

APPENDIX 2—Cetacean postcranial characters

This appendix includes a comprehensive list of 105 characters of the postcranial skeleton relevant to both cetacean higher phylogeny and relationships among archaic cetaceans. The majority of these have been accumulated from recent cladistic analyses (Thewissen and Madar, 1999; O'Leary and Geisler, 1999; Geisler, 2001; Thewissen et al., 2001b; Uhen and Gingerich, 2001; Geisler and Sanders, 2003), but 18 are new characters resulting from this study and previous work on artiodactyl limb osteology (Hussain et al., 1983). References that follow the characters cite their original derivation. Modified characters are noted. Regional clustering of characters follows that of the manuscript. A character matrix including scores for pakicetids, early marine archaeocete *Ambulocetus* and North American and Indo-Pakistani *Diacodexis* are found in Appendix 3.

Axial Skeleton

1. *Occipital condyles*.—Broadly rounded in lateral view (0); V-shaped in lateral view, in posterior view the condyle is divided into a dorsal and a ventral half by a transverse ridge (1) (Geisler, 2001).
2. *Anterovertebral border of occipital condyle*.—Tapers medially (0); flared laterally and ventrally to form stop for ventral movement of the cranium (1) (Geisler, 2001).
3. *Length of prelumbar vertebral column* (ordered).—Very short, length of cervical plus thoracic portions of vertebral column from 77% to 55% condylobasal length of skull (0); short, length of cervical plus thoracic portions of vertebral column from 100% to 83% skull length (1); long, from 123% to 114% skull length (2); very long, >135% skull length (3) (Geisler and Sanders, 2003, derived from Miller, 1923).
4. *Atlas* (ordered).—Ventral process larger than dorsal process (0); both processes are sub equal (1); dorsal process larger (2) (Geisler and Sanders, 2003, modified from Muizon, 1987, 1988a).
5. *Odontoid process of axis*.—Forms anteriorly pointed peg (0); spout-like, dorsal surface forms concave trough (1); bears central dorsal ridge that separates two spout-like troughs (2) (Geisler, 2001, modified from Webb and Taylor, 1980).
6. *Atlantoid facet of axis vertebra*.—Restricted below neural arch or extends slightly dorsal to the base of the neural pedicle (0); extended dorsally at least halfway up neural arch (1) (Geisler, 2001, modified from Webb and Taylor, 1980).
7. *Cervical vertebrae posterior to atlas* (ordered).—All are separate (0); only second and third are fused together (1); second through fourth are fused together (2); second through fifth are fused (3); second through sixth are fused (4); second through seventh are fused (5) (Geisler and Sanders, 2003, modified from Miller, 1923). Fusion of the cervical vertebrae is related to extreme shortening of the neck.
8. *Cervical vertebrae* (ordered).—Short, length shorter than centra of anterior thoracics (0); long, length of centrum greater than or equal to the centra of the anterior thoracics (1); very long, length closer to twice the length of the anterior thoracics (2) (Geisler, 2001, derived from Gingerich et al., 1995).
9. *Arterial canal for vertebral artery in cervical vertebrae 3–6*.—Posterior openings exterior to neural canal (0); inside neural canal (1) (Gentry and Hooker, 1988).
10. *Number of thoracic vertebrae* (ordered).—18–17 (0); 16–15 (1); 14 (2); 13 (3); 12 (4); 11 (5); 10 or fewer (6) (Uhen and Gingerich, 2001; Geisler and Sanders, 2003).
11. *Number of thoracic vertebrae with capitular articulations* (ordered).—eleven or more (0); ten (1); nine (2); eight (3); seven (4); six (5); four or five (6); three or fewer (7) (modified from Sanders and Barnes, 2002a).
12. *Capitular articulation facets of the posterior vertebrae*.—Facets gradually shift downward on sequential vertebrae to fuse with the tubercular facets (0); facets abruptly shift from a position on the neural arch to a pedestal that originates from the centrum on the subsequent vertebra (1) (Flower, 1869; Miller, 1923). Coding modified on the basis of observations in Heyning (1989a) (Geisler and Sanders, 2003).
13. *Anapophyses and metapophyses on posterior thoracic and lumbar vertebrae*.—Absent (0); present (1).
14. *Lateral edge of transverse processes of lumbar vertebrae*.—Oriented anteroposteriorly (0); angled anteromedially $45\pm$ or more, relative to a parasagittal plane (1) (Muizon, 1988).
15. *Transverse processes of lumbar vertebrae*.—Oriented ventrolaterally (0); oriented laterally and horizontally (1) (Sanders and Barnes, 2002a).
16. *Lumbar vertebrae*.—Transverse processes narrow distally or are approximately the same anteroposterior width as their bases (0); transverse processes bear greatly expanded distal ends (1) (Muizon, 1988).
17. *Centrum of anterior lumbar vertebrae* (ordered).—Short, length <63% the width (0); long, length between 79% and 136% the width (1); very long, length >147% the width (2) (Muizon, 1988; Barnes, 1990). The width is measured across the anterior face of the centrum (Geisler and Sanders, 2003).
18. *Number of lumbar vertebrae* (ordered).—One (0); 3 (1); 4 (2); 6 (3); 7–8 (4); 9–10 (5); 11–12 (6); 13–16 (7); 16–19 (8) (Uhen and Gingerich, 2001).
19. *Lumbar spinous processes*.—Process narrower at tip than base or midshaft (0); broader at tip than base or midshaft (1).
20. *Lumbar spinous process cross section*.—Process ovoid or discoidal (0); process deeply concave posteriorly (1).
21. *Lumbar zygapophyses*.—Revolvute (0); curved (1); flat (2); absent (3) (Uhen and Gingerich, 2001).
22. *Articulation between sacral vertebrae and ilium of pelvis* (ordered).—Broad area of articulation between pelvis and S1 and possibly S2 (0); narrow articulation of pelvis with end of transverse process of S1 (1); articulation absent (2) (Geisler and Luo, 1998).
23. *Number of sacral vertebrae* (ordered).—One (0); two or three (1); four (2); five or six (3). Cannot be scored for taxa that lack articulation of vertebral column to ilium (Thewissen and Domning, 1992; Gingerich et al., 1995).
24. *Sacral vertebral proportions*.—Terminal sacral centrum width equal or broader than centrum length (0); longer than broad (1).
25. *Sacral vertebral spinous process*.—Height of sacral spinous processes > height of S1centrum (0), equal height of S1centrum (1), double or greater the height of S1centrum (2).
26. *Number of caudal vertebrae* (ordered).—13–15 (0); 16–19 (1); 20–23 (2); 24–27 (3); 27–30 (4); 30–33 (5); 34–60 (6) (Geisler and Sanders, 2003).
27. *Caudal spinous processes*.—Typical single spine (0); bifid spines on anterior caudals (1).
28. *Anterior caudal vertebra*.—Breadth across transverse processes <2 × centrum breadth (0); breadth across transverse processes greater than 2 × centrum breadth (1).
29. *Anterior caudal vertebral length*.—No vertebral centrum in first half of caudal column elongate (0); some elements in first half of caudal column elongate (1) (modified from Uhen and Gingerich, 2001).
30. *Posterior caudal vertebral length*.—Vertebral centra in posterior half of caudal column nearly similar in length and depth (0); centra longer than deep (1) (modified from Uhen and Gingerich, 2001).
31. *Sternum form*.—Rod-like (0); dorsoventrally deep and broad (1); dorsoventrally flat and broad (2) (modified from Uhen and Gingerich, 2001).

Forelimb

32. *Scapular spine*.—Bears large acromion process that overhangs glenoid fossa (0); scapular spine with acromion process reduced or absent, does not encroach upon glenoid fossa (1); acromion process unreduced, directed anteriorly and does not encroach upon the glenoid fossa (2) (derived from O'Leary and Rose, 1995; O'Leary and Geisler, 1999).
33. *Supraspinatus fossa of the scapula*.—Large, portion on neck faces laterally and is equal to or larger than the infraspinatus fossa (0); small, portion on neck faces anterolaterally and is smaller than the infraspinatus fossa (1) (Geisler, 2001).
34. *Coracoid process of scapula*.—Present (0); absent or barely distinguishable from edge of glenoid fossa (1) (Muizon, 1987, 1994).
35. *Supraspinatus fossa of scapula*.—Present (0); absent or nearly absent, acromion process on anterior edge of scapula (1) (Muizon, 1987, 1994).
36. *Prominent deltoid crest on anterior edge of humerus*.—Present, forms greatest anteroposterior diameter along shaft (0); forms a

- knob-like tuberosity (1); tuberosity and crest absent (2) (Sanders and Barnes, 2002a).
37. *Deltpectoral tuberosity or farthest anterior point of crest* (ordered).—Closer to proximal head of humerus (0); approximately centered, proximodistally, on shaft (1); closer to distal end of humerus (2) (Muizon, 1988).
 38. *Humeral head*.—Rounded (0), mediolaterally narrow (1) (Thewissen et al., 2001b).
 39. *Humeral shaft*.—Nearly circular in section (0); anteroposteriorly compressed (1); mediolaterally compressed (2) (modified from Uhen and Gingerich, 2001).
 40. *Humerus* (ordered).—Longer than radius and ulna (0); approximately the same length as radius and ulna (1); shorter than radius and ulna (2) (Sanders and Barnes, 2002a).
 41. *Entepicondyle of humerus*.—Wide, width 50% or greater than the width of the ulnar and radial articulation facets (0); narrow, 25% or less than the width of the ulnar and radial articulation facets (1) (derived from O'Leary and Rose, 1995; Geisler and Luo, 1998).
 42. *Entepicondylar foramen*.—Present (0); absent (1) (Thewissen and Domning, 1992).
 43. *Olecranon fossa*.—Shallow (0); deep, sometimes perforate (1) (O'Leary and Geisler, 1999).
 44. *Distal articular surface of humerus*.—Restricted by medial edge of trochlea (0); expanded medially past trochlear edge to form convex surface (1) (Gentry and Hooker, 1988).
 45. *Distal humerus intercondylar ridge between capitulum and epicondyle*.—Absent (0); present (1) (Geisler, 2001, modified from Gentry and Hooker, 1988).
 46. *Radial and ulnar facets of humerus*.—Forms one articulation surface that is semicircular in lateral view (0); two distinct facets that in lateral view form an obtuse angle (1) (Barnes, 1990).
 47. *Olecranon process* (ordered).—Present as a distinct process (0); present as slightly raised proximal posterior edge (1); absent (2) (Barnes, 1990).
 48. *Length of olecranon process*.—Short, <10% of total ulnar length (0); long, >20% of ulnar length (1) (derived from O'Leary and Rose, 1995b; O'Leary and Geisler, 1999).
 49. *Ulnar coracoid* (ordered).—Projecting anteriorly from ulnar shaft (0); very reduced, radial facet(s) lie on ulnar shaft (1).
 50. *Posterior edge of ulna* (ordered).—Convex posteriorly (0); straight (1); concave posteriorly (2) (Geisler, 2001, derived from O'Leary and Rose, 1995).
 51. *Radius and ulna* (ordered).—Completely separate (0); fused distally (1); fused completely (2) (Webb and Taylor, 1980).
 52. *Radio-ulnar articulation*.—Convex and mobile (0); flat and immobile (1).
 53. *Proximal end of radius* (ordered).—Single fossa for edge of trochlea and capitulum of humerus (0); two fossae, for the medial edge of the trochlea and the capitulum (1); three surfaces, same as state 1 but with additional fossa for the lateral wall of the humeral articular surface (2) (modified from Geisler and Luo, 1998).
 54. *Distal articular surface of radius*.—Single concave fossa (0); split into scaphoid and lunate fossae (1) (Geisler and Luo, 1998, derived from O'Leary and Rose, 1995).
 55. *Centrale*.—Present (0); absent (1) (Thewissen, 1994).
 56. *Magnum and trapezoid*.—Separate (0); fused (1) (Webb and Taylor, 1980).
 57. *Manus*.—Pentadactyl (0); tetradactyl (1) (Yablokov, 1964).
 58. *Manus*.—Mesaxonic, axis of symmetry of foot passes along center of digit three (0); paraxonic, axis lies between digits three and four (1) (O'Leary and Geisler, 1999).
 59. *Second metacarpal contact with magnum*.—Present (0); absent, excluded by proximal end of metacarpal three (1) (Geisler, 2001).
 60. *Metacarpo-phalangeal proportions*.—Central (digits 2–4) metacarpals \geq 200% length of proximal phalanx (0); metacarpals \leq 150% proximal phalangeal length (1).
 61. *Second digit of forelimb* (ordered).—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metacarpal forms proximal splint or nodule (2); absent (3) (Geisler, 2001).
 62. *Width of middle portion of second metacarpal* (ordered).—Wide, 130% > minimum width of second metacarpal > 94% minimum width of third metacarpal (0); constricted, 78% > minimum width of second metacarpal > 51% minimum width of third metacarpal (1); highly compressed, 36% > minimum width of second metacarpal > 5% minimum width of third metacarpal (2) (Geisler, 2001).
 63. *Fifth digit of forelimb* (ordered).—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metacarpal forms proximal splint or nodule (2); absent (3) (Geisler, 2001).
 64. *Width of middle portion of fifth metacarpal* (ordered).—Wide, 100% > minimum width of fifth metacarpal > 78% minimum width of third metacarpal (0); constricted, 70% > minimum width of fifth metacarpal > 40% minimum width of third metacarpal (1); highly compressed, 35% > minimum width of fifth metacarpal > 15% minimum width of third metacarpal (2) (Geisler, 2001).
- #### Hindlimb
65. *Greater trochanter of femur* (ordered).—Below level of head of femur (0); approximately same level as head of femur (1); elevated dorsally well beyond head of femur (2) (O'Leary and Geisler, 1999, derived from O'Leary and Rose, 1995).
 66. *Third trochanter of femur* (ordered).—Present (0); highly reduced (1); absent (2) (Luckett and Hong, 1998; O'Leary and Geisler, 1999).
 67. *Patellar articular surface on femur*.—Wide (0); narrow (1) (O'Leary and Geisler, 1999).
 68. *Extensor sulcus of proximal tibia*.—Absent or wide (0); distinctly grooved and narrow (1).
 69. *Tibia and fibula* (ordered).—Separate (0); fused proximally (1); fused proximally and distally (2) (Webb and Taylor, 1980).
 70. *Fibula*.—Complete (0); incomplete (1) (Webb and Taylor, 1980).
 71. *Articulation between calcaneum and fibula*.—Absent (0); present (1) (Thewissen and Madar, 1999).
 72. *Proximal end of astragalus* (ordered).—Nearly flat to slightly concave (0); well grooved, but depth of trochlea < 25% its width (1); deeply grooved, depth > 30% its width (2) (Geisler, 2001, derived from Schaeffer, 1947; O'Leary and Geisler, 1999).
 73. *Astragalar canal*.—Present (0); absent (1) (Shoshani, 1986).
 74. *Navicular facet of astragalus* (ordered).—Convex (0); saddle-shaped (1); V-shaped (2) (Schaeffer, 1947; Thewissen and Domning, 1992; Geisler and Luo, 1998).
 75. *Head of the astragalus*.—Mediolaterally strongly convex (0); flat or concave (1) (Thewissen and Madar, 1999).
 76. *Distal end of astragalus contacts cuboid* (ordered).—Contact absent (0); contact present, articulating facet on astragalus forms a steep angle with the parasagittal plane (1); contact present and large, facet almost forms a right angle with the parasagittal plane (2) (Thewissen and Madar, 1999; Geisler, 2001).
 77. *Long axes of proximal and distal articulating surfaces of astragalus*.—If extrapolated, form angle that is obtuse and opens medially (0); parallel, no angle formed (1) (Geisler, 2001, modified from Gentry and Hooker, 1988).
 78. *Proximal half of lateral surface of astragalus*.—Concave (0); flat (1) (Geisler, 2001, modified from Gentry and Hooker, 1988).
 79. *Interarticular sulcus of astragalus*.—Deep (0), shallow or absent (1) (derived from Schaeffer, 1947).
 80. *Astragalocalcaneal facet*.—Ectal facet large, concave, plantar facing, and lies on a distinct lateral process, and is thus oblique to the parasagittal plane (0); elongate facet is laterally or plantolaterally oriented and its long axis is parasagittal to tibial trochlea (1); facet is parasagittal, but divided into two small plantolaterally oriented facets on the proximal and distal ends of tibial trochlea (2); single long parasagittal facet that forms the lateral margin of the sustentacular facet. A second bony flange may form a stop facet for calcaneal rotation at the distal end of the astragalus trochlea (3) (modified from Schaeffer, 1947; Thewissen and Madar, 1999).
 81. *Sustentacular facet of the astragalus*.—Facet mediolaterally concave (0); mediolaterally convex (1) (derived from Hussain et al., 1983).
 82. *Sustentacular facet of the astragalus*.—Narrow and positioned on medial half of astragalus; (0) elongate and positioned laterally upon the astragalus (1); elongate and covering nearly the entire width of

- the astragalus (2) (Schaeffer, 1947; Geisler and Luo, 1998; Thewissen and Madar, 1999).
83. *Sustentacular facet of the astragalus* (ordered).—Completely separated from navicular/cuboid facet (0); medial edge of sustentacular facet continuous (1); completely continuous with cuboid/navicular facet (2) (Geisler, 2001).
 84. *Distal calcaneal facet of astragalus*.—Indistinct from sustentacular facet (0); clearly distinct (1) (Thewissen and Madar, 1999).
 85. *Sustentacular facet length*.—Sustentacular facet length < 60% total astragalar length (0); facet length > 60% length (1) (Hussain et al., 1983; described by Martinez and Sudre, 1995).
 86. *U-shaped incurvation between the lateral margins of the proximal and distal astragalar trochleas in dorsal view*.—Present (0); absent (1) (derived from Hussain et al., 1983).
 87. *Articulation of calcaneus and cuboid*.—Flat, proximal articulating surface of the cuboid in one plane and corresponding surface of the calcaneus faces distally (0); sharply angled and curved, proximal surface of the cuboid has a distinct step between the facets for the calcaneus and astragalus (1) (Geisler, 2001, modified from Thewissen and Madar, 1999).
 88. *Proximal cuboid*.—Calcaneal facet dominant (0); divided into equal facets for astragalus and calcaneus (1).
 89. *Cuboid and navicular*.—Unfused (0); fused (1) (Webb and Taylor, 1980).
 90. *Ectocuneiform and mesocuneiform*.—Separate (0); fused (1) (Webb and Taylor, 1980).
 91. *Pes*.—Mesaxonic, axis of symmetry of foot passes along center of the third digit (0); paraxonic, axis lies between digits three and four (1); axis passes along center of digit four (2) (Thewissen, 1994; derived from Gingerich et al., 1990).
 92. *First metatarsal* (ordered).—Unreduced, length > 50% length of third metatarsal (0); reduced, length < 50% length of third metatarsal (1); highly reduced, metatarsal forms nodule or small splint or is absent (2) (O'Leary and Geisler, 1999).
 93. *Second metatarsal* (ordered).—Unreduced, length \geq 50% length of the third metatarsal (0); reduced, \leq the length of the third metatarsal (1); highly reduced in form of nodule, small splint or completely absent (2) (O'Leary and Geisler, 1999).
 94. *Second digit of hind limb*.—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, forms nodule or small splint (2); absent (3); reduced, distal end of phalanx terminates proximal to the distal end of the second phalanx of the third digit because the second metatarsal is 50% of the length of the third metatarsal (4) (Geisler, 2001).
 95. *Width of the middle portion of the second metatarsal* (ordered).—Wide, 100% > minimum width of second metatarsal > 75% minimum width of third metatarsal (0); constricted, 68% > minimum width of second metatarsal > 27% minimum width of third metatarsal (1); highly compressed, 18% > minimum width of second metatarsal > 9% minimum width of third metatarsal (2) (Geisler, 2001).
 96. *Fifth metatarsal* (ordered).—Unreduced, length \geq 50% length of third metatarsal (0); reduced, length \leq 50% length of third metatarsal; highly reduced in form of nodule or small splint or absent (2) (O'Leary and Geisler, 1999).
 97. *Fifth digit of hindlimb* (ordered).—Long, distal end of third phalanx terminates distal to distal end of second phalanx of third digit (0); reduced, distal end of third phalanx terminates proximal to distal end of second phalanx of third digit (1); highly reduced, metatarsal forms nodule or small splint (2); absent (3) (Geisler, 2001).
 98. *Width of middle portion of fifth metatarsal* (ordered).—Wide, 100% > Minimum width of fifth metatarsal > 70% minimum width of third metatarsal (0); constricted, 46% > minimum width of fifth metatarsal > 36% minimum width of third metatarsal (1); highly compressed, 26% > minimum width of third metatarsal > 10% minimum width of third metatarsal (2) (Geisler, 2001).
 99. *Elongation of third metatarsal*.—Absent, 20% < length of third metatarsal < 39% of the length of the femur (0); slight elongation, 47% < length of third metatarsal < 54% of the length of the femur (1); substantial elongation, 63% < length of third metatarsal < 95% of the length of the femur (2) (Geisler, 2001).
 100. *Keels on distal ends of the metapodials*.—Present, restricted to distal and plantar surfaces (0); present and extended onto dorsal surface (or anterior surface in a digitigrade stance) (1) (Webb and Taylor, 1980).
 101. *Fusion of third and fourth metatarsals*.—Absent (0); present (1) (Webb and Taylor, 1980).
 102. *Anterior surface of distal ends of third and fourth metatarsals*.—Unfused (0); fused, fusion forms prominent gully between third and fourth metatarsals (1) (Janis and Scott, 1987; Scott and Janis, 1993).
 103. *Metatarsal-proximal phalangeal proportions*.—Central (digits 3–4) metatarsals \geq 200% length of proximal phalanx (0); metatarsals \leq 150% proximal phalangeal length (1).
 104. *Intermediate phalanx*.—Intermediate phalanx \leq 25% length of corresponding metatarsal (0); intermediate phalanx \geq 33% length of corresponding metatarsal (1).
 105. *Ventral border of distal phalanges*.—Curved inferiorly (0); straight (1) (O'Leary and Geisler, 1999, derived from MacLeod and Rose, 1993).