0	0	9	1	1	9	0	0	9	2	0	0	9	0	9	0	9	0	9	9	9	9	9	1	9	
0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
9	1	0	0	0	0	2	9	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	1	
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
1	1	0	0	0	0	2	1	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
0	1	0	0	0	0	2	0	0	9	1	1	9	0	0	9	2	0	0	9	0	0	9	0	9	9	9	9	9	9	0	0	
0	9	1	0	0	0	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1	1	0	1	1	0	2	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
1	1	0	1	0	0	2	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
0	0	0	0	0	0	2	0	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
0	0	0	0	0	0	1	9	0	0	1	1	0	0	0	0	2	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	2	1	0	1	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	9	0	0	0	0	2	1	1	9	1	1	9	0	0	0	2	0	0	0	9	0	9	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	9	0	9	9	9	9	9	0	0	9	9	0	0	9	0	0	9	0	9	9	9	9	9	9	0	0	
0	0	0	0	0	0	9	0	9	0	9	9	1	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
0	0	0	0	0	0	9	0	9	0	9	9	1	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

some acanthopterygians. Although it could be argued that the short gut that lengthens during development in a few forms of myctophids represents the primitive condition, we consider the primitive myctophid condition a moderate-lengthed gut, with different derived states, short and long. (26) Although the caudal luminous organs are sexually dimorphic in about half the genera, we assume the original caudal organs were not sexually dimorphic. (27) No photophores are present on the described larvae of *Neoscopelus*. However the Br₂ develops in all larval myctophids except *Taaningichthys* and *Notolychnus*, and its universality indicates it was present in the ancestral myctophid. Other larval photophores however are present in fewer than half of the genera and we consider their presence derived. (30) The strongly developed caudal luminous organs found in *Lampadena* and *Taaningichthys* are clearly a more specialized state than the relatively unstructured organs found in many other genera. (34) See the discussion of character 17. (36) Although a strongly angled set of SAOs represents a linear position for the first two photophores, we consider this condition developed by the SAO, rising from a lower position in the weakly angled, plesiomorphic position. (59) We consider the absence of a keel or ridge on the fifth circumorbital of *Hintonia* to be secondarily derived through loss. This is the only character state we have used which is not present in all examined members of the line it defines.

We have thus attempted to determine polarity for 25 osteological, 17 larval and 17 photophore characters. We initially attempted a phylogenetic analysis utilizing the distribution of 23 larval characters at the species level. The resulting diagram split some genera into as many as three unrelated lines. We remain convinced that the myctophid genera as currently defined by larval morph, photophore pattern and osteology represent monophyletic lines (even though such genera as *Diaphus*, *Lampanyctus*, *Myctophum* and *Hygophum* may be formally divided as subgenera or genera by future work). These genera we use as the starting point in the present study. We have constructed a phylogenetic tree (Figs. 125, 126) based on our knowledge of the family and used the apomorphic states of the 59 characters to define the various branching points, which is the basis of the following discussion.

The subfamily Lampanyctinae is defined by two apomorphies restricted to all members of the subfamily (those characters found in all members of a lineage and nowhere else in the family are underlined in Figs. 125 and 126), the presence of a cleithral shelf and a single, fused extrascapular. The subfamily Myctophinae is defined by two apomorphies, short or moderate jaws and narrow larval eyes, but these features are also found in a few genera of the Lampanyctinae. The number of Prc photophores defines all members of one of the subfamilies (see discussion of character 4 above).

Notolychnus valdiviae, here considered a monotypic tribe, could not be placed with certainty in either subfamily. Moser and Ahlstrom (1970:138, 1974:409) and Paxton (1972:61) discussed the characters and problems of this enigmatic species. With long jaws and the lack of a cleithral shelf both considered plesiomorphies, the apomorphic number of Prc photophores unknown, and the larval eyes variable and intermediate in shape, future work is required to resolve this trichotomy.

We recognize three tribes in the subfamily Lampanyctinae (Fig. 125). The tribe Lampanyctini, with nine genera, is defined by the presence of a row of moderately to strongly hooked teeth in the posterior dentary; the only other genus with this feature is the myctophine *Diogenichthys*. These nine genera are also the only lampanyctines to lack a Dn orbital photophore, but we are unsure if this is a derived state (see discussion of character 6 above). Moser and Ahlstrom (1972) and Ahlstrom et al. (1976:148) placed five of these genera (*Lampadena*, *Taaningichthys*, *Bolinichthys*, *Lepidophanes*, *Ceratoscopelus*) in the tribe Gymnoscopelini, based primarily on larval photophore pattern. Photophores which appear in larvae of Lampanyctinae are essentially the same ones which develop in myctophine larvae (Moser et al., this volume) and, if they are adaptive as Moser (1981) has suggested, it is likely that they have appeared in these typical sites independently in a number of lineages. Moreover, these photophores develop at the end of the larval period, if at all, in *Bolinichthys* and no photophores develop in *Taaningichthys* larvae. Likewise, the larval pigment characters do not support the inclusion of these five genera in the Gymnoscopelini.

In addition to the distribution of hooked dentary teeth and Dn photophores, other features influenced our decision about these five genera. The ischial ligament is medium or long in all Lampanyctini except *Taaningichthys* (and some species of *Diaphus*), while the fifth circumorbital has a ridge or keel in all gymnoscopelines (but is lacking in some species of *Diaphus*) and no lampanyctines except *Bolinichthys* (thus the brackets around character 59 in Fig. 125). Finally all of the gymnoscopeline genera except *Notoscopelus* are restricted to the southern ocean (Moser et al., this volume: Table 59), while the Lampanyctini are found both north and south (except *Stenobranchius*) of the equator. Placement of the five genera in the Lampanyctini requires fewer character reversals and parallelisms.

Within the Lampanyctini, the development of larval photophores in addition to Br₂ (character 27) unites the five genera discussed above. We recognize *Dorsadena* as a subgenus of *Lampadena* until specimens other than the types are available for osteological study and the larvae are discovered. We have not found an apomorphic character that defines the line including *Stenobranchius*, *Triphoturus*, *Lampanyctus* and *Parvilux*. We are recognizing *Parvilux* on the basis of a weakly angled SAO and larval shape and pigmentation.

We consider the tribe Diaphini to be the sister group of the Gymnoscopelini. The relationships among the three genera of Diaphini are not clear. One of us (HGM) has re-examined the specimens on which the larval features of *Idiolychnus wolampus* were based (see Moser and Ahlstrom, 1974:405–406; Nafpaktitis and Paxton, 1978), and now thinks they could represent *Lobianchia gemellari*, with the larvae of *Idiolychnus* still un-

known. Two characters shared by *Lobianchia* and *Idiolychnus*, the presence of caudal organs and the absence of a luminous patch above the pectoral fin, are considered plesiomorphic, while the absence of a Vn and differences of photophore positions are not clearly apomorphic. The most unequivocal derived state is the presence of a wide pubic plate, indicating *Lobianchia* and *Diaphus* are the sister group pair.

Within the Gymnoscopelini the proposed generic relationships are based almost entirely on characters of the photophores and luminous tissue. No consistent osteological or larval features define generic groupings. Southern ocean larvae require more study. The larvae of *Hintonia* are unknown and not enough species of *Gymnoscopelus* have been studied to ascertain if the subgenus *Nasolychnus* can be defined by any larval characters. The species of *Notoscopelus* should also be studied to find supporting characters of the subgenus *Parieophus*.

Within the subfamily Myctophinae (Fig. 126), we also recognize three tribes, the Electronini, Myctophini and Gonichthyini. The Gonichthyini is clearly a derived lineage, with a number of osteological, photophore and larval characters distinguishing the four genera from the rest of the subfamily. We think the larval specializations of eyes and pectoral fins arose after the split of the two generic pairs.

Paxton (1972) was unable to find osteological characters to clearly separate the remaining genera of the Myctophinae into two lineages. We have utilized photophores to distinguish the Myctophini from the Electronini, while recognizing there is a mosaic of osteological and larval characters within these nine genera. We have little question of the sister group relationship of the generic pairs *Krefflichthys*—*Protomyctophum*, *Myctophum*—*Symbolophorus* and *Benthosema*—*Diogenichthys*. However two larval features, thin head and body and a bipartite gut, are shared by *Metelectrona* and some species of *Hygophum*. Since we think *Hygophum* is a monophyletic line, we consider these shared larval features parallelisms that do not indicate common ancestry. Paxton (1972) considered *Metelectrona* a synonym of *Electrona*. The description of a second species of *Metelectrona* (Hulley, 1981), coupled with its larval and photophore characters, convinced us to recognize the genus.

Of the 59 derived characters utilized in our analysis, only 20 are restricted to members of the lineage they define, and eight of these are autapomorphic at the generic level. The remaining 39 characters are not found in the apomorphic state in any member of the opposite lineage from the defined branching point, but are found in some members of other lineages within the family. This presumed homoplasy of larval, photophore and even osteological characters indicates that the proposed phylogeny was arrived at with some difficulty. Ten of our proposed lineages are undefined by derived characters. We think that future work will support our proposed phylogeny, although some details may be modified, and that new, less plastic characters and better definitions of polarity will help resolve the problems.

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