Supporting Information

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SI Text

Phylogenetic Analysis. *Outgroup taxa*. Given the current controversy regarding arthropod interrelationships (1), a number of arthropod and nonarthropod taxa were used to polarize relationships within Euchelicerata (Xiphosura + Eurypterida + Arachnida). Megacheirans ("great-appendage" arthropods) are represented herein by the Burgess Shale taxa *Leanchoilia superlata*, *Alalcomenaeus cambricus*, and the recently redescribed *Yohoia tenuis* (2). Trilobites are represented by *Olenoides serratus* from the Burgess Shale and *Eoredlichia intermedia* from the Chengjiang biota. Marrellomorphs have previously been used to root phylogenies of stem-chelicerates (3); they are represented herein by the marrellid *Marrella splendens* and the vachonisiid *Xylokorys chledophilia*. The crown-group crustaceans *Nebalia*, *Artemia*, and *Triopus* were also included to provide adequate character polarization.

The pycnogonids (sea spiders) are often allied with the euchelicerates as Chelicerata. However a number of studies have questioned this relationship (e.g., ref. 4). If pycnogonids are the sister-taxon to Euchelicerata then they represent an ideal candidate for polarizing relationships within. Four pycnogonids were included in this dataset: *Endeis*, *Colossendeis*, Ammotheidae (based on *Achelia*, *Ammothella* and *Tanystylum*—as per ref. 5), and the Silurian *Haliestes dasos*.

Nonarthropod outgroups were also included to ensure adequate polarization of relationships within Euarthropoda (Pycnogonida + Euchelicerata + Crustacea). The anomalocaridids are often considered the sister-taxon to the arthropods and are represented herein by *Anomalocaris canadensis* and *Opabinia regalis*. The entire phylogeny (Fig. S1) was rooted using the lobopodian *Aysheaia pedunculata*, for consistency with previous studies on arthropod phylogeny (e.g., ref. 6).

Ingroup taxa. Published hypotheses regarding relationships within Euchelicerata are generally consistent, except with regard to the position of Acari (mites and ticks; ref. 7) and Scorpiones (8, 9). Given the great diversity of mites and their poor early fossil record they were excluded from the current data set. Scorpions have a good fossil record, particularly from the Carboniferous (10). However, most are in need of redescription, and recent work has revealed major problems with their current taxonomy (10, 11). For this reason a single Silurian fossil exemplar *Proscorpius osborni* was employed. Extant scorpions were represented by the supra-generic taxa Scorpionidae (*Heterometrus* and *Pandinus*) and Buthidae (*Androctonus*, *Lychas* and *Centruroides*), following ref. 5. Eurypterids (sea scorpions) have also played a key role in discussions of chelicerate phylogeny. In the past eurypterids have been considered either the sister-taxon of xiphosurans (horseshoe crabs), or scorpions and other arachnids. This latter hypothesis was tested by Dunlop and Braddy (8), who contended that scorpions were the sister-taxon of eurypterids despite resolving scorpions and opiliones as sister-taxa in their phylogenetic analysis. For this reason a number of eurypterids (*Rhenopterus*, *Parastylonurus*, *Pterygotus*, and *Baltoeurypterus*) and opiliones (*Siro*, *Equitius*, and *Nipponopsalis*) were included. The remaining arachnids were represented by pantetrapulmonates including the recently redescribed trigonotarbid *Anthracomartus* (12), the spider *Cupiennius*, the whip spider *Phrynus*, and the whip scorpion *Mastigoproctus*.

Although many xiphosurans are known from the fossil record (13), only those with well preserved appendages were included in our data set, namely the Herefordshire taxa *Offacolus* and *Dibasterium* (described herein), the synziphosurid *Weinbergina*, and the xiphosurid *Alanops*. Extant xiphosurans were represented by *Limulus* and *Carcinoscorpius*.

Phylogenetic Characters. Characters were obtained from a number of sources including previous phylogenetic analyses and new observations. In total 163 characters were used in this study; they include characters for determining both ingroup and outgroup relationships. Numbers in square brackets refer to previous data sets that have included a character (publications listed below). The reader is referred to these publications for further discussion of these characters.

1. *Trunk annuli: (0) absent, (1) present*. [(4) character 18]
2. *Sclerotization of cuticle: (0) absent, (1) present*. [(4) character 20]
3. *Calcified cuticle: (0) absent, (1) present*. [(4) character 21]
4. *Anterior sclerite associated with ocular segment: (0) absent, (1) present*. [(14) character 14]
5. *Tergal covering of all head segments fused as cephalic shield: (0) absent, (1) present*. [(4) character 83; (15) character 3]
6. *Anterior end of prosoma with medial marginal or submarginal process: (0) absent, (1) present*. [(9) character 3]
7. *Anterolateral spines: (0) absent, (1) present*. [(16) character 2]
8. *Mediolateral spines: (0) absent, (1) present*. [(16) character 3]
9. *Expanded cephalic doublure: (0) absent, (1) present*.
10. *Cephalic tagmosis (number of limb-bearing segments): (0) one limb-bearing segment (antenna or frontal appendage), (1) two limb-bearing segments, (2) three limb-bearing segments, (3) four limb-bearing segments, (4) five limb-bearing segments, (5) cephalosoma with four post-pedipalpal locomotory limbs*. [(4) character 84]
11. *Transverse furrows on prosomal carapace corresponding to margins of segmental tergites: (0) absent, (1) present*. [(4) character 86]
12. *Mesopeltidium divided medially by a shallow sulcus: (0) absent, (1) present*.
13. *Cardiac lobe: (0) absent, (1) present*. [(4) character 87]
14. *Genal spines (posterior corners of head shield extended): (0) absent, (1) present, short (2) present (as long as trunk)*.
15. *Prosoma-opisthosoma coupling mechanism: (0) absent, (1) present*. [(9) character 96]
16. *Post-oral prosomal plate: (0) absent, (1) present*.
17. *Sternum: (0) undivided, (1) divided*. [(17) character 8]
18. *Sternum shape: (0) triangular, (1) pentagonal*. This character refers to the sternum of scorpions only.
19. *Paired tergal carinae: (0) absent, (1) present*. [(18) character 20]
20. *Fusion of paratergal folds into a dorsal shield: (0) absent, (1) present*. [(16) character 1]
21. *Articulating half ring: (0) absent, (1) present*.
22. *Raised axial region: (0) absent, (1) present*.
23. *Number of opisthosomal somites: (0) nine, (1) 10, (2. 11, (3) 12*. [(9) character 95]
24. *Fusion of opisthosomal somites 2 and 3: (0) absent, (1) present*. [(9) character 100]
25. *First mesosomal somite: (0) shorter than or equal in length to second mesosomal somite, (1) longer than second mesosomal somite*.
26. *Anterior transverse ridge on mesosomal tergites: (0) absent, (1) present*.
27. *Fusion of all opisthosomal tergites behind the opercular tergite into the thoracetron: (0) absent, (1) present*. [(4) character 240]

28. *Opisthosoma greatly reduced, forming a slender tube emerging from behind the posteriormost legs, with a terminal anus: (0) absent, (1) present*. [(4) character 241]
29. *Opisthosoma consisting of a single segment: (0) absent, (1) present*.
30. *Width of first opisthosomal segment: (0) broad, (1) narrow, developed as pedicel*. [(4) character 250]
31. *Abdomen (limb-free somites between the terminal segment and the limb-bearing trunk segments, posterior to expression domain of Ubx, abdA and abdB): (0) absent, (1) present*. [(4) character 252]
32. *Caudal metasoma: (0) absent, (1) present*.
33. *Number of metasomal somites: (0) zero, (1) two, (2) three, (3) five*. [(9) character 116]
34. *Carinae on metasoma: (0) absent, (1) present*.
35. *Posterior tagmata composed of three paired tail flaps: (0) absent, (1) present*. [(4) character 317]
36. *Articulate furcal rami: (0) absent, (1) present*. [(4) character 320]
37. *Telson shape: (0) styliform, (1) paddle-shaped, (2) lanceolate, (3) anal operculum*.
38. *Length of telson: (0) shorter than half the length of the trunk, (1) longer than half the length of the trunk*.
39. *Telson fringed with setae: (0) absent, (1) present*. [(18) character 24]
40. *Frontal appendage with row(s) of elongate spines along inner margin: (0) absent, (1) present*. [(4) character 146]
41. *Frontal appendages attached or fused basally: (0) separated, (1) basally attached or fused*. [(4) character 147; (19) character 6]
42. *Strongly sclerotised, articulated limbs with pivot joints: (0) absent, (1) present*. [(4) character 277]
43. *Number of podomeres in arthropodised limbs: (0) 8 or more, (1) 7 or less*.
44. *Biramy in post-antennal limbs: (0) absent, (1) present*. [(4) character 278]
45. *Protopodite: (0) absent (protopodite undifferentiated from limb stem), (1) present*. [(4) character 279]
46. *Protopodite of post-mandibular limbs elongate, fleshy, extended as numerous soft, setiferous endites: (0) absent, (1) present*. [(4) character 280]
47. *Bilobate exopod shaft: (0) absent (exopod is an undivided flap), (1) present*. [(4) character 285]
48. *Exopod shaft consisting of numerous segments each bearing a single seta: (0) absent, (1) present*. [(16) character 16]
49. *Appendage of second (deuterocerebral) head segment: (0) antenna (antennula in crustaceans), (2) raptorial great-appendage chelicerae / chelifore with few podomeres, terminal podomeres bearing spines on outer side of distal margins, with terminal pincer*. [(4) character 149]
50. *Great-appendage / cheliceral segmentation: (0) five segments, (1) four segments, (2) three segments, (3) two segments*.
51. *Number of spine-bearing articles on chelate appendage: (0) three+moveable finger, (1) two+moveable finger, (2) one +moveable finger; (3) moveable finger*. [(18) character 5]
52. *Antenniform chelicerae: (0) absent, (1) present*.
53. *Long spinose projections on distal part of terminal three podomeres of chelate appendage bearing flagellum: (0) absent, (1) present*. [(18) character 6]
54. *Plagula ventralis: (0) absent, (1) present*. [(4) character 161]
55. *Cheliceral tergo-deteromerite muscle: (0) absent, (1) present*. [(4) character 162]
56. *Appendage on third (tritocerebral) head segment: (0) unspecialised locomotory limb, (1) second antenna, (2) pedipalp, (3) subchelate appendage, (4) "swimming paddle"*. [(4) character 163]
57. *Palpal chelae: (0) absent, (1) subraptorial, (2) chelate, (3) scorpionoid*. [(4) character 166]
58. *Pedipalp patella: (0) shorter than, or equal in length to manus, (1) longer than manus*.
59. *Exopod on tritocerebral segment much longer than endopod: (0) absent, (1) present*. [(16) character 9]
60. *Oviger: (0) absent, (1) present*. [(4) character 189]
61. *Walking leg I antenniform: (0) absent, (1) present*. [(9) character 46]
62. *Walking leg II longer than adjacent leg and modified as feeler: (0) absent, (1) present*. [(4) character 190]
63. *Coxal swing: (0) absent, (1) present*. [(4) character 287]
64. *Musculi lateralis: (0) absent, (1) present*. [(4) character 292]
65. *Coxotrochanteral joint: (0) simple, (1) complex*. [(4) character 293]
66. *Trochanterofemoral joint of walking legs: (0) transverse bicondylar, (1) vertical bicondylar*. [(4) character 296]
67. *Patellotibial joint of walking legs: (0) dorsal monocondylar, (1) simple bicondylar, (2) vertical bicondylar, dorsal hinge*. [(4) character 300]
68. *Walking leg femur: (0) shorter than, or equal in length to patella, (1) longer than patella*.
69. *Femoropatellar joint: (0) transverse dorsal hinge, (1) bicondylar articulation*. [(4) character 301]
70. *Elastic arthrodial sclerites spanning the tibia-tarsus joints: (0) absent, (1) present*. [(4) character 304]
71. *Divided tarsus (basitarsus and telotarsus): (0) absent, (1) present*. [(9) character 82]
72. *Telotarsus in adults with two or more tarsomeres: (0) absent, (1) present*. [(9) character 84]
73. *Three tarsomeres on walking legs 2–4: (0) absent, (1) present*. [(9) character 85]
74. *Tarsal organ: (0) absent, (1) present*. [(4) character 306]
75. *Pretarsal depressor muscle origin: (0) on tarsus, (1) on tibia or patella*. [(4) character 307]
76. *Apotele on walking leg 1: (0) absent, (1) present*. [(9) character 90]
77. *Distal ends of walking legs chelate: (0) absent, (1) present*.
78. *Mandible: (0) absent, (2) present*.
79. *Mandibular palp: (0) present, (1) absent*. [(4) character 176]
80. *Maxilla 1: (0) absent, (1) present*. [(4) character 193]
81. *First maxillary palps: (0) present (including telopodite of positionally equivalent limb in chelicerates), (1) absent*. [(4) character 196]
82. *Second maxillae on fifth metamere: (0) appendage developed as trunk limb, (1) well developed maxilla differentiated as mouthparts, (2) vestigial appendage, (3) long antenniform appendage*.
83. *Trunk endopods: (0) absent, (1) present*.
84. *Appendage on first opisthosomal segment: (0) appendage present in post-embryonic stage, (1) appendage absent*. [(4) character 247]
85. *Opisthosomal appendage VI modified into a pusher: (0) absent, (1) present*.
86. *Opisthosomal appendage VI modified into a swimming paddle: (0) absent, (1) present*.
87. *Podomere 7a on appendage VI: (0) absent, (1) present*.
88. *Appendage of seventh metamere incorporated into cephalic tagmata: (0) absent, (1) present*.
89. *Appendage VII reduced and spinose along margin: (0) absent, (1) present*.
90. *Limb VII as chilaria: (0) absent, (1) present*. [(4) character 248]
91. *Pectines: (0) absent, (1) present*. [(4) character 249]
92. *Plate-like opisthosomal appendages: (0) absent, (1) present*.
93. *Opisthosomal silk glands and spigots: (0) absent, (1) present*.
94. *Opisthosomal spinnerets: (0) absent, (1) present*.
95. *Trunk limbs with lobate endites formed by folds in limb bud: (0) absent, (1) present*. [(4) character 281]
96. *Trunk endopod endites: (0) spiniferous, (1) rounded*. [(16) character 13]
97. *Pretarsal claws: (0) paired, (1) unpaired*. [(4) character 309]
98. *Trunk exopod setae: (0) short, fine setae, (1) long, flattened,*

tapering distally, with slight separation, (2) lamellate setae, (3) filamentous. [*cf*. (4) character 242; *cf*. (18) character 29]
99. *Paddle-like epipods: (0) absent, (1) present*. [(4) character 286]
100. *Rhabdomeric lateral eyes with new elements formed at a proliferation zone at side of developing eye field: (0) absent, (1) present*. [(4) character 94]
101. *Form of lateral eyes: (0) facetted, (1) simple lens with cup-shaped retina*.
102. *Proliferation zone of lateral eye field: (0) row-by-row addition, (1) morphogenetic front*.
103. *Compound eye stalked, basally articulated: (0) absent (eye sessile), (1) present*. [(4) character 98; (14) character 12]
104. *Visual surface with calcified lenses bounded by circumocular suture: (0) absent, (1) present*. [(3) character 21; (20) character 4]
105. *Ophthalmic ridges (0) absent, (1) present*. [(4) character 100]
106. *Number of corneagenous cells: (0) many, (1) two*. [(4) character 101]
107. *Ommatidium with crystalline cone: (0) cone absent, (1) cone present*. [(4) character 106]
108. *Optic chiasma between lamina and medulla: (0) absent, (1) present*. [(4) character 112]
109. *Number of median eyes: (0) none, (1) two, (2) three, (3) four, (4) one*. [(4) character 118]
110. *Ocular tubercle: (0) absent, (1) present*. [(4) character 125]
111. *Slit sensilla: (0) absent, (1) present*. [(4) character 46]
112. *Trichobothria innervated by several sensory cells, with dendrites having only indirect contact with the hair base: (0) absent, (1) present*. [(4) character 126]
113. *Appendage III with coxapophyses forming preoral chamber: (0) absent, (1) present*. [(9) character 50]
114. *Appendage IV with coxapophyses forming preoral chamber: (0) absent, (1) present*. [(9) character 51]
115. *Mouth position: (0) terminal, (1) ventral*. [(4) character 128]
116. *Head / mouth orientation: (0) prognathous, mouth directed anteroventrally, (1) hypognathous, mouth directed ventrally, (2) mouth directed posteriorly*. [(4) character 129]
117. *Radially arranged cicumoral structures (papillae, plates or lamellae): (0) absent (bilaterally symmetrical mouthparts), (1) present*. [(4) character 130]
118. *Circumoral structures as a circlet of overlapping plates with teeth on their inner margins ("Peytoia apparatus"): (0) absent, (1) present*. [(4) character 131]
119. *Epistome-labrum / clypeolabrum: (0) absent, (1) present*. [(4) character 132]
120. *Sclerotization of epistome-labrum/clypeolabrum (hypostome): (0) absent, (1) present*.
121. *Fleshy labrum: (0) absent, (1) present*. [(4) character 133]
122. *Sclerotic sternum formed by antennal to maxillulary sternites, including paragnaths on mandibular sternum: (0) absent, (1) present*. [(4) character 136]
123. *Intercheliceral epipharygeal sclerites: (0) absent, (1) present*. [(9) character 191]
124. *Tritosternum: (0) absent, (1) present*. [(4) character 137]
125. *Proboscis: (0) absent, (1) present*.
126. *Triradiate pharyngeal lumen: (0) absent, (1) present*. [(4) character 141]
127. *Three-branched epistomal skeleton supporting the pharyngeal dilator muscles: (0) absent, (1) present*. [(4) character 143]
128. *Gut caecae: (0) absent, (1) present along the midgut, (2) restricted to the anterior part of the midgut*. [(4) character 234]
129. *Serially repeating midgut glands: (0) absent, (1) reniform, metameric midgut glands with submillimetric lamellae*. [(14) character 16]
130. *Peritrophic membrane: (0) absent, (1) present*. [(4) character 238]
131. *Coxal gland orifice, leg I: (0) absent, (1) present*. [(4) character 32]
132. *Malpighian tubules formed as endodermal extensions of the midgut: (0) absent, (1) present*. [(4) character 35]
133. *Pair of repugnatorial glands in the carapace: (0) absent, (1) present*. [(4) character 380]
134. *Aculeus with sting / opisthosomal venom gland: (0) absent, (1) present*. [(4) character 382]
135. *Posterior oblique muscles of Box-Truss Axial System (BTAMS): (0) absent, (1) present*. [(9) character 127]
136. *Endosternum (ventral tendons fused into prosomal endosternum): (0) absent, (1) present*. [(4) character 259]
137. *Dorsal endosternal suspensor of fourth postoral segment with anterolateral carapacal insertion: (0) absent, (1) present*. [(4) character 260]
138. *Longitudinal muscles attach to intersegmental tendons: (0) absent, (1) present*. [(4) character 275]
139. *Haemoglobin: (0) absent, (1) present*. [(4) character 39]
140. *Respiratory exites: (0) absent, (1) present*.
141. *Dorsal bands of blade-like gills: (0) absent, (1) present*. [(4) character 261; (14) character 41]
142. *Lamellate respiratory organ derived from posterior wall of opisthosomal limb buds: (0) absent, (1) present*. [(4) character 243]
143. *Spines on lamellar margin: (0) absent, (1) present*.
144. *Respiratory lamellae on opisthosomal somite 2: (0) absent, (1) present*. [(9) character 121]
145. *Respiratory lamellae on opisthosomal somite 3: (0) absent, (1) present*. [(9) character 122]
146. *Respiratory lamellae on opisthosomal somites 4–6: (0) absent, (1) present*. [(9) character 123]
147. *Respiratory lamellae on opisthosomal somite 7: (0) absent, (1) present*. [(9) character 124]
148. *Intrasternite stigmata: (0) absent (opening to book-lungs at margin of sternite), (1) present*. [(4) character 246]
149. *Ovipositor: (0) absent, (1) present*. [(4) character 333]
150. *Sclerotised spermatophore: (0) absent, (1) present*.
151. *Penis (spermatopositor) opening on anteroventral part of opisthosoma: (0) absent, (1) present*. [(4) character 336]
152. *Penis form: (0) short, membranous, undivided, (1) long, chitinous, divided into shaft and glans*. [(4) character 337]
153. *Medial genital appendage: (0) absent, (1) present*.
154. *Female gonopore parity: (0) paired, (1) medium, unpaired*. [(4) character 341]
155. *Genital operculum divided, incorporated into pedicel: (0) absent, (1) present*. [(4) character 342]
156. *Genital operculum overlapping third opisthosomal sternite: (0) absent, (1) present*. [(4) character 343]
157. *Postgenital appendages: (0) opercular and/or lamellar, (1) poorly sclerotized or eversible, (2) absent*. [(4) character 344]
158. *Nucleus of sperm forms spiral ridge: (0) absent, (1) present*. [(4) character 368]
159. *Sperm nucleus with manchette of microtubules: (0) absent, (1) present*. [(4) character 369]
160. *Coiling of spermatozoa flagellum: (0) absent (filiform), (1) present*. [(4) character 370]
161. *Sperm conjugation: (0) absent, (1) present*. [(4) character 372]
162. *Blastodermal cuticle (cuticular egg envelope): (0) absent, (1) present*. [(4) character 6]
163. *Fate of embryologic growth zone (in chelicerates): (0) with a growth zone rising to both the prosoma and opisthosoma, (1) with a growth zone giving rise to the opisthosoma*. [(4) character 12]

Results. The phylogenetic analysis produced a single MPT (most parsimonious tree) of 13.03 steps; this is provided as Fig. 2 in the main paper. *Dibasterium* (Movie S1) resolved as sister-taxon to the synziphosurid *Weinbergina*. This result is supported by two unequivocal synapomorphies: the presence of a three segmented

metasoma (character 33) and a divided tarsus (character 71). The synziphosurids have previously been considered paraphyletic with regard to the xiphosurids (xiphosurans with a fused opisthosoma; Anderson and Selden 1997). Although the current data set are too limited to test this hypothesis, the morphological similarities between *Dibasterium* and other synziphosurids indicate that it belongs to this group. The monophyly of Xiphosura (*Offacolus* + Synziphosurida + Xiphosurida) is supported by four synapomorphies: the presence of a raised axial region (character 22), an elongate telson (character 38), chelate walking legs (character 77), and the incorporation of a spinose 7th appendage pair into the cephalic tagma (character 88). Character mapping indicates that biramy may either be a plesiomorphic feature in xiphosurans or convergently acquired in xiphosurans and the crustacean stem-group. This topology may be influenced by the inclusion of the uniramous pycnogonids which resolve as sister-taxon to all other arthropods. When these taxa are removed two MPTs of 11.29 steps are produced. These trees resolve megacheirans on the euarthropod stem and indicate that biramy is the plesiomorphic condition for euarthropods and is retained in xiphosurans. It should be noted that megacheirans resolved as stem-crustaceans in the first set of analyses but this relationship was not obtained during symmetric resampling which placed them in a polytomy with crustaceans and their stem group, and Euchelicerata.

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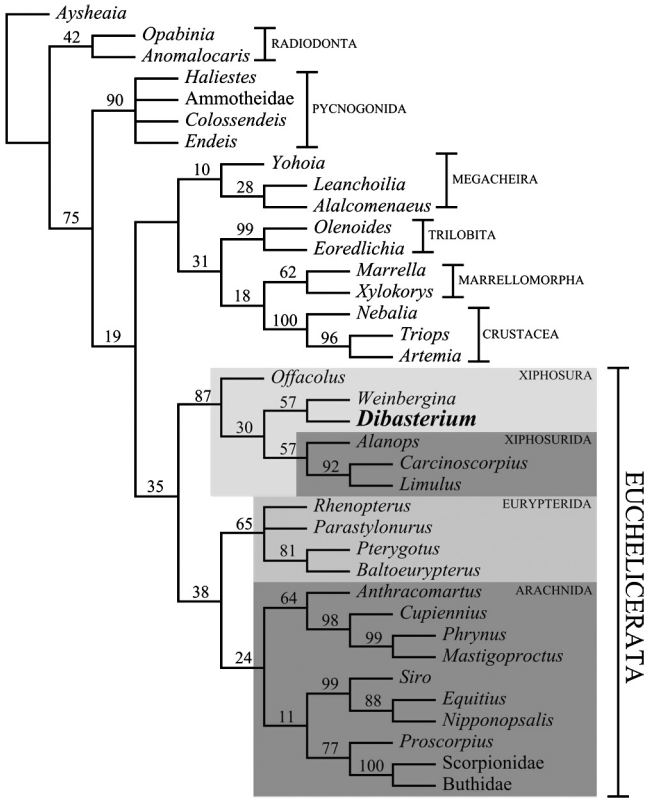
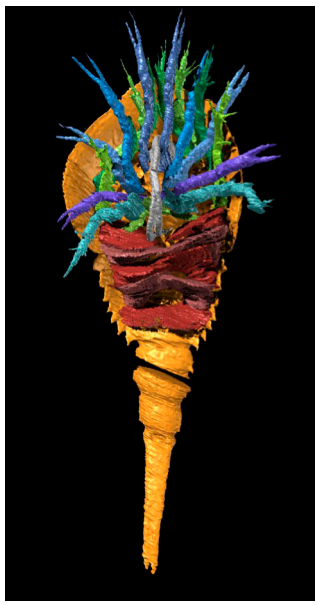


Fig. S1. Arthropod phylogeny, generated as explained in *Methods* (main article) and *SI Text*, showing the position of the new Silurian horseshoe crab *Dibasterium durgae*.



Movie S1 Reconstruction of the new Silurian horseshoe crab *Dibasterium durgae* generated as described in *Methods* (main article).
Movie S1 (AVI)

Other Supporting Information Files

Dataset S1 (PDF)

Nexus file of phylogenetic data.