SHORTER CONTRIBUTIONS

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Comments on Begle's "Monophyly and Relationships of Argentinoid Fishes"

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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 steps. In the analyses described above, polymorphisms for states (0) and (1) were treated as (0). With polymorphisms treated as (?) and character 65 ordered, 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.

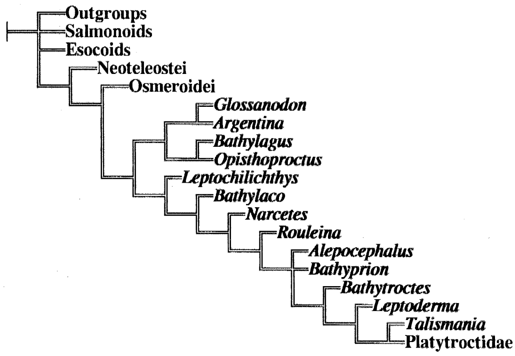

Fig. 1. Begle's (1992, fig. 2) tree of lower euteleosts, based on his data (Appendixes). Strict consensus of four shortest trees (length 215 steps; see text for details) found with Hennig86 (vers. 1.5, J. S. Farris, Port Jefferson, NY, 1988, unpubl.). As in Begle's published tree, the 15 taxa of osmeroids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

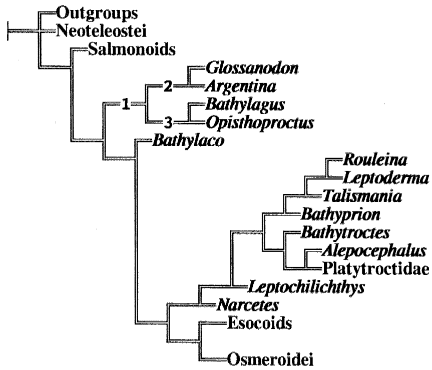

Fig. 2. Tree for the same taxa as Figure 1 after correction of Begle's data, as in Appendix 1. Strict consensus of three shortest trees (length 232 steps; C.I. 0.42, R.I. 0.73) found with Hennig86 (vers. 1.5, J. S. Farris, Port Jefferson, NY, 1988, unpubl.). Nodes common to this tree and Figure 1 are numbered. As in Figure 1, 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

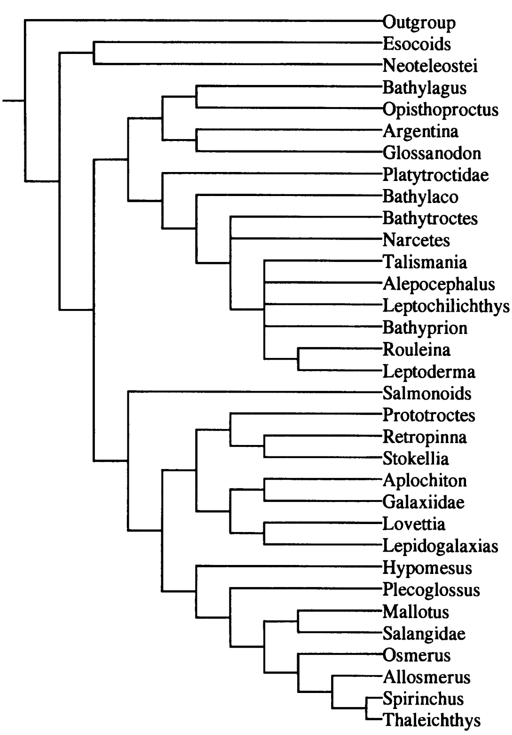

Fig. 3. Relationships of the taxa in Figures 1 and 2 as inferred by Johnson and Patterson (1996). Tree produced with Clados (vers. 1.2, K. C. Nixon, Trumansburg, NY, 1992, unpubl.).

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 primitively 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 platytroctid alepocephaloids, and we found them also in the alepocephalids *Bajacalifornia*, *Bathylaco*, *Bathytroctes*, *Leptochilichthys*, *Rinoctes*, 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, nonhomologous 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 $32 \times (108 - 12) = 3072$. 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 laminar bone on anterior margin of hyomandibula," is a character that we discarded because we could not confirm differences between

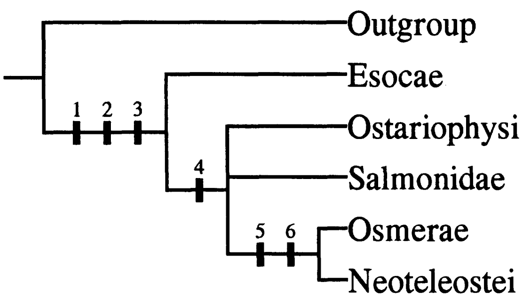

Fig. 4. Begle's (1992) interpretation of the relationships of lower eutelosts (after Begle, 1992, fig. 9). Tree produced with Clados (vers. 1.2, K. C. Nixon, Trumansburg, NY, 1992, unpubl.).

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 *Nansenia* (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 uroneural." 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 uroneural, 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

Ahlstrom, E. H., H. G. Moser, and D. M. Cohen. 1984. Argentinoidei: development and relationships. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1: 155–169.

Begle, D. P. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. Syst. Zool. 40:33–53.

———. 1992. Monophyly and relationships of the argentinoid fishes. Copeia 1992:350–366.

BOULENGER, G. A. 1904. Systematic account of Teleostei, p. 541–727. *In:* Fishes, ascidians, etc. The Cambridge natural history. Vol. 7. S. F. Harmer and A. E. Shipley (eds.). Macmillan, London.

CHAPMAN, W. MCL. 1942. The osteology and relationships of the Argentinidae, a family of oceanic fishes. J. Wash. Acad. Sci. 32:104–117.

COLLETTE, B. B. 1977. Epidermal breeding tubercles and bony contact organs in fishes. Symp. Zool. Soc. Lond. 39:225–268.

FINK, W. L. 1984. Basal euteleosts: relationships. Am. Soc. Ichthyol. Herpetol. Spec. Publ. 1:202–206.

———, AND S. H. WEITZMAN. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos.* Bull. Mus. Comp. Zool. 150:31–93.

FUJITA, K. 1990. The caudal skeleton of teleostean fishes. Tokai Univ. Press, Tokyo, Japan.

GOSLINE, W. A. 1960. Contributions toward a classification of modern isospondylous fishes. Bull. Br. Mus. (Nat. Hist.), Zool. 6:325–365.

GREENWOOD, P. H., AND D. E. ROSEN. 1971. Notes on the structure and relationships of the alepocephaloid fishes. Am. Mus. Novit. 2473:1–41.

HOWES, G. J., AND C. P. J. SANFORD. 1987a. Oral ontogeny of the ayu, *Plecoglossus altivelis* and comparisons with the jaws of other salmoniform fishes. Zool. J. Linn. Soc. 89:133–169.

———, AND ———. 1987b. The phylogenetic position of the Plecoglossidae (Teleostei, Salmoniformes), with comments on the Osmeridae and Osmeroidei. Proc. 5th Congr. Europ. Ichthyol., Stockholm 1985:17–30.

JOHNSON, G. D., AND C. PATTERSON. 1996. Relationships of lower euteleostean fishes, p. 251–332. *In:* Interrelationships of fishes. M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson (eds.). Academic Press, San Diego, CA.

KOBYLIANSKY, S. H. 1986. Materials for a revision of the family Bathylagidae (Teleostei, Salmoniformes). Trudy P. P. Shirsov Inst. Oceanol. 121a:6–50 (In Russian).

———. 1990. Taxonomic status of microstomatid fishes and problems of classification of suborder Argentinoidei (Salmoniformes, Teleostei). *Ibid.* 125: 148–177 (In Russian).

LE, H. L. V., G. LECOINTRE, AND R. PERASSO. 1993. A 28S rRNA-based phylogeny of the gnathostomes: first steps in the analysis of conflict and congruence with morphologically based cladograms. Mol. Phylog. Evol. 2:31–51.

MCALLISTER, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. Bull. Nat. Mus. Can. 221:1–239.

NELSON, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Am. Mus. Nat. Hist. 141:475–552.

NELSON, J. S. 1984. Fishes of the world. 2d ed. John Wiley and Sons, New York.

PATTERSON, C. 1993. Teleostei, p. 619–654. *In:* The fossil record 2. M. J. Benton (ed.). Chapman and Hall, London.

———, AND G. D. JOHNSON. 1997. The data, the matrix and the message: comments on Begle's "Relationships of the osmeroid fishes." Syst. Biol. 40.

ROSEN, D. E. 1962. Comments on the relationships of the north American cave fishes of the family Amblyopsidae. Am. Mus. Novit. 2109:1–35.

———. 1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides.* Bull. Am. Mus. Nat. Hist. 153:265–326.

———, AND C. PATTERSON. 1969. The structure and relationships of the paracanthopterygian fishes. *Ibid.* 141:357–474.

SAZONOV, Y. I. 1986. Morphology and classification of the fishes of the family Platytroctidae (Salmoniformes, Alepocephaloidei). Trudy P. P. Shirsov Inst. Oceanol. 121a:51–96 (In Russian).

WEITZMAN, S. H. 1967. The origin of the stomiatoid fishes with comments on the classification of salmoniform fishes. Copeia 1967:507–540.

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APPENDIX 1. BEGLE'S (1992, APPENDIX) MATRIX OF 108 CHARACTERS IN 33 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 *Bathyprion*). 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.

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CHARACTER                                                                    7777                                  111111111
                              111111111122222222223333333333444444444455555555556666666666771111777777778888888888999999999900000000
                     1234567890123456789012345678901234567890123456789012345678901ABCD23456789012345678901234567890123456789012345678

Outgroups            0000000000000000000000000000000000000000000000000000000000000     000000000000000000000000000000000000
Outgroups            00000000000000000X000X00000000000000000000XX0000000000000000XXX00X000X00000XX00X00000X000000000X000XXX0000X000
                                                                                                       *         *                  2
Salmonoids           00000000000000000000000000000000000000?0000000000000000     000000000000000000000000000000000000100
Salmonoids           1020000000000000000X000X000000000?000000000XX0000000000000000XXX00X000X00000XX00X00000X000000000X000XXX0000X000
                     * *                          *            *           *                       *         *              *   8
Neoteleosts          0000000000000000000000000000000000000000000011000000000000000     00000000001000000000000000100000000
Neoteleosts          00000000000000000X000X0000000001000000000XX000010001100000XXX00X000X00000XX00X00000X000000000X000XXX0000X001
                                                  *                 *                                                           * 3
Galaxiidae           1110111121121111211000?011010000110000110010001000100001111000100111111     0010000000110000000000000000100000100
Galaxiidae           0110121121112112O1X000X0B1B10000100000110B1XX0B0001000011110OXXX01X000X01B00XXB0X00001X0000000000X100XXX1000X101
                     *    *          *     * *     *        *  *  *                   ***      *                   *   *     *     * 17
Lovettia             1110111121121111211000?0000000000100001100000010001000011110001000000011     00000000011010000000000000100000100
Lovettia             01101211210121121 1X000X0000000000000000011011XX020001000011110OXXX00X000X1???0XX10X00001X000001000 1X100XXX1000X101
                     *    *    *           *             ****                   **        *           *   * * * *     *     * 18
Aplochiton           1110111121121111211000?001000000110000110010000000100001111000100111011     000000000110000000000000000100000100
Aplochiton           21101211211112112 11?01X100X001000000010000011001XX00000100001111 00XXX01X100X01100XX00X00001X0000000000X100XXX10?0X101
                     *    *        ** *         *          *                        *                    *   *    * *   * 13
Salangidae           1120211101121111200000?00000000011010000000100111100010011110001000000010     00?0000000110100000000000000100000400
Salangidae           212120110011210?00X000X0000000000010100????XX12111001000 11200XXX00X000X1???0XX10X00001X0100000?01X000XXX10?0X001
                     * * *   *  **           *  *  *******      *    *  *           **        *                *  *       * *  * * 27
Retropinna           11101111110000000011111100000100010000000010001000110000110000110000000     000000000110000000000000020100000100
Retropinna           11100111101010 0000X111X10000010001000000011XX0100011000011200XXX00X000X01000XX10X00001X0000000000X000XXX0000X101
                         *   **                        * ** *        *                 *                 *                 * 11
Stokellia            11101111110000000011111100000100010000000010001000110000110000110000001     000000000110000000000000021100000100
Stokellia            11100111101020 0000X111X10000010001000000001XX0100011000011000XXX00X000X01100XX10X00001X0000000000X100XXX1000X101
                         *   ** *                        * *                          *                 *   *    *    * 11
Prototroctes         1110111111000000001111110000100011000000000100010001100001100001100000001     00000000011000000000000002000000100
Prototroctes         11100111101010 0000X111X10000100011000000001XX0100011000011000XXX00X000X01100XX10X00001X0000000000X100XXX1000X101
                         *   ** *                        * *                          *                 *   *    *    * 11
Plecoglossus         11112000000000000000000000100101101121100000110000000000011000111100000 1     01000000001000000000000000100000100
Plecoglossus         0111200000000100000X001X0010010110112110000XX000010000001 1000XXX10X000X00112XX00X00000X0000001200X000XXX1000X101
                     *          *    *                 *                           *              **          *     * 9
Allosmerus           11112000000000000000000000100000001110200001100001000000110111112000001     10100000000110000000000000001100000100
Allosmerus           11112000000010000 0X000X001000000011202000 0XX0000100000011211XXX20X000X00112XX10X00000X1000001B00X000XXX1000X101
                                                 *        *                              * *                **          *     * 9
Hypomesus            111120000000000000000000001000000011202000000100001000000011000111100000 1     00100000000100000000000000101000000000
Hypomesus            B1112000000010000 0X000X1010000000102020000XX0000100000011200XXX10X000X00100XX00X00B00X000000 1000X000XXX1000X001
                     *                 *                                                    *              **          *     * 10
Osmerus              111120000000000100000001010000100112120000110000000000011000111100000 1     01000000000100000000000000101000000100
Osmerus              11112000000000100100X000X1010000000112020000XX0000100000011200XXX10X000X00011XX00X00000X0000001200X000XXX1000X101
                                 *              *     *    *                              **                **          *    * 11
Spirinchus           1111200000000000000000000010000000111020000110000100000001011111200000 1     10100000000100000000000000101000000100
Spirinchus           111120000000100000 0X000X001000000011202000 0XX0000100000011211XXX10X000X00012XX00X00000X0000001200X000XXX1000X101
                                 *              *        *                              *  *           **          *    * 11
Mallotus             11112000000000000000000000100000001110100001100001001000110001112000001     00100000000100000000000000101000000000
Mallotus             11112000000010000 0X000X0010000000101020000XX0000100100011210XXX20X000X00100XX00X00000X0001001000X000XXX1000X001
                                 *                  *       *           **                 *              **          *     * 10
Thaleichthys         11111000000000000000000010000000001120200001100000000000110100111000001     000000000010000000000000011100000100
Thaleichthys         11112000000010000 0X000X1000000000112020000XX0000100000011211XXX10X000X00012XX00X00000X0000001200X000XXX1000X101
                         *       *                        *        *  * *                 **                 **       *    * 11
Lepidogalaxias       01200111200211001100000000110000100000001110001000102111110000100000111     000111000001100000000000000100000400
Lepidogalaxias       0120031120012100 11X000X0011100001000001 0111XX020001121110 1?00XXX00X011X00100XX10X00001X010001000 0X100XXX1000X400
                          *       *           *          *  ** *   * *                 *   *  * *  *   *         * 16
Esocoids             00000010000000000000000000000000000000000000000000000000000000000     00011100000000000000000000000000000
Esocoids             01200011000B210000X000X001B100000100000000000XX02002000000B1?00XXX00X000X00000XX11X00001X0000000100X100XXX0000X000
                     **   *  ***           ***   *         * *  ***                                                                  18
Argentina            002010000001000000000000000000000000100000000000000000100000000000000100000000     000000111101001011000001000010110031 0
Argentina            00201000000000000000X000X1000000000100000000000XX000010000000000000XXX00X000X00000XX00X10100X0010110100X100XXX1110X30B
                         *               *                                                             * *                  ** 8
Alepocephalus        00201001000000020000000000000000010000000000000000000000000110000110000000     000000111111000000110111010011000 0400
Alepocephalus        002000010000200200X000X00001000010000001000XX000000000000000011XXX00X000X00000XX00X12101X00010010 01X100XXX1000X400
                         *    *         *           *            *      ** **               * *    *            *       12
Bathylagus           002010100000000000000000000100000000010000000000000000100000011000010000000000     0000011110101100101100100001011 00411
Bathylagus           00201010000021 0000X000X00000000010000000000XX00001000000B0010XXX00X000X00000XX00X11110X000001000 0X100XXX1110X401
                               **                       *           ** *                              **        *       *   * 11
Talismania           0020B00100000000002000000000000100000000000000000000000000000000110000000     000000111111010100110110010011001040 0
Talismania           002000010000200000X000X00001000010000001000XX00000000000000000XXX00X000X00000XX00X10101X0101001001X000XXX0001X400
                         *    *    *      *          *                                    * *                *   *      9
Platytroctidae       0020B0000000000200020000000000001000000000000000000000000BB0000110000000     0000001111110100001B01101100110001400
Platytroctidae       0010000100000B00000XB00X00001000010000001000XX0000000000000BB011XXX00X000X00000XX00X12101X0B01001B00X011XXX0000X10B
                       *  *  *  *  *  *     *          *                 **                  * *   * *    *      *    * * 18
Leptoderma           0020?011010000120000000000000000100000000000000000000000000000110000000     0000001111110100001101110101110001400
Leptoderma           002000110101201201X000X00001000010000001000XX00000000000000000XXX00X000X00000XX01X12101X0100000001X100XXX0001X401
                          *   **   *       *          *                               *  * *      *       *   *   *   * 14
Leptochilichthys     0020100000000000000000000000000100000000000000000000000100000110000000     000000111111000000010011010001000 1?00
Leptochilichthys     002000010000200000X000X00001000010000001000XX00000000000011000XXX00X000X00000XX00X10101X0001001000X101XXX0000X?00
                          *  *  *          *          *                *                   * *    *  *        *        11
Opisthoproctus       00201010000000000000000000000001000000000000000001000000110000010000000     000000111101011011011001000010110040 1
Opisthoproctus       002000100000210000X000X00000?0001000000000000XX01000000010110 00XXX0?X000X00000XX00X01110X0110010010X100XXX1110X410
                          *    **         *             *  *   *         *                *    *    *            *    ** 14
Bathyprion           0020101000000000200000000000000100000000000000000000000011000011 0000000     0000001111110000001101100101110010400
Bathyprion           002000110000?00200X000X00001000010000000?000XX000000000000011000XXX00X000X00000XX00X0?101X000?001001X000XXX0001X400
                          *  *            *                                               *            *   *   *    7
Bathytroctes         002010000000000020000000000000010000000000000000000000010000011000000000     0000001111110000001100100101110001400
Bathytroctes         002000010000200200X000X00001000010000000000XX00000000000000000XXX00X000X00000XX00X12101X0001001000X000XXX0000X400
                          *  *  *          *                     *                         * *    *          *   *     10
Bathylaco            0020?000000000000000000000000001000000000000000000000000000000110000000     00000011111100000001002001011100 10400
Bathylaco            002000010000000000X000X00001000010000000000XX000000000000000000XXX10X000X00000XX00X00100X000100?000X000XXX0000X400
                          *  *             *                           *                   * **    *        *   *   *     11
Glossanodon          0020100000010000000000000000000010000000000000000010000001000000100000000     000000111010B101100000100001011 00210
Glossanodon          00201000000000000 0X000X0000000000100000000000XX00001000000000000XXX00X000X00000XX00X10100X0B10110B00X100XXX1110X20B
                               *                          *         *                        * *        *          *    ** 9
Narcetes             0020100000000000000000000000000100000000000000000000000011000011000000     0000001111110000000100100101010000400
Narcetes             002000010000200000X000X00001000010000001000XX00000000000000000XXX00X000X00000XX00X10101X000000?000X000XXX0000X400
                          *  *  *          *          *            **                      * *                *   *     11
Rouleina             0020100001000000000000000000000010000000000000000000000110000110000000     000000111111010000010110010111000 0400
Rouleina             002000010100200200X000X00001000010000001000XX00000000000000000XXX00X000X00000XX00X10101X0100001001X000XXX0000X400
                          *  *    *  *          *          *            **                 * *      *      *   *     13
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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.
9. Principal caudal rays. 0 = 10/9; 1 = 9/9; 2 = 8/8.
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 *Argentina* and *Glossanodon,* with Chapman (1942) as source. Chapman chose to call the dermopterotic of *Argentina* the supratemporal and described it as fused to the pterotic (= autopterotic), 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 infraorbital 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 ("beryciform 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 *Plecoglossus*).]
23. Location of ectopterygoid. 0 = posterior to autopalatine; 1 = ventral to autopalatine. [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. Basioccipital lateral pegs. 0 = basioccipital 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 articular process not tightly adhering to maxillary head; 1 = syndesmosis between the two bones. [Premaxilla absent in *Opisthoproctus,* here coded (?).]

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 medial tusk-like process.
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 of 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. [In Begle (1991) state (1) was absence of the bone. "Reduced" might have been added in Begle (1992) to excuse his (1991) coding of absence in alepocephaloids and argentinoids.]
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. Epihyal. 0 = without foramen; 1 = with midlateral foramen.
63. Pterosphenoid. 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. Epihyal. 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.

APPENDIX 2. CONTINUED.

71. Pterosphenoid. 0 = without ventral processes; 1 = with small ventral flange midway along its length.
72. Anterior margin of prootic. 0 = rounded and smooth; 1 = notched with a small dorsal projection.
73. Prootic/pterosphenoid contact. 0 = at dorsal margin of prootic; 1 = more medial, contact by interdigitation.
74. Lateral spine on sphenotic. 0 = blunt; 1 = rodlike.
75. Pyloric caeca. 0 = present; 1 = absent.
76. Uroneurals. 0 = more than one; 1 = one.
77. First preural centrum (PU1). 0 = more than one neural arch over PU1; 1 = a single rudimentary neural arch over PU1.
78. Accessory cartilage at tip of fifth ceratobranchial. 0 = absent; 1 = present.
79. Fourth ceratobranchial. 0 = unmodified; 1 = in dorsal view, much wider than first three ceratobranchials, sometimes with distal end expanded.
80. Fourth gill arch. 0 = unmodified; 1 = with fleshy membrane along joint of ceratobranchial and epibranchial partitioning crumenal pouch from orobranchial chamber.
81. Gillrakers on fourth and fifth arches. 0 = unmodified; 1 = expanded/elongate.
82. Opercle. 0 = extending dorsally above articulation with hyomandibular; 1 = not extending above articulation.
83. Premaxilla. 0 = without postmaxillary process (premaxilla and maxilla serially arranged); 1 = with postmaxillary (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.]
84. Midlateral band of silver pigment. 0 = absent; 1 = present.
85. Pelvic splint. 0 = present; 1 = absent.
86. Shape of interhyal. 0 = elongate, rodlike; 1 = short, dumbbell-shaped.
87. Branchiostegal cartilages. 0 = absent; 1 = small cartilages present, connecting branchiostegals with hyoid arch. [See comments in text.]
88. Ventral arm of symplectic. 0 = short, less than half length of dorsal arm; 1 = elongate, longer than dorsal arm.
89. Metapterygoid. 0 = large, broad; 1 = reduced and rodlike.
90. Medial shelf on metapterygoid. 0 = absent; 1 = present.
91. Uncinate process on fourth epibranchial. 0 = present; 1 = absent.
92. Fifth epibranchial. 0 = short, much less than half length of fourth; 1 = long, almost equal in length to fourth.
93. Ventral coracoid process [= postcoracoid process]. 0 = short, not extending below ventral margin of pectoral girdle; 1 = narrowly elongate, extending below pectoral girdle.
94. Dilatator spine on dorsal margin of opercle. 0 = absent; 1 = present; 2 = large, extending dorsally. [Character discarded, see comment in text.]
95. Maxillary teeth. 0 = present; 1 = absent. [See comment in text.]
96. Shoulder organ. 0 = absent; 1 = present.
97. Elevated median basibranchial ridge. 0 = absent; 1 = present, separating right and left portions of branchial basket.
98. Lateral ridge on hyomandibular. 0 = short, less than half length of hyomandibular; 1 = longer, sometimes occupying entire shaft of bone; 2 = absent. [Character discarded, see comment in text.]
99. Lateral ridge on hyomandibular. 0 = contacts preopercle; 1 = does not contact preopercle. [Character discarded, see comment in text.]
100. Laminar extension on anterior margin of hyomandibular. 0 = present; 1 = greatly reduced or absent. [Character discarded, see comment in text.]
101. Teeth on gillrakers. 0 = absent; 1 = present. [See comments in text.]
102. Mouth. 0 = large; 1 = very small.
103. Vomer. 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 (?).]
104. Ovarian tunic. 0 = absent; 1 = ovaries covered more-or-less completely with membranous tunic.
105. Opercular process of hyomandibular. 0 = straight, dorsally located; 1 = ventrally curved, dorsally located; 2 = located at or below midpoint of hyomandibular. [Character discarded, see comment in text.]
106. Basihyal teeth. 0 = scattered over basihyal; 1 = fangs on margin; 2 = small teeth on terminus only; 3 = fangs on terminus; 4 = absent.
107. Development of pectoral fins. 0 = small, relatively late in ontogeny; 1 = large, relatively early in ontogeny.
108. Fusion of PU1 to U1. 0 = no; 1 = yes. [See comments in text.]