
Supplementary information

A Jurassic acanthocephalan illuminates the origin of thorny-headed worms

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Supplementary Note 1. Characters used in phylogenetic analysis

Below is a list of characters and characters states with descriptions used in all the phylogenetic analyses. The matrix was derived primarily from ref. 1, with an increased taxon sampling of rotifers and acanthocephalans. Additional characters were added to accommodate this increased taxonomic sampling, as well as the combination of features seen in *Juracanthocephalus daohugouensis*. Characters that were not included in the dataset of ref. 1 are marked with an asterisk (*) and sources and justifications for the character and character states are provided. Many additional characters were scored from refs. 2–4 for Acanthocephala and Rotifera. Note that as most characters were derived from ref. 1, our descriptions outlined below focus on newly introduced characters, amendements to these characters and justifications for characters state codings for newly introduced taxa, primarily rotifers, acanthocephalans and *Juracanthocephalus daohugouensis*.

List of characters and modifications to previous matrices

1. Collar complex.
 - . 0 absent
 - . 1 present
2. Multicellularity with extracellular matrix.
 - . 0 absent
 - . 1 present
3. Septate junctions (SJs). Acanthocephalans are scored as absent because they have tight junctions, see character 4.
 - . 0 absent
 - . 1 present
4. Tight junctions (TJs). This character is present in acanthocephalans^{5–7}.
 - . 0 absent
 - . 1 present
5. Gap junctions (GJs).
 - . 0 absent

- . 1 present
- 6. Adherens junctions (AJs). Scored from ref. 8.
 - . 0 absent
 - . 1 present
- 7. Hemidesmosomes.
 - . 0 absent
 - . 1 present
- 8. Epithelia.
 - . 0 absent
 - . 1 present
- 9. Basal laminae. Scored from ref. 9.
 - . 0 absent
 - . 1 present
- 10. Collagen. All rotifers are scored as absent according to ref. 10, but collagen-like filaments are present in *Seison*¹¹, thus coded as ? for *Seison*. Collagen is abundant in *Acanthocephala*^{11,12}.
 - . 0 absent
 - . 1 present
- 11. Nerve cells.
 - . 0 absent
 - . 1 present
- 12. Acetylcholine used as a neurotransmitter. Scored from refs. 13,14.
 - . 0 absent
 - . 1 present
- 13. Diffuse nervous system. Scored from refs. 2,15.
 - . 0 absent

- . 1 present
14. Epidermis with pulsatile bodies.
- . 0 absent
 - . 1 present
15. Ciliated epidermis. This character is present in all rotifers¹⁶. Although Sørensen and Giribet⁴ mentioned a ciliated epidermis as present in *Seison*, Ahlrichs¹⁶ considered *Seison* as lacking cilia on the whole body surface, thus we code this character as uncertain for *Seison*. This character is absent in acanthocephalans⁴.
- . 0 absent
 - . 1 present
16. Multiciliate epidermal cells. Contingent on the presence of ciliated epidermis (character 15). This character is present in all rotifers^{16,17} but absent in acanthocephalans^{4,10}. We code this character as uncertain for *Seison* (see details in character 15 above).
- . 0 absent
 - . 1 present
17. Ciliation absent on the lateral and dorsal regions and restricted to the anterior. Contingent on the presence of ciliated epidermis (character 15). This character is present in all rotifers and acanthocephalans^{4,16}. We code this character as uncertain for *Seison* (see details in character 15 above).
- . 0 absent
 - . 1 present
18. Ciliated corona with paired nerves. This character is a chaetognath synapomorphy distinct from the corona of rotifers.
- . 0 absent
 - . 1 present
19. Rotifer corona. The corona of *Seison* is strongly reduced but still present^{4,18}.

This character is absent in *Juracanthocephalus* and acanthocephalans.

- . 0 absent
- . 1 present

20. *Corona with auricles. Score from ref. 4. Contingent on the presence of a rotifer corona (character 19). The character refers to the presence of auricles, which are large, paired rostral extensions.

- . 0 absent
- . 1 present

21. *Pseudotroch forms tufts with stiff cirri. Score from ref. 4. Contingent on the presence of a rotifer corona (character 19). The character refers to the presence of a pseudotroch with stiff cirri formed by modification of cilia in the buccal field.

- . 0 absent
- . 1 present

22. *Corona with trochal discs on pedicles, separated by broad upper lip. Score from ref. 4. Contingent on the presence of a rotifer corona (character 19).

- . 0 absent
- . 1 present

23. Cilia covered by cuticle. This character is unique to gastrotrichans.

- . 0 absent
- . 1 present

24. Ventral locomotory cilia.

- . 0 absent
- . 1 present

25. Cilia restricted to ventral surface. Contingent on the presence of character 24 (ventral locomotory cilia).

- . 0 absent
- . 1 present

26. Ventral cilia in two rows. Contingent on the presence of character 24 (ventral locomotory cilia).
- . 0 absent
 - . 1 present
27. Ventral surface modified into foot.
- . 0 absent
 - . 1 present
28. Xenacoelomorph cilia.
- . 0 absent
 - . 1 present
29. Striated ciliary rootlets.
- . 0 absent
 - . 1 present
30. Triploblasts built of three germ layers.
- . 0 absent
 - . 1 present
31. Direct development.
- . 0 absent
 - . 1 present
32. Cleavage.
- . 0 radial
 - . 1 spiral
33. Apical cross.
- . 0 absent
 - . 1 present

34. 4d mesentoblast.
- . 0 absent
 - . 1 present
35. Colloblasts.
- . 0 absent
 - . 1 present
36. Coelenteron (gastrovascular cavity).
- . 0 absent
 - . 1 present
37. Cnidae.
- . 0 absent
 - . 1 present
38. Structure of mitochondrial DNA. Circular in Rotifera including *Seison*, and Acanthocephala^{19,20}.
- . 0 circular
 - . 1 linear
39. Actinopharynx.
- . 0 absent
 - . 1 present
40. Siphonoglyph (sulcus).
- . 0 absent
 - . 1 present
41. Planulae.
- . 0 absent
 - . 1 present
42. Polyp stage.

- . 0 absent
 - . 1 present
43. Medusoid stage.
- . 0 absent
 - . 1 present
44. Gut. A gut is present in Rotifera including *Seison*, but acanthocephalans have degenerated their guts^{21,22}. Although a potential alimentary tract can be observed within the proboscis, we score the gut of *Juracanthocephalus* as uncertain.
- . 0 absent
 - . 1 present
45. Through-gut. Contingent on the presence of a gut (character 44). This character is present in Rotifera including *Seison*, but acanthocephalans have degenerated their guts^{21–23}. Although a potential mouth and anus can be observed, we score the through-gut of *Juracanthocephalus* as uncertain.
- . 0 absent
 - . 1 present
46. U-shaped gut. Contingent on the presence of a gut (character 44).
- . 0 absent
 - . 1 present
47. Dorsal anus or anal pore. Contingent on the presence of a through-gut (character 45). The dorsal anus is a character shared by all gnathiferans, but acanthocephalans have degenerated their guts and thus have no anus^{21–24}. Although a dorsal anus may present in *Juracanthocephalus*, we code it as uncertain.
- . 0 absent
 - . 1 present
48. Transient anal pore. Contingent on the presence of a through-gut (character

- 45).
- . 0 absent
 - . 1 present
49. Subterminal ventral anus. Contingent on the presence of a through-gut (character 45). Although a dorsal anus may present in *Juracanthocephalus*, we code it as uncertain.
- . 0 absent
 - . 1 present
50. Anus in midbody anterior of trunk septum. Contingent on the presence of a through-gut (character 45).
- . 0 absent
 - . 1 present
51. Longitudinal muscle bands. This character is present in Rotifera, including *Seison*, and Acanthocephala^{25,26}.
- . 0 absent
 - . 1 present
52. Helicoidal muscles enwrap pharynx.
- . 0 absent
 - . 1 present
53. Helicoidal muscles enwrap midgut.
- . 0 absent
 - . 1 present
54. Head with cerebral eyes. Rotifera usually have cerebral eyes, but this character is absent in *Seison*²⁷, and is also absent in *Juracanthocephalus* and Acanthocephala.
- . 0 absent
 - . 1 present

55. Cephalic sensory appendages. Dorsal antennae are usually absent in rotifers except *Adineta*. This character is absent in *Juracanthocephalus* and acanthocephalans.
- . 0 absent
 - . 1 present
56. Sensory appendage type. Contingent on the presence of cephalic sensory appendages (character 55).
- . 0 smooth cephalic tentacles
 - . 1 articulated cephalic tentacles
 - . 2 contractile annelid type palps
 - . 3 anterodorsal papillae
57. Number of pairs of anterior appendages. Contingent on the presence of cephalic sensory appendages (character 55). The rotifer *Adineta* has an unpaired dorsal appendage.
- . 0 one pair
 - . 1 two pairs
 - . 2 three pairs
 - . 3 unpaired dorsal antennae
58. Caudal organ.
- . 0 absent
 - . 1 present
59. Frontal organ.
- . 0 absent
 - . 1 present
60. Female organ with germovitellarium. A syncytial germovitellarium is present in all rotifers except Seisonidea. Absent in Acanthocephala⁴.
- . 0 absent
 - . 1 present

61. Retrocerebral organ. This character is present in all Rotifera, but absent in *Acanthocephala*^{2,9,15,28}.
- . 0 absent
 - . 1 present
62. Nuchal organs.
- . 0 absent
 - . 1 present
63. *Head or neck region retractable. This character is present in *Adineta*, *Rotaria*, *Seison*, but absent in other rotifers; this character is also present in acanthocephalans. This character is unknown for *Juracanthocephalus*. We also re-coded the introverts of Kinorhyncha and Loricifera as retractable heads.
- . 0 absent
 - . 1 present
64. Distinct inflated head with constricted neck region. This character is present in *Adineta*, *Rotaria*, *Seison*, but absent in other rotifers; this character is also present in *Juracanthocephalus*. This character is absent in acanthocephalans.
- . 0 absent
 - . 1 present
65. Type of neck constriction. Contingent on the presence of a distinct inflated head with constricted neck region (character 64). In gnathiferans and chaetognaths, the pharyngeal region is located near the jaws. The pharyngeal region in *Seison* (behind the jaws) and *Juracanthocephalus* (in front of the jaws) is strongly depressed.
- . 0 slight depression of the pharyngeal region
 - . 1 strong depression of the pharyngeal region
 - . 2 constriction at the level of the frontal adhesive tubes
 - . 3 constriction at the level of the pharyngeal pores
 - . 4 constriction at the caudal end
 - . 5 depression of the whole trunk

- . 6 constriction at the level of the mouth
66. Mouth position. The mouth position is located as ventral in all rotifers. We score this character as uncertain for *Juracanthocephalus*.
- . 0 terminal
 - . 1 subterminal
 - . 2 ventral
67. Post oral cavity between mouth and pharynx. A cavity is present between the mouth opening and the pharynx in most Rotifera, as well as *Juracanthocephalus*; this character is not applicable for Acanthocephala since they lack a mouth.
- . 0 absent
 - . 1 present
68. Cavity shape. Contingent on the presence of a post oral cavity (character 67). Mastax is present in all rotifers.
- . 0 V-shaped
 - . 1 cylindrical
 - . 2 conical
 - . 3 wide funnel
 - . 4 rounded lumen (mastax)
 - . 5 slit like
 - . 6 with ventral membrane
69. Mouth supportive structures.
- . 0 absent
 - . 1 present
70. Mouth support type. Contingent on the presence of mouth supportive structures (character 69).
- . 0 cuticularized club
 - . 1 mouth basket
 - . 2 longitudinal ridges

- . 3 cuticular pedicles
 - . 4 small hooks
 - . 5 triangular, pointed projections
 - . 6 mouth equipped with lips
 - . 7 cuticularised plate
71. Body dorsoventrally flattened (width twice the depth of the body).
- . 0 absent
 - . 1 present
72. Body dorsally shortened.
- . 0 absent
 - . 1 present
73. Anterior gut with differentiated tubular pharynx.
- . 0 absent
 - . 1 present
74. Origin of pharyngeal musculature. Contingent on the presence of a differentiated pharynx (character 73).
- . 0 myoepithelial
 - . 1 mesodermal
75. Shape of pharyngeal lumen. Contingent on the presence of a differentiated pharynx (character 73).
- . 0 approximately round
 - . 1 Y shape
 - . 2 inverted Y shape
 - . 3 quadrate
76. Pharyngeal pores. Contingent on the presence of a differentiated pharynx (character 73).
- . 0 absent
 - . 1 present

77. Position of pharyngeal pores. Contingent on the presence of pharyngeal pores (character 73).
- . 0 near the end of the pharynx
 - . 1 in the caudal third of the pharynx
 - . 2 around the middle of the pharynx
78. Pharyngeal tooth like elements. Tooth-like structures are present in both representatives of Macrodasysida (*Lepidodasys*) and several chaetodontids (e.g. *Arenotus*). This character is distinguished from other similar digestive structures (e.g. the jaws of gnathiferans) by its occurrence at the anterior tip of a differentiated pharynx, rather than the occurrence in a mastax or as grasping spines.
- . 0 absent
 - . 1 present
79. Cuticularised hindgut. Contingent on the presence of a through-gut (character 44).
- . 0 absent
 - . 1 present
80. Nephridia. Rotifers have protonephridia²⁹, but this character is only present in some acanthocephalans like *Macracanthorhynchus*^{2,4,30}.
- . 0 absent
 - . 1 present
81. Nephridial type. Contingent on the presence of nephridia (character 80). Rotifers have protonephridia²⁹, but protonephridia are only present in some acanthocephalans like *Macracanthorhynchus*^{2,4,30}.
- . 0 protonephridia
 - . 1 transitional
 - . 2 metanephridia
82. Cilia-microvilli arrangement in protonephridium. Contingent on the presence

of protonephridia (character 80). In some rotifers like *Brachionus*, *Adineta*^{29,31}, all cilia are surrounded by a common wreath of microvilli in their protonephridia, but there is not enough information for other rotifers about this character, which is also the situation in *Macracanthorhynchus*^{32,33}.

- . 0 each cilium with single wreath of microvilli
- . 1 all cilia surrounded by a common wreath of microvilli
- . 2 irregular arrangement

83. Cilial condition of terminal cells of protonephridia. Contingent on the presence of protonephridia (character 80). In rotifers^{31,34} and *Macracanthorhynchus*^{29,30,32,33}, terminal cells are multiciliated in their protonephridia.

- . 0 monociliated
- . 1 biciliated
- . 2 multiciliated

84. Cellularity of the nephridium collecting canal. In some rotifers like *Brachionus*, *Adineta* and *Seison*^{31,34}, cellularity of the nephridium collecting canal is syncytial, but there is not enough information for other rotifers for this character. In *Macracanthorhynchus*, it also has a syncytial nephridial collecting canal^{29,30,32,33}.

- . 0 unicellular
- . 1 multicellular
- . 2 syncytial

85. Shape of nephridial canal. In some rotifers like *Brachionus*, *Adineta* and *Seison*^{31,34}, the nephridial canal is branching, but there is not enough information for other rotifers for this character. *Macracanthorhynchus* also has a branching nephridial canal^{29,30,32,33}.

- . 0 straight
- . 1 branching

86. Annelid type cuticle.

- . 0 absent

- . 1 present
87. Intracellular lamellar cuticle. Adopted from refs. 35,36.
- . 0 absent
 - . 1 present
88. Epidermis syncytial. This character is shared with rotifers and acanthocephalans, scored according to refs. 16,21.
- . 0 absent
 - . 1 present
89. *Epidermis with an intra-syncytial lamina. This character is shared with rotifers and acanthocephalans, scored according to refs. 16,21.
- . 0 absent
 - . 1 present
90. *Distal plasma membrane of the epidermis with crypt-like infoldings. This character is shared with rotifers and acanthocephalans, scored according to refs. 16,21.
- . 0 absent
 - . 1 present
91. *Infoldings of the distal plasma membrane widen inside the epidermis to larger caverns. Contingent on the presence of a distal plasma membrane of the epidermis with crypt-like infoldings (character 90). This character is shared with Seisonidea and acanthocephalans, scored according to refs. 16,21.
- . 0 absent
 - . 1 present
92. *Epidermis containing larger filament bundles. This character is shared with Seisonidea and acanthocephalans, scored according to refs. 16,21, and it has also been mentioned as present in Phoronida, Tardigrada, Nematoda and Nematomorpha.
- . 0 absent

- . 1 present
93. Cuticular plates on head (cephalion) formed from thickening of the endocuticle. This character is present in very few genera of Gastrotricha.
- . 0 absent
 - . 1 present
94. Ventral postoral cuticular formation.
- . 0 absent
 - . 1 present
95. Cuticular spines and scales beneath cuticle. This refers specifically to the condition in Gastrotricha.
- . 0 absent
 - . 1 present
96. Spines and scales as solid thickenings of endocuticle. Contingent on the presence of cuticular spines and scales beneath the cuticle (character 95).
- . 0 absent
 - . 1 present
97. Head scales. Contingent on the presence of cuticular spines and scales beneath the cuticle (character 95).
- . 0 absent
 - . 1 present
98. Head scale shape. Contingent on the presence of head scales (character 97).
- . 0 an cres
 - . 1 placoid
 - . 2 polygonal cuticular plates
 - . 3 long and oval scales with two longitudinal keels
 - . 4 spined
 - . 5 keeled scales
 - . 6 circular scales

- . 7 polygonal scales
 - . 8 rhombic scales
 - . 9 stalked
 - . 10 compound scales
99. Trunk scales. Contingent on the presence of cuticular spines and scales beneath cuticle (character 95).
- . 0 absent
 - . 1 present
100. Sclerites reduced or absent in mid-trunk region. Contingent on the presence of cuticular spines and scales beneath cuticle (character 95).
- . 0 absent
 - . 1 present
101. Trunk scale shape. Contingent on the presence of trunk scales (character 99).
- . 0 an cres
 - . 1 long and oval scales
 - . 2 spined
 - . 3 circular
 - . 4 keeled
 - . 5 polygonal
 - . 6 rhombic
 - . 7 stalked
 - . 8 compound
 - . 9 ornamented
102. Spines covering entire ventral surface. Contingent on the presence of cuticular spines and scales beneath the cuticle (character 95).
- . 0 absent
 - . 1 present
103. Epidermal glands.
- . 0 absent

- . 1 present
104. Duo gland adhesion.
- . 0 absent
 - . 1 present
105. Shape of posterior end. Rotifers *Brachionus*, *Proales*, *Lepadella*, *Adineta* and *Rotaria* have a bilobed end. In acanthocephalans, they usually have a rounded end. In *Juracanthocephalus* and *Seison*, the posterior is blunt.
- . 0 tapering
 - . 1 rounded
 - . 2 blunt
 - . 3 bilobed
106. Bilobed end shape. Contingent on the presence of a bilobed posterior (character 105).
- . 0 fin-shaped
 - . 1 blunt pedicles
 - . 2 simple lobes
 - . 3 inverted Y-shaped fork
 - . 4 simple dichotomous fork
 - . 5 elongated dichotomous fork
 - . 6 closely arranged, parallel furca
 - . 7 furcette
 - . 8 oval lobes
 - . 9 short appendages at the angles of the blunt caudal end
107. Adhesive tubes on bilobed end/ posterior furca. Contingent on the presence of a bilobed posterior (character 105).
- . 0 absent
 - . 1 present
108. Number of adhesive tubes per branch. Contingent on the presence of furcal adhesive tubes (character 105).

- . 0 one
- . 1 two
- . 2 three
- . 3 four
- . 4 five
- . 5 eight
- . 6 nine
- . 7 thirteen
- . 8 fifteen
- . 9 sixteen

109. Bilobed end secondary adhesive tubes. Contingent on the presence of adhesive tubes on the bilobed posterior (character 105).

- . 0 absent
- . 1 present

110. Median tail cone. This character is only present in some gastrotrichans.

- . 0 absent
- . 1 present

111. Frontal adhesive tubes. This character is only present in gastrotrichans.

- . 0 absent
- . 1 present

112. Number of frontal adhesive tubes per side. Contingent on the presence of frontal adhesive tubes (character 111).

- . 0 6 and more
- . 1 fewer tubes per side

113. Frontal adhesive tube arrangement. Contingent on the presence of frontal adhesive tubes (character 111).

- . 0 in convex arch
- . 1 in concave arch
- . 2 in tuft

- . 3 hand like organ
- . 4 two diagonal rows
- . 5 in W shape
- . 6 in two ventrolateral longitudinal fields

114. Ventral adhesive tubes.

- . 0 absent
- . 1 present

115. Lateral adhesive tubes.

- . 0 absent
- . 1 present

116. Lateral adhesive tube shape. Contingent on the presence of lateral adhesive tubes (character 115).

- . 0 raised cuticularized tubes
- . 1 mastoid uprisings
- . 2 double tubes

117. Number of lateral adhesive tubes per side. Contingent on the presence of lateral adhesive tubes (character 115).

- . 0 many tubes per side
- . 1 one tube per side
- . 2 few tubes per side
- . 3 thirty per side

118. Dorsolateral adhesive tubes.

- . 0 absent
- . 1 present

119. Dorsolateral adhesive tube shape. Contingent on the presence of dorsolateral adhesive tubes (character 118).

- . 0 raised cuticularized tubes
- . 1 rudimentary tubes

120. Number of dorsolateral tubes per side. Contingent on the presence of dorsolateral adhesive tubes (character 119).
- . 0 up to 10 tubes per side
 - . 1 more than 10 tubes per side
121. Caudal adhesive tubes.
- . 0 absent
 - . 1 present
122. Body cuticle with chitin.
- . 0 absent
 - . 1 present
123. Body cuticle with alpha-chitin. Contingent on the presence of chitin (character 122).
- . 0 absent
 - . 1 present
124. Body cuticle moulted.
- . 0 absent
 - . 1 present
125. Lorica. Lorica is present in *Brachionus*, *Lepadella*, and absent in other rotifers and acanthocephalans.
- . 0 absent
 - . 1 present
126. Lobopods or segmented/arthropodised limbs. Limbs absent and subordinate characters inapplicable in Acanthocephala and rotifers.
- . 0 absent
 - . 1 present
127. Limb type. Contingent on the presence of lobopods or segmented/

- arthropodised limbs (character 126).
 - . 0 lobopods
 - . 1 arthropodised limbs

- 128. Posteriorly facing last pair of limbs. Contingent on the presence of lobopods or segmented/ arthropodised limbs (character 126).
 - . 0 absent
 - . 1 present

- 129. Slime papillae.
 - . 0 absent
 - . 1 present

- 130. Telescoping mouth cone with protrudable stylets.
 - . 0 absent
 - . 1 present

- 131. Respiration via metameric tracheae and spiracles.
 - . 0 absent
 - . 1 present

- 132. Mixocoel (haemocoel) surrounded by segmented mesoderm.
 - . 0 absent
 - . 1 present

- 133. Teloblastic segmentation.
 - . 0 absent
 - . 1 present

- 134. Longitudinal ventral or lateral nerve cord(s). This character is present in Rotifera and also Acanthocephala^{2,29,37,38}.
 - . 0 absent
 - . 1 present

135. Paired ventral or lateral nerve cords. Contingent on the presence of longitudinal ventral or lateral nerve cords (character 134). This character is present in Rotifera and also Acanthocephala^{2,29,37}.
- . 0 absent
 - . 1 present
136. Circumoral nerve ring. There is no anterior nerve ring in Acanthocephala, the cerebral ganglion connecting directly to the lateral nerves.
- . 0 absent
 - . 1 present
137. Circum-pharyngeal, collar-shaped brain with anterior and posterior rings of perikaryal separated by ring-shaped neuropil. There is either a dorsal or ventral cerebral ganglion in Acanthocephala, so this character is absent.
- . 0 absent
 - . 1 present
138. Brain with dorsal and ventral lobes.
- . 0 absent
 - . 1 present
139. Introvert with scalid rings.
- . 0 absent
 - . 1 present
140. Flosculi.
- . 0 absent
 - . 1 present
141. Preoral larval ciliary band (prototroch). The development of *Seison* has not been studied, thus coded as uncertain for all of the developmental characters³⁹. The acanthor larva does not have ciliary bands.
- . 0 absent
 - . 1 present

142. Downstream or upstream food collection. Contingent on the absence of direct development (character 31).
- . 0 downstream
 - . 1 upstream
143. Metatroch. Contingent on the absence of direct development (character 31) and absent in acanthocephalans.
- . 0 absent
 - . 1 present
144. Apical organ. Contingent on the absence of direct development (character 31). There is no apical organ in the acanthor larva.
- . 0 absent
 - . 1 present
145. Apical organ with muscles extending to the hyposphere. Contingent on the absence of direct development (character 31).
- . 0 absent
 - . 1 present
146. Segmental metanephridia sacculus.
- . 0 absent
 - . 1 present
147. Chitinous appendages secreted by microvilli (chaetae).
- . 0 absent
 - . 1 present
148. Chaetae in bundles. Contingent on the presence of chaetae (character 147).
- . 0 absent
 - . 1 present
149. Paleae. Contingent on the presence of chaetae (character 147).

- . 0 absent
- . 1 present

150. Mineralised chaetae. Contingent on the presence of chaetae (character 147).

- . 0 absent
- . 1 present

151. Serially repeated chaetal bundles. Contingent on the presence of chaetae (character 147).

- . 0 absent
- . 1 present

152. Parapodia.

- . 0 absent
- . 1 present

153. Head with prostomium and peristomium.

- . 0 absent
- . 1 present

154. Dorsal cirri. Contingent on the presence of parapodia (character 152).

- . 0 absent
- . 1 present

155. Ventral cirri. Contingent on the presence of parapodia (character 152).

- . 0 absent
- . 1 present

156. Pygidial cirri.

- . 0 absent
- . 1 present

157. Shell plates/conch.

- . 0 absent

- . 1 present
158. Protoconch. Contingent on the presence of shell plates/conch (character 157).
- . 0 absent
 - . 1 present
159. Head valve. Contingent on the presence of shell plates/conch (character 157).
- . 0 absent
 - . 1 present
160. Opposing dorsal and ventral valves. Contingent on the presence of shell plates/conch (character 157).
- . 0 absent
 - . 1 present
161. Ventrally attached conveyor belt of teeth with continual replacement (radula).
- . 0 absent
 - . 1 present
162. Radula tooth rows. Contingent on the presence of a radula (character 161).
- . 0 few rows
 - . 1 many rows
163. Discrete, chitinous, bilaterally symmetrical jaw apparatus. This character codes for the jaws of chaetognaths and gnathiferans²¹ following the justification in ref. 1, therefore excluding the jaws of panarthropods, which are continuous with the epicuticle and are not discrete elements. The jaw apparatus with discrete solid parts is a character present both in chaetognaths and gnathiferans, but in all extant chaetognaths the jaws become grasping spines. While gastropod jaws may meet this definition, they are not present in *Tritia*. This character is also present in *Juracanthocephalus* where jaws are present as discrete elements.
- . 0 absent
 - . 1 present

164. Tube like support rods in jaw. Contingent on the presence of a jaw apparatus (character 163). This character codes as present for rotifers^{15,40–42}. The situation is unknown for *Juracanthocephalus*.
- . 0 absent
 - . 1 present
165. Jaw with symphysis. Contingent on the presence of a jaw apparatus (character 163). The symphysis is a bilateral structure that fuses two elements at the midline, which can be seen in all rotifers^{15,40–42}. *Juracanthocephalus* does not possess this feature.
- . 0 absent
 - . 1 present
166. Grasping spines. Contingent on the presence of a jaw apparatus (character 163). This character is shared by all extant chaetognaths.
- . 0 absent
 - . 1 present
167. Grasping spines in discrete clusters. Contingent on the presence of grasping spines (character 166).
- . 0 absent
 - . 1 present
168. *Rami stout, appearing triangular in dorso-ventral view. Scored from ref. 3. Contingent on the presence of a jaw apparatus (character 163). This character refers to the rami found in taxa with virgate trophi. The situation is unknown in *Juracanthocephalus*.
- . 0 absent
 - . 1 present
169. *Trophi with unci. Scored from ref. 3. Contingent on the presence of a jaw apparatus (character 163). This character refers to the presence of unci. Scored as unknown in *Juracanthocephalus*.

- . 0 absent
- . 1 present

170. *Fulcrum and rami connected by large hypopharyngeal muscle working as a piston. Scored from refs. 3,4. Contingent on the presence of a jaw apparatus (character 163). Scored as unknown in *Juracanthocephalus*.

- . 0 absent
- . 1 present

171. Teeth. Contingent on the presence of a jaw apparatus (character 163). This character refers to the teeth of Chaetognatha that are usually situated at the outside of the mouth.

- . 0 absent
- . 1 present

172. Anterior teeth. Contingent on the presence of teeth (character 171).

- . 0 absent
- . 1 present

173. Posterior teeth. Contingent on the presence of teeth (character 171).

- . 0 absent
- . 1 present

174. Type of teeth. Contingent on the presence of teeth (character 171).

- . 0 stout teeth arranged in fan shape
- . 1 slender teeth arranged in comb shape

175. Jaw apparatus position. Contingent on the presence of a jaw apparatus (character 163). The jaw apparatus is inside in rotifers and *Juracanthocephalus*.

- . 0 external
- . 1 internal

176. *Internal jaws with denticles. Contingent on the presence of an internal jaw

apparatus (character 175). This is a character that shared by Gnathifera as well as *Juracanthocephalus* and *Amiskwia*⁴³. In *Timorebestia*, this character is uncertain¹.

- . 0 absent
- . 1 present

177. Unpaired basal plate. Contingent on the presence of a jaw apparatus (character 163). A basal plate is only present in gnathostomulids³, *Amiskwia*⁴³, and *Timorebestia*¹.

- . 0 absent
- . 1 present

178. Position of jaw. Contingent on the presence of a jaw apparatus (character 163). In most gnathiferans and *Timorbestia*, the jaw is within the anterior part of the trunk¹. In *Seison*², *Amiskwia*⁴³ and chaetognaths¹, the jaws are situated within or externally on the head region.

- . 0 anteriormost trunk
- . 1 within or on head

179. Ctenidia.

- . 0 absent
- . 1 present

180. Ventral ciliated locomotor organ separated from dorsum by cavity (mantle cavity).

- . 0 absent
- . 1 present

181. Peripheral mantle cavity. Contingent on the presence of a mantle cavity (character 180).

- . 0 absent
- . 1 present

182. *Head specialized as a hooked proboscis. This character is only present in

acanthocephalans, including *Juracanthocephalus*.

- . 0 absent
- . 1 present

183. *Proboscis shape. Scored from ref. 2. Contingent on the presence of a proboscis (character 182). The head is round in *Macracanthorhynchus* and *Juracanthocephalus*, and elongate to fusiform in other acanthocephalans.

- . 0 round
- . 1 elongate to fusiform

184. *Arrangement of hooks. Scored from ref. 2. Contingent on the presence of a hooked proboscis (character 182). Spiral for *Macracanthorhynchus* and *Juracanthocephalus*, and longitudinal for all other acanthocephalans.

- . 0 spiral
- . 1 longitudinal

185. Eversible proboscis surrounded by rhynchocoel.

- . 0 absent
- . 1 present

186. Tripartite body plan with septum.

- . 0 absent
- . 1 present

187. *Termination of body specialised as a bursa. Scored from ref. 2. This character is only present in acanthocephalans, including *Juracanthocephalus*.

- . 0 absent
- . 1 present

188. Body with lateral fins.

- . 0 absent
- . 1 present

189. Anterior lateral fins. Contingent on the presence of fins (character 188).

- . 0 absent
- . 1 present

190. Tegumentary bridge connecting anterior and posterior lateral fins. Contingent on the presence of fins and anterolateral fins (characters 188 and 189).

- . 0 absent
- . 1 present

191. Ray less zone in the lateral fins. Contingent on the presence of trunk fins (character 188).

- . 0 absent
- . 1 present

192. Caudal fin supported by rays. Contingent on the presence of a caudal fin (character 188).

- . 0 absent
- . 1 present

193. Trunk fins continuous with caudal fin. Contingent on the presence of a caudal fin (character 188).

- . 0 absent
- . 1 present

194. Trunk fins supported by rays. Contingent on the presence of fins (character 188).

- . 0 absent
- . 1 present

195. Gelatinous masses in the lateral fins. Contingent on the presence of trunk fins (character 188).

- . 0 absent
- . 1 present

196. Phragms.

- . 0 absent
- . 1 present

197. Phragms in trunk.

- . 0 absent
- . 1 present

198. Phragms in tail.

- . 0 absent
- . 1 present

199. Type of phragms.

- . 0 super contraction
- . 1 normal contraction

200. Intestinal diverticulae.

- . 0 absent
- . 1 present

201. *Anterior insertion of sperm flagellum. Scored from ref. 21. This character refers to the anterior portion of the sperm flagellum and is present in all Rotifera and Acanthocephala.

- . 0 absent
- . 1 present

202. *Two rows of electron-dark bodies alongside sperm flagellum. Scored from ref. 21. Contingent on the presence of an anterior insertion of the sperm flagellum (character 201). This character refers to the two rows of electron-dark bodies that accompany the anterior portion of the sperm flagellum and is present in Seisonidea and Acanthocephala.

- . 0 absent
- . 1 present

203. Seminal vesicles. This character is presented in some rotifers like

Brachionus^{44,45} and *Seison*¹⁵, but remains unknown in many rotifers. Seminal vesicles are also found in many acanthocephalans^{2,46-48}.

- . 0 absent
- . 1 present

204. Type of seminal vesicles. Contingent on the presence of seminal vesicles (character 203). This character remains unknown in most rotifers, but the shape is oval in *Seison*¹⁵. Acanthocephalans are scored from refs. 2,46,48-50.

- . 0 elongated with a lateral opening
- . 1 elongated and an anterior protruding part usually roundish
- . 2 roundish or slightly oval with a lateral opening
- . 3 elongated with an anterior opening
- . 4 small indentations present
- . 5 oval with bulb-like shape

205. Position of seminal vesicles relative to fins. Contingent on the presence of fins (character 188) and seminal vesicles (character 203).

- . 0 touching neither lateral fins nor tail fin but closer to lateral fins
- . 1 touching neither lateral fins nor tail fin but closer to tail fin
- . 2 touching, or close to, lateral fins and well separated from tail fin
- . 3 touching, or close to, tail fin and well separated from lateral fins
- . 4 touching both lateral fins and tail fin

206. Median posterior adhesive structure. In Rotifera this would refer to the pedal glands that can secrete an adhesive substance.

- . 0 absent
- . 1 present

207. *Pedal glands. Scored from ref. 4. This character refers to the presence of pedal glands. Contingent on the presence of a posterior adhesive structure (character 206). This character is present in all rotifers.

- . 0 absent
- . 1 present

208. *Number of pedal glands. Scored from ref. 3. This character refers to the number of pedal glands. Contingent on the presence of pedal glands (character 207).
- . 0 one pair
 - . 1 multiple glands
209. *Female organs with differentiated bursa and prebursa. Scored from ref. 4. This character is only present in gnathostomulids.
- . 0 absent
 - . 1 present
210. Stomatogastric ganglia connected directly to brain. According to ref. 51, this character is not clear in Seisonidea, and in acanthocephalans there is no anterior ganglion apart from the brain/cerebral ganglion.
- . 0 absent
 - . 1 present
211. Stomatogastric ganglion with ciliated receptors. Contingent on the presence of stomatogastric ganglia (character 210).
- . 0 absent
 - . 1 present
212. Ventral ganglion with lateral somata. All acanthocephalans lack such a large ganglion with lateral somata which is unique to chaetognaths.
- . 0 absent
 - . 1 present
213. Head covered by cuticular hood.
- . 0 absent
 - . 1 present
214. Secretory ventral gland.
- . 0 absent
 - . 1 present

215. *Mode of reproduction. Scored from refs. 4,52–60. This character refers to reproductive strategy. Seisonidea and Acanthocephala are obligate gamogenetic, Bdelloidea are obligate parthenogenetic, and all monogononts are metagenetic¹⁸.

- . 0 obligate gamogenesis
- . 1 obligate parthenogenesis
- . 2 metagenesis

216. AP axis.

- . 0 absent
- . 1 present

217. Dorsoventral axis.

- . 0 absent
- . 1 present

218. Origin of mesoderm. Acanthocephala do not gastrulate and are coded as uncertain.

- . 0 from the blastopore lips and as ectomesoderm
- . 1 from the walls of the archenteron or neural crest

219. Coelom.

- . 0 absent
- . 1 present

220. Coelom formation. Contingent on the presence of a coelom (character 219).

- . 0 schizocoelous
- . 1 enterocoelous

221. Serially repeated paired coelomic cavities. Contingent on the presence of a coelom (character 219).

- . 0 absent
- . 1 present

222. Pharyngeal slits.

- . 0 absent
- . 1 present

223. Endostyle (or homologues).

- . 0 absent
- . 1 present

224. Notochord.

- . 0 absent
- . 1 present

225. Stomochord.

- . 0 absent
- . 1 present

226. Haemal system with axial complex.

- . 0 absent
- . 1 present

227. Calcareous endoskeleton composed of separate ossicles.

- . 0 absent
- . 1 present

228. Tornaria type larva.

- . 0 absent
- . 1 present

229. Longitudinal dorsal nerve cord.

- . 0 absent
- . 1 present

230. Zig zag myomeres.

- . 0 absent
- . 1 present

231. Endothelium that lines the inner wall of blood vessels

- . 0 absent
- . 1 present

232. Neural crest.

- . 0 absent
- . 1 present

233. Neurogenic placodes.

- . 0 absent
- . 1 present

234. Body symmetry.

- . 0 radial
- . 1 bilateral
- . 2 biradial

235. Mesoglea.

- . 0 absent
- . 1 present

236. Cydippid larvae.

- . 0 absent
- . 1 present

237. Ciliary rosettes.

- . 0 absent
- . 1 present

238. Lophophore.

- . 0 absent

- . 1 present

239. Hox/ParaHox genes. The following characters (240–247) are contingent on the presence of Hox/ParaHox genes. Rotifera and Acanthocephala scored from refs. 61,62.

- . 0 absent
- . 1 present

240. ftz.

- . 0 absent
- . 1 present

241. Ubx/abd-A.

- . 0 absent
- . 1 present

242. AbdB.

- . 0 absent
- . 1 present

243. lox5.

- . 0 absent
- . 1 present

244. Duplication of UbdA into lox4 and lox2.

- . 0 absent
- . 1 present

245. Post.

- . 0 absent
- . 1 present

246. Duplication into Post1 and Post2.

- . 0 absent

. 1 present

247. MedPost.

. 0 absent

. 1 present

SUPPLEMENTARY REFERENCES

- 1 Park, T.-Y. S. *et al.* A giant stem-group chaetognath. *Sci. Adv.* **10**, eadi6678 (2024).
- 2 Monks, S. Phylogeny of the Acanthocephala based on morphological characters. *Syst. Parasitol.* **48**, 81–115 (2001).
- 3 Sørensen, M. V. On the evolution and morphology of the rotiferan trophi, with a cladistic analysis of Rotifera. *J. Zool. Syst. Evol. Res.* **40**, 129–154 (2002).
- 4 Sørensen, M. V. & Giribet, G. A modern approach to rotiferan phylogeny: Combining morphological and molecular data. *Mol. Phylogenet. Evol.* **40**, 585–608 (2006).
- 5 Bosi, G., DePasquale, J. A., Rossetti, E. & Dezfuli, B. S. Differential mucins secretion by intestinal mucous cells of *Chelon ramada* in response to an enteric helminth *Neoechinorhynchus agilis* (Acanthocephala). *Acta Histochem.* **122**, 151488 (2020).
- 6 Silva, R. Z., Pereira, J. & Cousin, J. C. B. Histological patterns of the intestinal attachment of *Corynosoma australe* (Acanthocephala: Polymorphidae) in *Arctocephalus australis* (Mammalia: Pinnipedia). *J. Parasit. Dis.* **38**, 410–416 (2014).
- 7 Skorobrechova, E. M., Nikishin, V. P. & Lisitsyna, O. I. Structure of capsule around acanthocephalan *Corynosoma strumosum* from uncommon paratenic hosts—lizards of two species. *Parasitol. Res.* **110**, 459–467 (2012).
- 8 Hochberg, R., Yang, H. & Moore, J. The ultrastructure of escape organs: setose arms and cross-striated muscles in *Hexarthra mira* (Rotifera: Gnesiotrocha: Flosculariaceae). *Zoomorphology* **136**, 159–173 (2017).
- 9 Herlyn, H. & Ehlers, U. Organisation of the praesoma in *Acanthocephalus anguillae* (Acanthocephala, Palaeacanthocephala) with special reference to the muscular system. *Zoomorphology* **121**, 13–18 (2001).

- 10 Garey, J. R., Schmidt-Rhaesa, A., Near, T. J. & Nadler, S. A. in *Rotifera VIII: A Comparative Approach. Developments in Hydrobiology* (eds Wurdak, E., Wallace, R., & Segers, H.) 83–91 (Springer Netherlands, 1998).
- 11 Ferraguti, M. & Melone, G. Spermiogenesis in *Seison nebaliae* (Rotifera, Seisonidea): further evidence of a rotifer-acanthocephalan relationship. *Tissue Cell* **31**, 428–440 (1999).
- 12 Cain, G. D. Collagen from the giant acanthocephalan *Macracanthorhynchus hirudinaceus*. *Arch. Biochem. Biophys.* **141**, 264–270 (1970).
- 13 Preston, B. L., Snell, T. W., Robertson, T. L. & Dingmann, B. J. Use of freshwater rotifer *Brachionus calyciflorus* in screening assay for potential endocrine disruptors. *Environ. Toxicol. Chem.* **19**, 2923–2928 (2000).
- 14 Sangster, N. C. & Mettrick, D. F. Effects of cholinergic drugs on muscle contraction in *Moniliformis moniliformis* (Acanthocephala). *J. Parasitol.* **73**, 998–1004 (1987).
- 15 Ricci, C., Melone, G. & Sotgia, C. Old and new data on Seisonidea (Rotifera). *Hydrobiologia* **255**, 495–511 (1993).
- 16 Ahlrichs, W. H. Epidermal ultrastructure of *Seison nebaliae* and *Seison annulatus*, and a comparison of epidermal structures within the Gnathifera. *Zoomorphology* **117**, 41–48 (1997).
- 17 Funch, P., Sørensen, M. V. & Obst, M. in *Rotifera X: Rotifer Research: Trends, New Tools and Recent Advances* (eds Herzig, A., Gulati, R. D., Jersabek, C. D., & May, L.) 11–28 (Springer Netherlands, 2005).
- 18 Hagemann, L., Mauer, K. M., Hankeln, T., Schmidt, H. & Herlyn, H. Nuclear genome annotation of wheel animals and thorny-headed worms: inferences about the last common ancestor of Syndermata (Rotifera s.l.). *Hydrobiologia* **851**, 2827–2844 (2023).
- 19 Sielaff, M. *et al.* Phylogeny of Syndermata (syn. Rotifera): Mitochondrial gene order verifies epizotic Seisonidea as sister to endoparasitic Acanthocephala within monophyletic Hemirotifera. *Mol. Phylogenet. Evol.* **96**, 79–92 (2016).
- 20 Song, R. *et al.* Characterization of the complete mitochondrial genome of *Brentisentis yangtzensis* Yu & Wu, 1989 (Acanthocephala, Illiosentidae). *ZooKeys* **861**, 1–14 (2019).
- 21 Herlyn, H. in *The Evolution and Fossil Record of Parasitism: Identification*

- and *Macroevolution of Parasites* (eds De Baets, K. & Huntley, J. W.) 273–313 (Springer International Publishing, 2021).
- 22 Sørensen, M. V., Segers, H. & Funch, P. On a new *Seison* Grube, 1861 from coastal waters of Kenya, with a reappraisal of the classification of the Seisonida (Rotifera). *Zool. Stud.* **44**, 34–43 (2005).
 - 23 Leasi, F., Rouse, G. W. & Sørensen, M. V. A new species of *Paraseison* (Rotifera: Seisonacea) from the coast of California, USA. *J. Mar. Biol. Assoc. UK* **92**, 959–965 (2012).
 - 24 Boell, L. A. & Bucher, G. Whole-mount in situ hybridization in the Rotifer *Brachionus plicatilis* representing a basal branch of lophotrochozoans. *Dev. Genes Evol.* **218**, 445–451 (2008).
 - 25 Leasi, F., Neves, R. C., Worsaae, K. & Sørensen, M. V. Musculature of *Seison nebaliae* Grube, 1861 and *Paraseison annulatus* (Claus, 1876) revealed with CLSM: a comparative study of the gnathiferan key taxon Seisonacea (Rotifera). *Zoomorphology* **131**, 185–195 (2012).
 - 26 Albrecht, H., Ehlers, U. & Taraschewski, H. Syncytial organization of acanthors of *Polymorphus minutus* (Palaeacanthocephala), *Neoechinorhynchus rutili* (Eoacanthocephala), and *Moniliformis moniliformis* (Archiacanthocephala) (Acanthocephala). *Parasitol. Res.* **83**, 326–338 (1997).
 - 27 Fontaneto, D. & De Smet, W. H. in *Handbook of Zoology, Gastrotricha, Cycloneuralia and Gnathifera* (ed Schmidt-Rhaesa, A.) 217–316 (De Gruyter, 2015).
 - 28 Hochberg, R., Araújo, T. Q., Walsh, E. J., Mohl, J. E. & Wallace, R. L. Fine structure of the retrocerebral organ in the rotifer *Trichocerca similis* (Monogononta). *Invertebr. Biol.* **142**, e12396 (2023).
 - 29 Ahlrichs, W. Ultrastructure of the protonephridia of *Seison annulatus* (Rotifera). *Zoomorphology* **113**, 245–251 (1993).
 - 30 Dunagan, T. T. & Miller, D. M. A review of protonephridial excretory systems in Acanthocephala. *J. Parasitol.* **72**, 621–632 (1986).
 - 31 Riemann, O. & Ahlrichs, W. H. The evolution of the protonephridial terminal organ across Rotifera with particular emphasis on *Dicranophorus forcipatus*, *Encentrum mucronatum* and *Erignatha clastopis* (Rotifera: Dicranophoridae). *Acta Zool.* **91**, 199–211 (2010).
 - 32 Dunagan, T. T. & Miller, D. M. Protonephridia in male *Macracanthorhynchus*

- hirudinaceus* (Acanthocephala): An SEM study. *J. Parasitol.* **71**, 427–432 (1985).
- 33 Krapf, K. & Dunagan, T. T. Structural features of the protonephridia in female *Macracanthorhynchus hirudinaceus* (Acanthocephala). *J. Parasitol.* **73**, 1176–1181 (1987).
 - 34 Wilson, R. A. & Webster, L. A. Protonephridia. *Biol. Rev.* **49**, 127–160 (1974).
 - 35 Bekkouche, N. & Gąsiorowski, L. Careful amendment of morphological data sets improves phylogenetic frameworks: re-evaluating placement of the fossil *Amiskwia sagittiformis*. *J. Syst. Palaeontol.* **20**, 1–14 (2022).
 - 36 Van Der Land, J. & Nørrevang, A. in *The origins and relationships of lower invertebrates* (eds Conway Morris, S., George, J. D., Gibson, R., & Platt, H. M.) 261–273 (Oxford University Press, 1985).
 - 37 Bekkouche, N. & Worsaae, K. Nervous system and ciliary structures of Micrognathozoa (Gnathifera): evolutionary insight from an early branch in Spiralia. *Roy. Soc. Open Sci.* **3**, 160289 (2016).
 - 38 Dunagan, T. T. & Miller, D. M. Major nerves in the anterior nervous system of *Macracanthorhynchus hirudinaceus* (Acanthocephala). *Comp. Biochem. Phys.* **37**, 235–242 (1970).
 - 39 Nielsen, C. *Animal evolution: interrelationships of the living phyla* (Oxford University Press, 2012).
 - 40 Markevich, G. I. SEM observations on *Seison* and phylogenetic relationships of the Seisonidea (Rotifera). *Hydrobiologia* **255**, 513–520 (1993).
 - 41 Wulfken, D. & Ahlrichs, W. H. The ultrastructure of the mastax of *Filinia longiseta* (Flosculariaceae, Rotifera): Informational value of the trophi structure and mastax musculature. *Zoo. Anz.* **251**, 270–278 (2012).
 - 42 Wulfken, D., Wilts, E. F., Martínez-Arbizu, P. & Ahlrichs, W. H. Comparative analysis of the mastax musculature of the rotifer species *Pleurotrocha petromyzon* (Notommatidae) and *Proales tillyensis* (Proalidae) with notes on the virgate mastax type. *Zoo. Anz.* **249**, 181–194 (2010).
 - 43 Caron, J.-B. & Cheung, B. *Amiskwia* is a large Cambrian gnathiferan with complex gnathostomulid-like jaws. *Commun. Biol.* **2**, 164 (2019).
 - 44 Gu, S. *et al.* Spermatozoon of the freshwater rotifer *Brachionus calyciflorus* (Rotifera, Monogononta): Advances in morphological and ultrastructural

- studies. *Micron* **76**, 6–13 (2015).
- 45 Snell, T. W. & Childress, M. Aging and loss of fertility in male and female *Brachionus plicatilis* (Rotifera). *Int. J. Invertebr. Reprod. Dev* **12**, 103–110 (1987).
- 46 Datta, M. N. & Soota, T. D. On a new species of the genus *Acanthocephalus* from *Rana* sp. and a new host record of *Centrorhynchus cinctus* (Rudolphi). *Rec. Zoo. Surv. India* **52**, 185–188 (1955).
- 47 Hughes, R. C. & Moore, G. A. *Acanthocephalus van-cleavei*, a new echinorhynchid worm, from a salamander. *Am. Midl. Nat.* **29**, 724–729 (1943).
- 48 Chandler, A. C. A revision of the genus *Rhadinorhynchus* (Acanthocephala) with descriptions of new genera and species. *Parasitology* **26**, 352–358 (1934).
- 49 Foata, J., Culioli, J.-L. & Marchand, B. Ultrastructure of spermiogenesis and the spermatozoon of *Macracanthorhynchus hirudinaceus* (Pallas, 1781) (Acanthocephala: Archiacanthocephala), a parasite of the wild boar *Sus scrofa*. *J. Parasitol.* **91**, 499–506 (2005).
- 50 Foata, J., Dezfuli, B. S., Pinelli, B. & Marchand, B. Ultrastructure of spermiogenesis and spermatozoon of *Leptorhynchoides plagicephalus* (Acanthocephala, Palaeacanthocephala), a parasite of the sturgeon *Acipenser naccarii* (Osteichthyes, Acipenseriformes). *Parasitol. Res.* **93**, 56–63 (2004).
- 51 Herlyn, H. Enigmatic Gnathostomulida (Gnathifera, Spiralia): about monociliated pharyngeal receptors and the pharyngeal nervous system. *Zoomorphology* **136**, 425–434 (2017).
- 52 Mortimer, K. & Mackie, A. S. Y. Morphology, feeding and behaviour of British “*Magelona*” (Annelida: Magelonidae), with discussions on the form and function of abdominal lateral pouches. *Mem. Mus. Vic.* **71**, 177–201 (2014).
- 53 Olive, P. J. W., Garwood, P. R., Bentley, M. G. & Wright, N. Reproductive success, relative abundance and population structure of two species of *Nephtys* in an estuarine beach. *Mar. Biol.* **63**, 189–196 (1981).
- 54 Petraitis, P. S. Occurrence and reproductive success of feminized males in the polychaete *Capitella capitata* (Species Type I). *Mar. Biol.* **97**, 403–412 (1988).
- 55 Olive, P. J. W. Reproductive biology of *Eulalia viridis* (Müller) (Polychaeta:

- Phyllodocidae) in the north eastern UK. *J. Mar. Biol. Assoc. UK* **55**, 313–326 (1975).
- 56 Gibbs, P. E. Gametogenesis and spawning in a hermaphroditic population of *Golfingia minuta* (Sipuncula). *J. Mar. Biol. Assoc. UK* **55**, 69–82 (1975).
- 57 Giannakara, A. & Ramm, S. A. Self-fertilization, sex allocation and spermatogenesis kinetics in the hypodermically inseminating flatworm *Macrostomum pusillum*. *J. Exp. Biol.* **220**, 1568–1577 (2017).
- 58 Guidi, L. *et al.* Comparative sperm ultrastructure of *Neodasys ciritus* and *Musellifer delamarei*, two species considered to be basal among Chaetonotida (Gastrotricha). *Zoomorphology* **122**, 135–143 (2003).
- 59 Hummon, M. R. Reproduction and sexual development in a freshwater gastrotrich. *Zoomorphology* **104**, 33–41 (1984).
- 60 Sørensen, M. V. in *Invertebrate Zoology: A Tree of Life Approach* (eds Schierwater, B. & DeSalle, R.) 279–300 (CRC Press, 2021).
- 61 Mauer, K. *et al.* The genome, transcriptome, and proteome of the fish parasite *Pomphorhynchus laevis* (Acanthocephala). *PLOS ONE* **15**, e0232973 (2020).
- 62 Fröblius, A. C. & Funch, P. Rotiferan *Hox* genes give new insights into the evolution of metazoan bodyplans. *Nat. Commun.* **8**, 9 (2017).