

Supplementary Data

Phylogenetic analysis

For the phylogenetic analysis, a character matrix of 38 characters was generated for 27 taxa. The characters and states are listed below in the supporting text, with explanations where appropriate. The character matrix can be seen in Table S1. Cladistic analysis of these lobopodians, and some arthropods was conducted in PAUP* version 4.0b10. A branch and bound search under implied weights ($k=2$) resulted in 3 trees. The strict consensus of these trees is shown in Fig. 4, with character optimizations depicted in Fig. S1. Cycloneuralia was used as the outgroup.

Phylogenetic Analysis Character List

1. Proboscis

0 absent

1 present

The proboscis is a typical character of Cycloneuralia and some lobopodians: *Aysheia*⁴, *Paucipodia*²⁵ and *Diania* also bear a similar structure. The poor preservation of *Xenusion*¹⁴ and *Hadranax*²⁶ makes it difficult to determine whether or not a proboscis was present in these two taxa. In *Microdictyon*²⁷, the orientation is still controversial. Ramsköld²⁸ claimed that the extended, limbless part is the anterior, a view was endorsed by Chen *et al.*²⁹ and Ramsköld and Chen⁶; while Hou *et al.*³⁰ insisted on a reversed orientation. Based on our specimens and the reasonable explanations of Ramsköld and Chen⁶, we here accept the orientation of Ramsköld²⁸ and treat the extended, limbless part as a proboscis. *Halluciginia*⁶, has a round head

and probable eyes spot on it^{18, 31}; here we code the proboscis as absent.

2. Oral papillae

0 absent

1 present

Oral papillae are a unique feature of modern onychophorans. *Aysheaia*⁴ also bears three finger-like projections (also scored here as papillae) that surrounded the mouth. The poor preservation of *Xenusion*¹⁴ and *Hadranax*²⁶ makes it difficult to determine whether or not oral papillae were present.

3. 'Peytoia'-like oral structures

0 absent

1 present

This character refers to the mouth parts of the anomalocaridids and the circumoral plates of *Pambdelurion*³² and *Megadictyon*¹².

4. A set of anterior appendages ventrally at the base of the head

0 absent

1 present

This refers to a slightly different number of appendage pairs in the head region in front of the most anterior pair of sclerites of lobopodians, e.g. *Hallucigenia*⁶ with two pairs, *Cardiodictyon*^{6, 30} with at least one pair. Although *Onychodictyon ferox* doesn't show any sign of anterior appendages, *Onychodictyon gracilis* shows one pair³³, so here we code this character as 1.

5. Frontal/great appendages

0 absent

1 present

This indicates the anteriormost head appendages of the lobopodians *Kerygmachela*^{9,10}, *Pambdelurion*³², *Jianshanopodia*¹³, *Megadictyon*¹² and *Aysheaia*⁴, the anomalocaridids³⁴, and the ‘short’ great appendages of *Leanchoilia*³⁵. Whether there is a pair of frontal appendage in *Fuxianhuia*³⁵ has proved controversial. Some regard the structures thought to be a pair of frontal appendages as gut diverticulae instead³⁶,³⁷. Strong support for these structures being appendicular is provided by Scholtz and Edgecombe³⁸ and Budd³⁹. Here we accept the latter view and code character state 1 for *Fuxianhuia*.

6. Position of frontal appendage

0 lateral

1 latero-ventral

2 ventral

7. Arthropodized frontal appendage

0 absent

1 present

Character state 0 denotes for the frontal appendage of *Opabinia*⁴⁰, *Kerygmachela*^{9,10}, *Pambdelurion*³², *Jianshanopodia*¹³, *Megadictyon*¹² and *Aysheaia*⁴, that they are annulated, not arthropodized or sclerotized. For the anomalocaridids, including *Hurdia*⁴¹ and *Schinderhannes*²⁴, the frontal appendages are considered to be arthropodized, or at least cuticularized (if not sclerotized to some extent).

8. Frontal appendage structure

0 robust with at least one terminal spine and one joint, and fewer than 4 lateral spines

1 more than 4 spines developed along inner margin

This feature distinguishes the anomalocaridid-like great appendage (state 1) from the ‘short’ great appendages of *Leancoilia*³⁵ and *Fuxianhuia*³⁵.

9. Body size

0 normal

1 giant (>20cm)

2 small (<1cm)

This character recognizes the different sizes of the animals. Giant refers to the large size of the lobopodians *Xeunsiion*¹⁴, *Hadranax*²⁶, *Pambdelurion*³², *Jianshanopodia*¹³, *Megadictyon*¹² and the anomalocaridids. Small size refers to, e.g., Tardigrada and the lobopodian *Orstenotubulus*¹⁶.

10. Distinct head

0 absent

1 present

This character indicates that a head is clearly distinguishable from a trunk.

11. Bipartite trunk expressed via the appendages

0 absent

1 present

This character indicates that the trunk of the lobopodians, Collins’ monster⁴², *Miraluolishania*¹¹ and *Diania* is bipartite, based on the form and orientation of the

two batches of appendages.

12. Mouth position

0 terminal

1 ventral

13. Eyes

0 absent

1 present

14. State of the eyes

0 ocellus-like or pigment spots

1 compound / ommatidial-type

This character distinguishes the ocelli of the onychophorans and tardigrades from the compound and stalked eyes of some stem- and crown- group arthropods.

Miraluolishania, bears small eyes with a miniscule lens⁴³, which resembles the ocelli of onychophorans and here we code the state as 0. *Halluciginia* and *Cardiodictyon* possess similar eyes to *Miraluolishania*, they both are coded as 0 for this character⁴⁴.

With respect to the eyes of *Luolishania*⁴⁵ and the doubts of Ma *et al.*¹⁸ about *Miraluolishania* and *Luolishania* being synonyms, Liu *et al.* clarified this problem in 2008⁴⁶ and here we prefer to maintain them here as independent taxa. The character states of *Luolishania* are thus based on features of the holotype of *Luolishania*⁴⁵.

15. Antennae/Antenna

0 absent

1 present

16. Trunk limbs

0 absent

1 present

This character refers to a series of repeated, paired, latero-ventral or ventral locomotory limbs of any form. The presence of lobopod limbs in *Opabinia* is a controversial issue. Serially repeated reflective triangular structures originally thought to be gut diverticulae or musculature were regarded as lobopod limbs by Budd⁴⁷ based on their morphology and taphonomy, while Zhang and Briggs⁴⁸ explained these triangular structures as gut diverticulae based on element mapping. Whether *Opabinia* bears lobopodous walking limbs or gut diverticulae is still a controversial issue, here we coded this character as ?. Current study indicates that there are no walking limbs in *Anomalocaris*^{49,50}, *Hurdia*⁴¹ or *Laggania*⁵⁰.

17. State of the trunk limbs

0 lobopod

1 arthropod

This character distinguishes the jointed limbs of *Diania*, *Schinderhannes*²⁴ and euarthropods from the lobe-like limbs of lobopodians.

18. Trunk limbs with appendiculae or branches

0 absent

1 present

This character refers specifically to the lobopodian *Onychodictyon* which has two rows of small and relatively soft appendiculae (i.e. non-spinous projections) that run

along the inner and outer margins of limbs^{6, 30, 33}. We are not convinced by previous interpretations of appendicules being present on the limbs of other lobopodians, as per character 29 of the *Hurdia* description⁴¹. Their interpretations seem to be based on a misunderstanding of appendiculae as spines. Compared to spines, appendiculae are invariably quite soft and do not end in a sharp point (Fig 2C in Liu *et al.*³³).

*Jianshanopodia*¹³ and *Megadictyon*¹² also bear tree-like or lamellate-like branches on the dorsal surface of the limbs similar to, and potentially homologous with, appendiculae.

19. Trunk limbs with spines/papillae

0 absent

1 present

Unlike the appendiculae/branches on the limbs of *Onychodictyon*, *Jianshanopodia* and *Megadictyon* (see above), spines/papillae on the limbs are observed in *Miraluolishania*¹¹, *Diania*, *Aysheaia*⁴, *Xenusion*¹⁴, Collins' monster⁴², Onychophora and Tardigrada.

20 Terminal limb claws

0 absent

1 present

The poor preservation of *Xenusion*¹⁴, *Kerygmachela*⁹ and slightly superficial description of the Collins' monster⁴² makes it difficult to determine whether terminal limb claws were present here or not.

21. More than 2 claws on limbs

0 absent

1 present

The lobopodian *Cardiodictyon* is reported to bear two curved, pointed claws⁶; alternative ideas indicate that there are four or five terminal claws in *Cardiodictyon*^{5, 30}. In light of the controversy surrounding the number of terminal claws in *Cardiodictyon*, we have coded this state as ?

The holotype of *Luolishania*⁴⁵ indicates three or more claws per limbs. All the specimens of *Miraluolishania* suggest unquestionably two claws terminally per limb^{11, 46}.

22. Lateral lobes

0 absent

1 present

This character refers to the body extending laterally into imbricated, unscleerotized flaps, which are expressed clearly in anomalocaridids and some lobopodians. In *Hurdia*⁴¹, the lateral lobes are not as prominent as in other anomalocaridids, but still visible. The condition in *Schinderhannes*²⁴, with wing-like head appendages, is considered not to be homologous with the lateral lobes of anomalocaridids and some lobopodians.

23. Posterior tapering of lateral lobes

0 absent

1 present

This character is prominent in *Anomalocaris*^{49, 50} and *Laggania*⁵⁰, while other

lobe-bearing taxa bear a more even body outline.

24. Pro-biramous limbs/both a lateral lobe and a lobopod being present

0 absent

1 present

This character refers specifically to the presence of lateral lobes plus the lobopodous limbs of *Kerygmachela*^{9, 10} and *Pambdelurion*³², where it has been suggested that these two structures could have united during arthropodisation to form the biramous limb (see below) by Budd¹⁰.

25. Biramous limbs

0 absent

1 present

This character refers explicitly to the biramous condition seen in the ground pattern of the euarthropods, with a basal element giving rise to two branches.

26. Multisegmented endopod

0 absent

1 present

This character refers to the number of endopod segments in the biramous limbs. *Schinderhannes*²⁴, with about 3 or more podomeres, is coded as state 0.

27. Sclerotized tergite

0 absent

1 present

A hard, articulated tergal exoskeleton is found only in the upper stem- and crown-

group arthropods. The bodies of *Diania*, anomalocaridids⁵⁰ and *Opabinia*⁴⁷ were probably not sclerotized, based on the observation of soft-deformation and no signs of brittle breakage.

28. Trunk annulation

0 absent

1 present

This character refers to the repeated superficial ring structures of lobopodians and onychophoran bodies. Some tardigrade taxa⁸ have ring-shaped wrinkling in between the dorsal shields and legs, but this is not interpreted here as the same structure as the annulations of lobopodians and onychophorans.

29. Heteronomous annulation

0 absent

1 present

Heteronomous annulation means that annulation differs between segments. This is usually considered as a more derived character than homonomous annulation.

30. Trunk with plates or nodes

0 absent

1 present

A variety of plates or nodes are seen in armoured lobopodians, onychophoran and tardigrade bodies.

31. Plates or nodes with elongated spines

0 absent

1 present

This character refers to elongated spines protruding from the plates in some lobopodians, such as *Halluciginia*⁶ and *Onychodictyon*^{6,33}

32. More than 2 plates or nodes on each trunk segment

0 absent

1 present

33. 11-segmented trunk

0 absent

1 present

This character refers to a ‘central body of 11 segments’, which exclude the tail and head segments of *Anomalocaris*.

34. Gut with diverticulae

0 absent

1 present

This character refers to midgut glands notably in *Leancoilia*⁵¹, *Laggania*³⁴, *Pambdelurion*³², *Jianshanopodia*¹³ and *Megadictyon*¹². For *Opabinia*, we coded this character here as ? (See comments for character 16).

35. Posterior protrusion

0 absent

1 present

This character indicates that the last pair of limbs and/or lateral lobes is not terminal.

36. Tail spine

0 absent

1 present

Long tail spines occur in *Kerygmachela*⁹, *Anomalocaris*⁴⁹ and *Schinderhannes*²⁴. *Opabinia*⁴⁸ and *Fuxianhuia*³⁵ also possess tail spines, although admittedly these are much shorter than those of *Anomalocaris*, *Kerygmachela* and *Schinderhannes*.

37. Tail composed of multiple flaps

0 absent

1 present

Three paired tail flaps occur in *Anomalocaris*⁴⁹ and *Opabinia*⁴⁸. A single pair of tail flaps is visible in *Jianshanopodia*¹³, *Hurdia*⁴¹ and *Schinderhannes*²⁴. The posterior region of *Pambdelurion*³², *Megadictyon*¹² and *Hadranax*²⁶ is unknown.

38. Conspicuous, unpaired genital opening

0 absent

1 present

This character refers to the slit-like unpaired opening observed in *Orstenotubulus*¹⁶, which is probably equivalent to the gonopore of Onychophora and cloaca of Tardigrada.

Comments on the results of the phylogenetic analysis

The resulting consensus tree supports previous contentions⁹⁻¹² that lobopodians are not a monophyletic clade, but that they can be broadly divided into at least two major lineages. One contains the bulk of the lobopodians, and includes the crown-group Onychophora and its sister taxon, the eyed lobopodian *Miraluolishania*. The other appears to be part of the arthropod stem-group and includes animals like the anomalocarids and various lobopodians preserving, e.g., gill flaps (*Kergymachela*) – or in the present case with putative jointed appendages (*Diania*).

In fact it is this apparent mosaic of characters which makes reconstructing the arthropod stem so challenging. Different taxa preserve different components of the eventual arthropod ground pattern, but the known fossil record does not, presently, yield a clear scenario of stepwise character accumulation. *Diania* is a prime example of this. It resolves here in a derived position in our analysis based primarily on the presence of jointed trunk appendages (Fig. S1: box 23); a key arthropod character and the one which gives the group its name. Despite this, it lacks the eyes, gill flaps or large frontal appendages of other putative stem-arthropod taxa, which in our analysis resolve more basally due to the absence of jointed legs.

In this context we concede that the most problematic part of our strict consensus tree is the fact that the somewhat simply constructed and worm-like *Diania* resolves between Radiodonta (i.e. *Anomalocaris* and similar forms) and *Schinderhannes*; despite the latter taxa both looking rather similar and sharing potential apomorphies in the form of a radial mouth and the large, grasping anterior appendages. The characters

responsible for our results are the fact that the Radiodonta do not preserve any trunk appendages (Fig. S1: box 21), while *Diania* and *Schinderhannes* have jointed trunk appendages; a character which they share with arthropods, as noted above. In the original *Schinderhannes* description these trunk appendages were also interpreted as biramous (Fig. S1: box 24) – the authors themselves noting that the fossil preserved an unusual combination of anomalocaridid and euarthropod characters – and this begs the question whether arthropodan trunk limbs were part of the radiodontan ground plan, only to be lost in fossils such as *Anomalocaris* and/or outgroups like *Opabinia*.

In such a scenario, the derived position resolved here for *Diania* could turn out to be an artifact, and our fossil might instead occupy a key position, albeit slightly further down the tree where it reflects a grade of organization where truly jointed appendages first made an appearance. Although some authors have recovered radiodontans as paraphyletic, forming a successive series of sister clades to the Arthropoda, one could envisage less specialized *Diania*-like animals – with simple jointed legs – yielding a lineage leading to the rather specialized Radiodonta (+ *Schinderhannes*?) and another leading to Arthropoda *sensu stricto*. Where the gilled or eyed lobopodians fit into this scenario is a moot point, and exploring such hypotheses further would be premature, as new finds from the Cambrian in particular continue to provide new data. *Diania* is nevertheless important in that it shows that there are lobopodians to be discovered which can have a bearing on our understanding of the early phases of arthropod evolution. It is also the closest thing we have to the proverbial ‘worm with legs’ which was traditionally envisaged as an ‘ancestral’

arthropod.

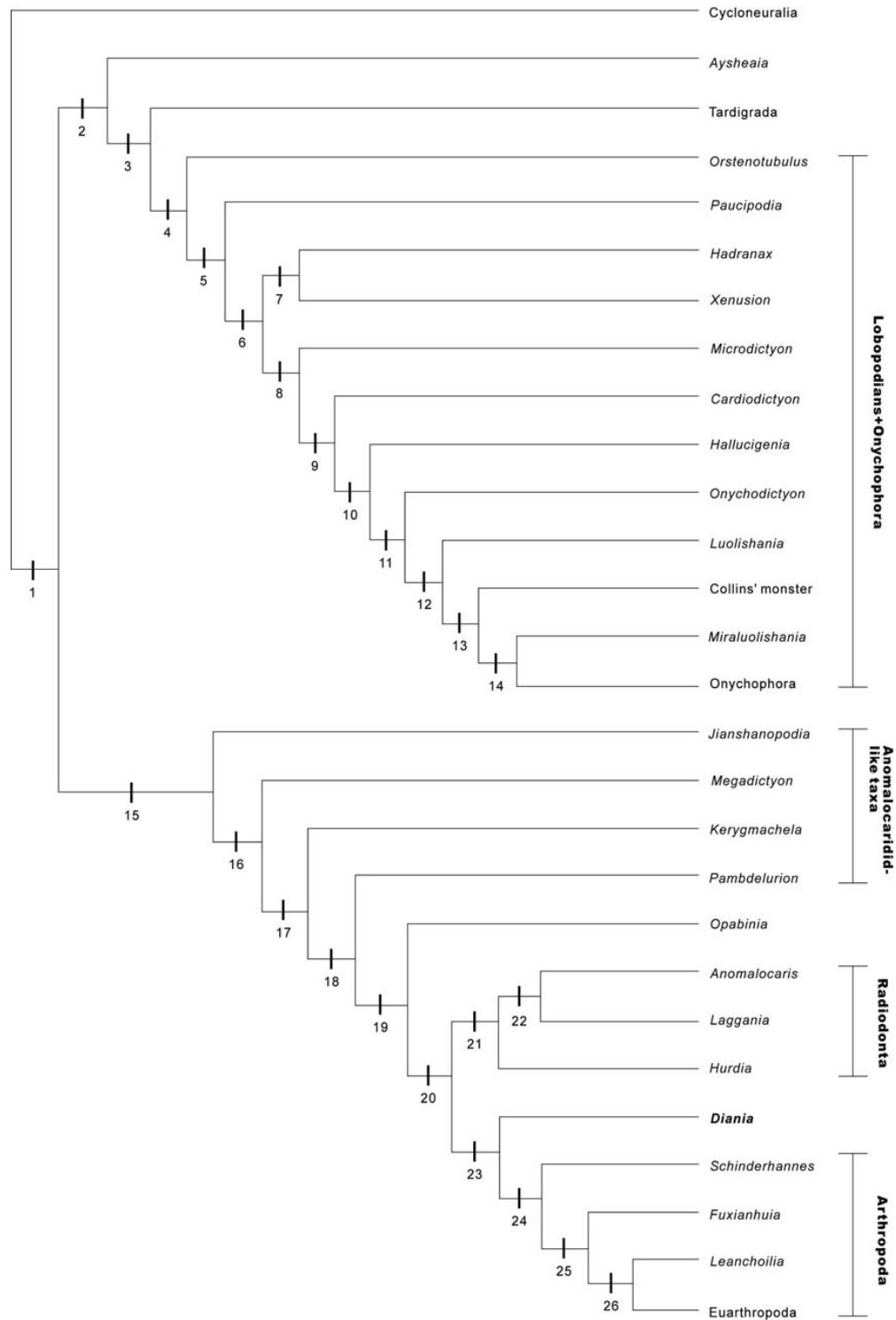


Figure S1. Cladistic analysis of Cambrian lobopodians and some arthropods showing character optimizations. Strict consensus of three trees found using branch and

bound search under implied weights ($k=2$). Tree length 130. Character states: 1. Homonomous annulation, terminal mouth. 2. Uniramous lobopod limbs, undifferentiated head region. 3. Small size, genital opening. 4. Limbs of subequal lengths along trunk, without differentiation. 5. Loss of small size. 6. Enlarged nodes or plates on the body. 7. Large size, large nodes on the trunk, relatively wide, well-defined trunk annulations, lack of claws. 8. Terminal claws, simple eyes? 9. Differentiation of head from body, a set of anterior appendages ventrally at the base of the head. 10. Elongate spine with plate-like armour on the trunk and the shape and size of spines variable. 11. Heteronomous annulation. 12. Loss of anterior appendages ventrally at the base of head. 13. Bipartite trunk expressed in the appendages. 14. Antennae/antenna. 15. Specialization and differentiation of limbs, such as frontal appendages or trunk limbs. 16. Lobe-like trunk limbs without spines or tubercles. 17. Trunk exits as lateral lobes. 18. Oral structure like 'Peytoia' or proboscis. 19. Eyes present?, terminal protrusion or differentiation of trunk to form tail flap. 20. Arthropodization of appendages. 21. Trunk limbs absent. 22. Posterior tapering of lateral lobes. 23. Loss of lateral lobes and trunk limbs jointed. 24. Biramous limbs and hard, articulated tergal exoskeleton. 25. 'Peytoia'-like mouth structures and proboscis absent; short great appendage style. 26. Protopodites with gnathobasic endites.

Table S1. Character matrix used for phylogenetic analysis of Cambrian lobopodians and arthropods.

| Characters: | 1-5 | 6-10 | 11-15 | 16-20 | 21-25 | 26-30 | 31-35 | 36-38 |
|------------------------|-------|-------|-------|-------|-------|-------|-------|-------|
| <i>Cycloneuralia</i> | 100-- | ---?0 | -00-0 | 0---- | -0--- | -0101 | 010-- | 000 |
| <i>Paucipodia</i> | 10000 | ---00 | 000-0 | 10001 | 00-00 | -0100 | --001 | 000 |
| <i>Microdictyon</i> | 10000 | ---00 | 000-0 | 10001 | 00-00 | -0101 | 00001 | 000 |
| <i>Hallucigenia</i> | 00010 | ---01 | 00100 | 10001 | 00-00 | -0101 | 10001 | 000 |
| <i>Cardiodictyon</i> | 00010 | ---01 | 00100 | 10001 | ?0-00 | -0101 | 00001 | 000 |
| <i>Onychodictyon</i> | 00010 | ---01 | 000-1 | 10101 | 00-00 | -0111 | 10000 | 000 |
| <i>Luolishania</i> | 00000 | ---01 | ?0??? | 10001 | 10-00 | -0111 | 01001 | 000 |
| <i>Miraluolishania</i> | 00000 | ---01 | 11101 | 10011 | 00-00 | -0111 | 10001 | 000 |
| <i>Jianshanopodia</i> | 00001 | 10111 | 000-0 | 10100 | -0-00 | -0110 | --?11 | 010 |
| <i>Megadictyon</i> | 00101 | 10111 | 010-0 | 10100 | -0-00 | -0110 | --?1? | ??? |
| <i>Diania</i> | 10000 | ---00 | 100-0 | 11011 | 00-00 | -0101 | 00001 | 000 |
| <i>Aysheaia</i> | 11001 | 00100 | 000-0 | 10011 | 10-00 | -0101 | 01000 | 000 |
| <i>Xenusion</i> | ????? | ??? | 0???? | 1001? | ?0-00 | -0101 | 1000? | ??0 |
| Collins' monster | 00000 | ---0? | 1???? | 1001? | ?0-00 | -0111 | 1000? | 000 |
| <i>Orstenotubulus</i> | ????? | ??? | 0???? | 1001? | ?0-00 | -0101 | 10?0? | ??1 |
| <i>Hadranax</i> | ????? | ??? | 0???? | 10010 | -0-00 | -0101 | 01?0? | ??? |
| <i>Kerygmachela</i> | 00001 | 00101 | 00?0 | 10000 | -1010 | -0111 | 01101 | 100 |
| <i>Pambdelurion</i> | 00101 | 10111 | 010-0 | 10000 | -1010 | -0110 | --11? | ??? |
| <i>Opabinia</i> | 00001 | 20101 | 01110 | ????? | ?10?0 | -00-0 | --0?1 | 110 |
| <i>Anomalocaris</i> | 00101 | 21111 | 01110 | 0---- | -1100 | -00-0 | --111 | 110 |
| <i>Laggania</i> | 00101 | 21111 | 01110 | 0---- | -1100 | -00-0 | --110 | 000 |
| <i>Hurdia</i> | 00101 | 21111 | 01110 | 0---- | -1000 | -00-0 | --0?1 | 010 |
| <i>Schinderhannes</i> | 00101 | 21101 | 01110 | 11000 | -0-01 | 010-0 | --001 | 110 |
| <i>Fuxianhuia</i> | 00001 | 21001 | 01111 | 11000 | -0-01 | 110-0 | --011 | 100 |
| <i>Leanchoilia</i> | 00001 | 21001 | 01110 | 11000 | -0-01 | 110-0 | --111 | 000 |
| Onychophora | 01000 | ---01 | 01101 | 10011 | 00-00 | -0101 | 01001 | 001 |
| Tardigrada | 00000 | ---20 | 00100 | 11011 | 10-00 | -00-1 | 00000 | 001 |
| Euarthropoda | 00000 | ---?1 | 01111 | 11001 | ?0-01 | 110-0 | --?11 | ?00 |

Character matrix consists of 38 characters and 27 taxa. *Cycloneuralia* was used as the out group. Uncertain characters are coded with question mark (?). Characters that are not applicable to certain taxa are coded with (-).

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