SHORTER CONTRIBUTIONS

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Comments on Begle’s “Monophyly and Relationships of Argentinoid Fishes”

COLIN PATTERSON AND G. DAVID JOHNSON

In 1992, Begle published a paper on the interrelationships of argentinoid fishes, with comments on the relationships of other lower euteleosts. The study was based on a matrix of 108 characters scored in 32 taxa and a hypothetical outgroup (a row of zeros). That matrix was an expansion of one in an earlier paper (Begle, 1991) comprising 84 characters scored in 19 taxa and an outgroup. Begle’s (1992) data differed by including 24 additional characters, modifying a few of the previous 84, and sampling 14 taxa of Argentinoidei (alepocephaloids and argentinoids), a group treated as a single terminal in the 1991 paper. In a revision of the interrelationships of lower euteleosts (Johnson and Patterson, 1996), we had to pay close attention to Begle’s two papers and found his two matrices to be rife with errors. We have a note (Patterson and Johnson, 1997) detailing errors in Begle’s 1991 matrix. Here we concentrate on his 1992 matrix, the characters newly introduced in it, and his conclusions. Appendixes 1 and 2 reproduce Begle’s (1992) matrix, together with our corrected coding and a summary of differences between the two versions. A detailed commentary is published elsewhere (Johnson and Patterson, 1996), and there is an abbreviated commentary on some characters in Appendix 2 and the text below.

Results.—When we ran Begle’s (1992) matrix, as published, on Hennig86, version 1.5 (J. S. Farris, Port Jefferson, NY, 1988, unpubl.), we found virtually the same solution as Begle (his published results are in square brackets): four shortest trees [Begle reported two], length 215 steps [215], with the same strict consensus (Fig. 1) as Begle’s (1992, fig. 2) published tree, and with C.I. 0.54 [0.56] and R.I. 0.82 [0.83] when the 11 autapomorphic characters are omitted (25, 27, 32, 41, 42, 46, 48, 49, 84, 87, and 96). The minor differences in tree statistics could be due to different treatment of multistate characters or polymorphism: we ran all but character 65 as unordered; with all characters unordered, we found the same four trees, length 213, C.I. 0.55 and R.I. 0.82 with autapomorphies omitted; or if all characters are unordered length 211, C.I. 0.56, R.I. 0.82 with autapomorphies omitted. The virtual coincidence between these results and Begle’s shows that our complaints do not merely concern misprints in Begle’s published matrix.

When we ran the corrected matrix (see Appendixes), not surprisingly we found a very different result. There are three equally parsimonious trees with the strict consensus in Figure 2. Comparison of Figures 1 and 2 shows that, of the 14 nodes in Figure 1, only three (less than a quarter) are reproduced in Figure 2 (numbered 1–3). Major differences between Figures 1 and 2 include the following: (1) the position of esocoids, which are in the basal polychotomy in Figure 1 and are the sister group of osmeroids in Figure 2; (2) Argentinoidei (the node beyond Osmeroidei in Fig. 1) are nonmonophyletic in Figure 2, with the argentinoid genera (Argentina, Glossanodon, Bathylagus, and Opisthoproctus) placed as the sister group of alepocephaloids + esocoids + osmeroids; (3) Alepocephaloidea are nonmonophyletic in Figure 2, with Bathylaco placed as the sister group of esocoids + osmeroids + the remaining alepocephaloids; and (4) relationships within the remaining alepocephaloids (Narcetes and the taxa distal to it in Fig. 2) are totally incongruent with the pattern in Figure 1. The differences between Figures 1 and 2 demonstrate the effects of Begle’s miscoding, but in our opinion, the corrected version (Fig. 2) does not have much to do with the relationships of the taxa concerned (Fig. 3); Figure 2 is more a reflection of Begle’s choice of characters. For example, the characters that place esocoids with osmeroids in Figure 2 are absence of the orbitosphenoid, mesocoracoid, and pubic symphysis and reduction of the articular and the dorsal portion of the opercle; in the context of a wider survey of lower euteleostean characters, these are not convincing evidence that the two groups are immediately related.

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Fig. 1. Begle's (1992, fig. 2) tree of lower euteleosts, based on his data (Appendixes). Strict consensus of four shortest trees (length 215 steps; see text for details) found with Hennig86 (vers. 1.5, J. S. Farris, Port Jefferson, NY, 1988, unpubl.). As in Begle's published tree, the 15 taxa of osmeroids (Galaxiidae to Lepidogalaxias in Appendix 1) are collapsed into a single node, Osmeroidei.

Comments on our recoding.—We discard 19 of the 108 characters in Begle's matrix. The majority (14) of them are among characters 1–84 from Begle (1991), and our reasons for discarding them are summarized in Patterson and Johnson (1997). Among the new characters introduced in Begle's 1992 paper, we discard six (83, 94, 98, 99, 100, and 105). Number 83 concerns the alveolar process of the premaxilla and is discarded because the supposed primitive state is apomorphic for a subgroup of salmonoids (Salmoninae). Number 94 is redundant, concerning features of the opercle dealt with under numbers 65 and 82. Numbers 98 and 99 concern the lateral ridge or strut on the hyomandibular. Number 98 mistakes the primitive state (a long ridge) for a derived state and codes as primitive a condition already coded (number 26) as derived. Number 99 is redundant in part (repeating 26) and self-contradictory in coding. Number 100 concerns laminar bone on the anterior margin of the hyomandibular and is discarded because we could not confirm differences between taxa. Number 105 concerns the opercular process of the hyomandibular and is discarded for the same reason as number 100.

In Begle's (1991) matrix, there were obvious warnings on the quality of the data in entries for undescribed states of several characters. The warnings in Begle (1992) are less obvious because they demand some knowledge of fishes. Three examples of errors in characters introduced in the 1992 paper are numbers 95, 101, and 108. Under character 95, presence or absence of maxillary teeth, a toothed maxilla was incorrectly assigned by Begle to esocoids; to the
retropinnids Prototroctes and Stokellia; and to Aplochiton, Lovettia, Lepidogalaxias, and galaxiids. Under character 101, gillrakers toothed or toothless, the primitive state was mistakenly taken to be toothless gillrakers; and the rakers of outgroups, salmonoids, neoteleosts, Retropinna, and esocoids were incorrectly coded as toothless. Under character 108, first preural centrum (PU1) and first ural centrum (U1) independent or fused, the derived fusion was coded by Begle only in Bathylagus and Opisthoproctus (in which it does not occur); the fusion universally found in galaxiids, neoteleosts, osmerids, salangids, retropinnids, etc., was miscoded. One could quibble about whether the true distribution of these three characters is general knowledge among ichthyologists. Nelson (1984), the standard text at the time of publication of Begle (1992), records the toothless maxilla in esocoids, Prototroctes, Aplochiton, Lovettia, and galaxiids, as did Boulenger (1904) for esocoids, Aplochiton, and galaxiids. That teleostean (or actinopterygian, or osteichthyan) gillrakers are primitives toothed should be obvious to anyone who has examined the gill arches in (say) Amia, Elops, and Salmo. As Nelson (1969:486) put it: “In Recent fishes there is a complete transition between ordinary tooth plates and well-developed gillrakers, and there can be no doubt that gillrakers are little more than modified plates.” Fusion between PU1 and U1 is a little more obscure, but since the condition was first distinguished, its distribution in lower euteleosts has been recorded repeatedly (e.g., Gosline, 1960; Weitzman, 1967; Rosen, 1974; Fujita, 1990) and should be familiar to anyone working in the osteology or higher-level systematics of these fishes. In our view, these errors should have been caught by someone during the procedures between Begle drafting his manuscript and its publication in the professional journal of ichthyologists.

Other errors in Begle’s matrix are more technical. A typical example taken from the characters introduced in Begle’s 1992 paper is number 87, branchiostegal cartilages connecting the branchiostegal rays with the hyoid arch. These were coded by Begle as present only in the alepocephalid Talismania but had previously been illustrated by Sazonov (1986, figs. 6–7) in seven genera of platypteroctid alepocephaloids, and we found them also in the alepocephalids BajaCalifornia, Bathylaco, Bathytroctes, Leptochilichthys, Rinocetes, and Alepocephalus tenebrosus and in the osmerids Mallotus and Hypomesus olidus. Many similar examples could be given. Character 71 was a particular problem. Begle’s original description concerned a ventral process on the pterosphenoid bone. On investigation, we had to delete the character and replace it by four two-state characters (71A–D in Appendix 1). The first concerns presence or absence of the pterosphenoid: it is absent in Lovettia and salangids, which must therefore be coded (?) for any feature of the bone. The other three characters (71B–D) concern three different, non-homologous processes on the pterosphenoid (one dorsomedial, one ventral, and one posteroventral, directed toward the prootic).

Statistics.—As shown in the Appendixes, according to our reading of the specimens and literature, Begle’s (1992) matrix contains errors in 92 (85%) of his 108 characters, leaving only 16 that we accept as he coded them. Of those 16, six (32, 46, 48, 49, 84, and 96) are autapomorphic, leaving only 10 that can be used to group taxa. And those 10 are all taken from previous cladistic analyses (7, 9, 19, 21, and 54 from Fink, 1984; 30 and 51 from Howes and Sanford, 1987a, 1987b; 53 from Rosen, 1974; and 80 and 102 from Greenwood and Rosen, 1971).

A more accurate way of assessing Begle’s error rate is to compare the number of asterisks in Appendix 1, each an error, with the total number of entries. Excluding 12 deleted characters (62–64, 67, 71, 74, 77, 94, 98–100, and 105) in which errors cannot be assessed for one reason or another, the total entries in the matrix are 32 × (108 – 12) = 3072. There are 382 asterisks in Appendix 1, giving an error rate of 12.5%. A more telling way of assessing Begle’s error rate is to compare the number of asterisks with the number of positive (nonzero) entries in the original matrix, since only the positive entries comprise Begle’s character information. Excluding the 12 problematic deleted characters, there are 657 positive entries in Begle’s matrix; the 382 asterisks in Appendix 1 give an error rate of 58%.

Begle’s conclusions on euteleostean interrelationships.—Begle (1992) summarized his conclusions on euteleostean interrelationships in a tree with six characters (Fig. 4). Two characters (numbers 5 and 6 in Fig. 4) link Begle’s Osmerae (alepocephaloids, argentinoids, osmeroids) with Neoteleostei; they are his characters 83 and 100. Number 83, “presence of alveolar process of premaxilla,” is incorrectly coded and characterizes all taxa in the diagram except for salmonine salmonoids and Opisthoproctus (which has no premaxilla). Number 100, “reduction in lamina bone on anterior margin of hyomandibula,” is a character that we discarded because we could not confirm differences between
taxa. One character (number 4) links ostariophysans and salmonoids with Osmerae + Neoteleostei, distinguishing them from esocoids; it is "loss of toothplate on fourth basibranchial" and is credited to Rosen (1974). But Rosen (1962, fig. 13; Rosen and Patterson, 1969, pl. 65, fig. 1) illustrated this toothplate in the percopsiforms Amblyopsis and Percopsis (it also occurs in Aphredoderus; Nelson, 1969, pl. 92, fig. 2), and Rosen (1974:273) reported it as present in the ostariophysan Ichthyborus and in Lepidogalaxias (cf. Fink and Weitzman, 1982:81; we did not find the toothplate in Lepidogalaxias, which is unusual in having the fourth basibranchial fully ossified). Among argentinoids, the toothplate also occurs in the primitive bathylagid Bathylagichthys (Kobyliansky, 1986, fig. 11) and the primitive microstomatid Nansenenia (Kobyliansky, 1990, fig. 8; pers. obs.). Thus the fourth basibranchial toothplate occurs in several euteleostean groups, and its absence cannot have the significance implied in Figure 4. Three characters in Begle's tree (1–3) link esocoids (Esocae of Rosen [1974] and Begle [1992]) with ostariophysans, salmonoids, and Osmerae + Neoteleostei; two are Begle's characters 28 (presence of adipose fin) and 33 (presence of nuptial tubercles), and the third, credited to Greenwood and Rosen ("1977", 1971 intended), is "membranous outgrowth of first urobranchial." Esocoids have no adipose fin (e.g., Boulenger, 1904; Nelson, 1984); Begle mistakenly coded them (and all sampled alepocephaloids) as having one (Appendix 1, number 28). Esocoids do not develop nuptial tubercles (Collette, 1977); Begle mistakenly coded them as having them (Appendix 1, number 33). Esocoids do have a membranous outgrowth on the first urobranchial, but argentinoids (Greenwood and Rosen, 1971) and ostariophysans (Johnson and Patterson, 1996) do not. In short, not one of the characters in Begle's diagram (Fig. 4) has the distribution indicated. As with Begle's matrix, the warnings are clear (adipose fin and nuptial tubercles reported in esocoids) and should have been caught before publication.

Conclusions.—Teleostean fishes are "the vertebrate group to which cladistic analysis was first applied, and, for that reason, teleost systematics has probably progressed further down the road from traditional phenetics towards a phylogenetic system than has the classification of any other vertebrate group" (Patterson, 1993:621). Begle's (1992) paper is a warning of how the application of cladistics in teleosts can lead the way toward chaos. One consequence of the cladistic revolution and the development of numerical cladistics is that a matrix and a computer-generated parsimony analysis are now the norm; if you do not provide them, referees will demand them. The larger the matrix (in number of taxa and of characters), the more impressive it is, but the greater is the likelihood that error will creep in. The advantage of requiring a matrix is that it presents data in unambiguous format, so that they may be checked. However, to check a large matrix as thoroughly as we checked Begle's requires resources: adequate material, technical knowledge, time, and above all will power or commitment. It may never have been done before, and we hope it never has to be done again. Those preparing similar matrices might take a hint from molecular systematists, who routinely deal with character data in quantity: "Each sequence [read 'character'] was read and entered twice by two different persons" (Le et al., 1993:32). In other words, get some help. Those supervising, editing, or refereeing works containing large matrices could use the same advice. Their responsibilities are heavy, because observations published in professional journals are inevitably regarded as having been prepared and vetted with sufficient care to approximate truth.

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Literature Cited


APPENDIX 1. BEGLE’S (1992, APPENDIX) MATRIX OF 108 CHARACTERS IN 35 TAXA, AS PRESENTED BY BEGLE AND AS RECODED AFTER CHECKING. We checked characters against specimens where possible or against the literature where specimens are inadequate (e.g., numbers 4, 24) or not at hand (we lacked Bathypriion). There are three rows for each taxon. The upper row is Begle’s coding, with (?) for missing data and (B) for polymorphism in states (0) and (1). The second row is our coding, with “X” for deleted characters and bold entries for inferred errors in Begle’s coding. The third row summarizes those errors with an asterisk beneath each error and a total at the end. These asterisks do not all coincide with differences between Begle’s coding and ours, because in some characters our coding differs through deleting nonexistent states.
APPENDIX 2. CHARACTERS, ABRIDGED FROM BEGLE (1992). Comments in square brackets detail changes we made or add explanation; characters 1–82 and 84 were included in Begle (1991) and our brief comments are in Patterson and Johnson (1997).

1. Vomer. 0 = composed of head and posterior shaft; 1 = shaft absent. [State (2) added for absence of vomer in *Aplochiton* and salangids.]
2. Articular. 0 = fused; 1 = absent or appearing late.
3. Mesopterygoid teeth. 0 = distributed over surface of bone; 1 = narrow band of larger teeth along medial border; 2 = absent.
4. Anchor membrane of egg. 0 = egg not adhesive; 1 = adhesive anchor membrane present.
5. Caudal fusion pattern. 0 = no fusion of rudimentary neural arches to any element in caudal skeleton; 1 = arches fuse first to centrum, followed in some case by fusion to first uroneural; 2 = arches fuse first to uroneural, followed in some case by fusion to centrum. [In Begle (1991) the character was two-state, discriminating osmerids and salangids from other taxa by fusion of first uroneural with centrum.]
6. Orientation of infraorbital sensory canal. 0 = posterodorsally deflected; 1 = posteroventrally deflected. [See also no. 19.]
7. Mesocoracoid. 0 = present; 1 = absent.
8. Dorsal fin position. 0 = anterior; 1 = posterior.
10. Palatine teeth. 0 = present; 1 = absent.
11. Ectopterygoid. 0 = present; 1 = absent. [See also no. 23.]
12. Extrascapular. 0 = present; 1 = attached to pterotic; 2 = absent. [In Begle (1991) the character was two-state; state (1) added in Begle (1992) for *Argentinia* and *Glossanodon*, with Chapman (1942) as source. Chapman chose to call the dermopterotic of *Argentinia* the supratemporal and described it as fused to the pterotic (= autoprotein), the normal teleostean condition. Begle followed Ahlstrom et al. (1984), not specimens, in interpreting Chapman’s supratemporal as the extrascapular. Begle’s state (1) is deleted and his (2) replaced by (1).]
13. Cleithrum process. 0 = cleithrum with ventral process descending to meet coracoid; 1 = without ventral process. [Two conditions are conflated under state (0). The primitive state, here coded (0), is a long-based, triangular process against which the coracoid lies. In osmerids and retropinnids, here coded (1), there is a narrow-based, columnar process that interdigitates with the coracoid. Absence is here coded (2).]
14. Posterior pubic symphysis. 0 = present; 1 = absent.
15. Scales. 0 = present; 1 = absent.
16. Vomerine teeth. 0 = present; 1 = “huge fangs”; 2 = absent. [Vomer absent in *Aplochiton* and salangids, here coded (?).]
17. Posterior border of operculum. 0 = rounded; 1 = incised or emarginate.
18. Number of hypurals. 0 = 6; 1 = 5.
19. Extent of infrarostral canal. 0 = not extending to preopercle; 1 = extending to preopercle. [State (1), in retropinnids, here added to no. 6, as state (2), and this character deleted.]
20. Ceratohyal border. 0 = more or less straight, with branchiostegals along most of its length; 1 = deeply concave anteriorly, with branchiostegals restricted to area posterior to concavity; 2 = ventral border with rectangular notch. [In Begle (1991) the character was two-state. State (2) added in Begle (1992) for *Talismania* and platytroctids. The notch is in the dorsal border of the ceratohyal, and is homologous with the fenestra ("beryiform foramen" of McAllister, 1968) primitively present in the teleostean ceratohyal.] 21. Horny midventral abdominal keel. 0 = absent; 1 = present.
22. Ovaries. 0 = left and right present; 1 = right only. [It is the left ovary only that is present in retropinnids (and *Plecopterus*).]
23. Location of ectopterygoid. 0 = posterior to autoplatine; 1 = ventral to autoplatine. [The bone is the dermopalatine (no. 11); character deleted.]
24. Cucumber odor. 0 = freshly caught specimens lacking cucumber odor; 1 = fresh specimens with distinctive cucumber odor.
25. Basiopterygial lateral pegs. 0 = basiopterygial without lateral extensions; 1 = with pegs projecting caudally along each side of first vertebra. [Character deleted; see comment in Patterson and Johnson (in press).]
26. Lateral hyomandibular spur. 0 = hyomandibular without lateral projection; 1 = with lateral spur, at or below level of its articulation with opercle. projecting caudally to contact preopercle.
27. Posterior border of caudal fin. 0 = incised or deeply forked; 1 = rounded or emarginate.
28. Adipose fin. 0 = present; 1 = absent.
29. Articulation of premaxilla with maxilla. 0 = premaxillary articulation process not tightly adhering to maxillary head; 1 = syndesmosis between the two bones. [Premaxilla absent in *Opisthophroctus*, here coded (?).]
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APPENDIX 2. CONTINUED.

30. Palatine-maxilla articulation. 0 = palatine without articulatory head meeting similar head on maxilla; 1 = maxilla and palatine with head-to-head articulation.
31. Symphysial cartilages. 0 = paired cartilages not present at dentary symphysis; 1 = paired cartilages present at symphysis.
32. Ectopterygoid flange. 0 = dorsal rim of ectopterygoid not directed laterally; 1 = dorsal rim directed laterally in a horizontal flange.
33. Nuptial tubercles. 0 = present; 1 = absent.
34. Pelvic girdle. 0 = without ventral condyle; 1 = with ventral condyle articulating with the first three or four hemitrichs.
35. Autopalatine. 0 = not in the shape of a dumbbell; 1 = in distinctive dumbbell shape.
36. Adipose cartilage. 0 = absent; 1 = present; 2 = present, pear-shaped.
37. Dentary symphysis. 0 = without medial process; 1 = with short lateral shelf; 2 = with prominent diagonal shelf.
38. Metapterygoid. 0 = without lateral shelf; 1 = with short lateral shelf; 2 = with prominent diagonal shelf.
39. Uncinate process on first epibranchial. 0 = present; 1 = absent.
40. Uncinate process on second epibranchial. 0 = present; 1 = absent.
41. Uncinate process on third epibranchial. 0 = present; 1 = absent.
42. Uncinate process on third pharyngobranchial. 0 = present; 1 = absent.
43. Uncinate process on second pharyngobranchial. 0 = present; 1 = absent.
44. Uncinate process on third pharyngobranchial. 0 = not extending over second epibranchial; 1 = extending well over body of second epibranchial.
45. Uncinate process of second pharyngobranchial. 0 = directed laterally or caudally; 1 = directed anteriorly.
46. Hyomandibula. 0 = not fused to palatine [palatoquadrate intended]; 1 = fused with palatine [palatoquadrate].
47. Third pharyngobranchial. 0 = with narrow anterior extension, reaching first pharyngobranchial; 1 = without anterior extension.
48. Occiput. 0 = not greatly depressed; 1 = greatly depressed.
49. Separate fourth hypobranchial. 0 = absent; 1 = present.
50. Levator process on fourth epibranchial. 0 = wide, its width at distal margin up to half the length of underlying epibranchial; 1 = very narrow, narrower than width of underlying epibranchial.
51. Nasal lamellae. 0 = arranged in rosette; 1 = parallel, longitudinal.
52. Preopercular and supraorbital sensory canal pores. 0 = five or more; 1 = three.
53. Anal rays/scales. 0 = not modified in males; 1 = scales anterior to dorsal margin of anal fin greatly enlarged, anal-fin rays and supports also more or less modified; 2 = as (1) but fin rays and supports extremely modified. [In Begle (1991) the character was two-state; state (2) added in Begle (1992) for Lepidogalaxias alone.]
54. Retractor dorsalis. 0 = absent; 1 = present.
55. Occipital condyle. 0 = formed by basioccipital; 1 = tripartite, formed by basioccipital and exoccipitals.
56. Temporal sensory canal. 0 = present; 1 = absent.
57. Basisphenoid. 0 = present; 1 = reduced or absent. [As no. 57 in Begle (1991).]
58. Orbitosphenoid. 0 = present; 1 = reduced or absent. [As no. 57 in Begle (1991).]
59. Fusion of fifth epibranchial to fourth. 0 = no; 1 = yes, to form circular foramen for efferent artery.
60. Quadrate. 0 = without linear ridges; 1 = narrow transverse ridges present, sometimes ramifying.
61. Metapterygoid. 0 = without linear ridges; 1 = ridges present, sometimes ramifying.
62. Epiphysial. 0 = without foramen; 1 = with midlateral foramen.
63. Pterosphosphenoid. 0 = not reduced, meeting on midline; 1 = reduced and widely separated, not meeting at midline.
64. First basibranchial. 0 = unmodified; 1 = with ventral cartilaginous vane.
65. Anterodorsal border of opercle. 0 = without spine, horizontal; 1 = with notch and spine; 2 = with deep narrow notch.
66. Ascending process of premaxilla. 0 = knoblike; 1 = sharply triangular. [Premaxilla absent in Opisthoproctus, here coded (?).]
67. Maxilla. 0 = more-or-less straight in lateral profile; 1 = curved dorsally in lateral profile.
68. Epiphysial. 0 = usually greater than half length of ceratohyal; 1 = short, very much less than half length of ceratohyal.
69. Fifth ceratobranchial. 0 = without bony laminar extensions near medial margin; 1 = with anterior laminar extension close to medial margin.
70. Palatine. 0 = contacting maxilla by small knob, if at all; 1 = lateral knob overlying maxilla.
<table>
<thead>
<tr>
<th>Character</th>
<th>Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pterosphenoid</td>
<td>0</td>
<td>without ventral processes; 1 = with small ventral flange midway along its length.</td>
</tr>
<tr>
<td>Anterior margin of prootic</td>
<td>0</td>
<td>rounded and smooth; 1 = notched with a small dorsal projection.</td>
</tr>
<tr>
<td>Prootic/pterosphenoid contact</td>
<td>0</td>
<td>at dorsal margin of prootic; 1 = more medial, contact by interdigation.</td>
</tr>
<tr>
<td>Lateral spine on sphenotic</td>
<td>0</td>
<td>blunt; 1 = rodlike.</td>
</tr>
<tr>
<td>Pyloric caeca</td>
<td>0</td>
<td>present; 1 = absent.</td>
</tr>
<tr>
<td>Uroaneals</td>
<td>0</td>
<td>more than one; 1 = one.</td>
</tr>
<tr>
<td>First preural centrum (PU1)</td>
<td>0</td>
<td>more than one neural arch over PU1; 1 = a single rudimentary neural arch over PU1.</td>
</tr>
<tr>
<td>Accessory cartilage at tip of fifth ceratobranchial</td>
<td>0 = absent; 1 = present.</td>
<td></td>
</tr>
<tr>
<td>Fourth ceratobranchial</td>
<td>0</td>
<td>unmodified; 1 = in dorsal view, much wider than first three ceratobranchials, sometimes with distal end expanded.</td>
</tr>
<tr>
<td>Fourth gill arch</td>
<td>0</td>
<td>unmodified; 1 = with fleshy membrane along joint of ceratobranchial and epibranchial partitioning crumenal pouch from orobranchial chamber.</td>
</tr>
<tr>
<td>Gillrakers on fourth and fifth arches</td>
<td>0 = unmodified; 1 = expanded/elongate.</td>
<td></td>
</tr>
<tr>
<td>Opercle</td>
<td>0 = extending dorsally above articulation with hyomandibular; 1 = not extending above articulation.</td>
<td></td>
</tr>
<tr>
<td>Premaxilla</td>
<td>0 = without postmaxillary process (premaxilla and maxilla serially arranged); 1 = with post-maxillary (alveolar) process extending beneath maxilla. [In Begle (1991) the character referred to the length of the alveolar process and was coded as autapomorphic for Stokellia. In Begle (1992) the coding distinguishes neoteleosts, argentinoids, alepocephaloids and osmeroids (all with 1) from esocoids, salmonoids and outgroups. See comments in text.]</td>
<td></td>
</tr>
<tr>
<td>Midlateral band of silver pigment</td>
<td>0 = absent; 1 = present.</td>
<td></td>
</tr>
<tr>
<td>Pelvic splint</td>
<td>0 = present; 1 = absent.</td>
<td></td>
</tr>
<tr>
<td>Shape of interhyal</td>
<td>0 = elongate, rodlike; 1 = short, dumbbell-shaped.</td>
<td></td>
</tr>
<tr>
<td>Branchiostegal cartilages</td>
<td>0 = absent; 1 = small cartilages present, connecting branchiostegals with hyoid arch. [See comments in text.]</td>
<td></td>
</tr>
<tr>
<td>Ventral arm of symplectic</td>
<td>0 = short, less than half length of dorsal arm; 1 = elongate, longer than dorsal arm.</td>
<td></td>
</tr>
<tr>
<td>Metapterygoid</td>
<td>0 = large, broad; 1 = reduced and rodlike.</td>
<td></td>
</tr>
<tr>
<td>Uncinate process on fourth epibranchial</td>
<td>0 = present; 1 = absent.</td>
<td></td>
</tr>
<tr>
<td>Fifth epibranchial</td>
<td>0 = short, much less than half length of fourth; 1 = long, almost equal in length to fourth.</td>
<td></td>
</tr>
<tr>
<td>Ventral coracoid process</td>
<td>0 = short, not extending below ventral margin of pectoral girdle; 1 = narrowly elongate, extending below pectoral girdle.</td>
<td></td>
</tr>
<tr>
<td>Dilator spine on dorsal margin of opercle</td>
<td>0 = absent; 1 = present; 2 = large, extending dorsally. [Character discarded, see comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Maxillary teeth</td>
<td>0 = present; 1 = absent. [See comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Shoulder organ</td>
<td>0 = absent; 1 = present.</td>
<td></td>
</tr>
<tr>
<td>Elevated median basibranchial ridge</td>
<td>0 = absent; 1 = present, separating right and left portions of branchial basket.</td>
<td></td>
</tr>
<tr>
<td>Lateral ridge on hyomandibular</td>
<td>0 = short, less than half length of hyomandibular; 1 = longer, sometimes occupying entire shaft of bone; 2 = absent. [Character discarded, see comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Lateral ridge on hyomandibular</td>
<td>0 = contacts preopercle; 1 = does not contact preopercle. [Character discarded, see comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Laminar extension on anterior margin of hyomandibular</td>
<td>0 = present; 1 = greatly reduced or absent. [Character discarded, see comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Teeth on gillrakers</td>
<td>0 = absent; 1 = present. [See comments in text.]</td>
<td></td>
</tr>
<tr>
<td>Mouth</td>
<td>0 = large; 1 = very small.</td>
<td></td>
</tr>
<tr>
<td>Vomer</td>
<td>0 = does not extend anteriorly beyond ethmoid cartilage; 1 = extends anterior to ethmoid cartilage. [Aplochiton and salangids, in which the vomer is absent, cannot be assessed for this character and should be coded (?)].</td>
<td></td>
</tr>
<tr>
<td>Ovarian tunic</td>
<td>0 = absent; 1 = ovaries covered more-or-less completely with membranous tunic.</td>
<td></td>
</tr>
<tr>
<td>Opercular process of hyomandibular</td>
<td>0 = straight, dorsally located; 1 = ventrally curved, dorsally located; 2 = located at or below midpoint of hyomandibular. [Character discarded, see comment in text.]</td>
<td></td>
</tr>
<tr>
<td>Basihyal teeth</td>
<td>0 = scattered over basihyal; 1 = fangs on margin; 2 = small teeth on terminus only; 3 = fangs on terminus; 4 = absent.</td>
<td></td>
</tr>
<tr>
<td>Development of pectoral fins</td>
<td>0 = small, relatively late in ontogeny; 1 = large, relatively early in ontogeny.</td>
<td></td>
</tr>
<tr>
<td>Fusion of PU1 to U1</td>
<td>0 = no; 1 = yes. [See comments in text.]</td>
<td></td>
</tr>
</tbody>
</table>