

Supplementary information to Dong *et al.* 'Fossil embryos from the Middle and Late Cambrian of Hunan, South China'

Notes on the interpretation of anatomy

The length of the animal was calculated by dividing the average surface area of annulae ($23\mu\text{m} \times 185\mu\text{m} = 3634\mu\text{m}^2$) into the area of the sphere ($4 \times \pi \times 200\mu\text{m}^2 = 502655\mu\text{m}^2$) to give the number of annulae (138.32), and multiplying this figure by the narrow width of each segment, which gives $3181.361\mu\text{m}$. Thus, the average size of an unwound embryo is approximately $3180\mu\text{m} \times 23 \mu\text{m}$.

Cladistic analysis

Data

This analysis is based in large part on the datamatrix presented in ref¹, but modified and extended to encompass gastrotrichs, nematodes, nematomorphs, and arthropods, utilising characters in refs²⁻⁵, as well as character states from the primary literature and personal observations.

Character definitions

1. Introvert invaginable: absent (0), present (1)
2. Degree to which the introvert can be invaginated: partially invaginable (i.e., part of zone 1) (0), completely invaginable into the trunk (i.e., to the base of zone 1) (1).
3. Zone I: unarmed (0), armed (2).
4. Arrangement of zone I armature: regular or irregular quincunxes (0), parallel longitudinal rows (1).
5. Pentaradial arrangement of zone I armature: absent (0), present (1).
6. Morphology of zone 1 armature: papillae (0), simple spines (1), hooks or spinose hooks (2), conical scalids (3), telescopiform scalids (4), curved scalids and dentoscalids (5), complex scalids (6), glandular scalids, trifid spines, sensory spines, and double, tentaculite scalids (7), scalids with pectinate hood (8), spinoscalids and clavoscalids (kinorhynchs and lorificerans) (9).
7. Number of elements in the anteriormost circlet of zone 1 armature: $>6 \leq 20$ (0), 25 (1), more than 25 (2), 6 (3).
8. Sequence of zone 1 elements: elements as a single series (all elements identical or with differing morphologies) (0), elements organised into two or more transverse bands or series, possibly with different element morphologies within each series, but the sequence of morphologies being comparable between subsequent series (1).
9. Basal circlet of zone 1 armature separated from more anterior by a constriction (as in lorificerans) or by insertion of longitudinal or circular muscles (kinorhynchs): absent (0), present (1).
10. Zone II: unarmed (0), armed (1).
11. Number of elements in the proximal circlet of zone II: numerous (more than eight) (0), eight (1), less than eight (2).
12. Zone III: unarmed (0), armed (1).
13. Number of circlets of zone III armature: one to four (1), six to eight (2), sixteen or more (3).
14. Morphology of proximal circlets of zone III armature ("teeth"): absent (0), spines or papillae (1), multispinose (2), multispinose but massively reduced (3), hooks (4), conical with a fringe of spines (5), sclerotized trabeculae (6), pectinate (7), conical papillae terminating in a long spine (prickle) (8), oral stylets (9).
15. Morphology of middle circlets of zone III armature (teeth): absent (0), spines (of any length) or papillae (1), multispinose (reduced or otherwise) (2), pectinate (3).
16. Morphology of the distal circlets of zone III armature (teeth): absent (0), spines (of any length) (1), multispinose (reduced or otherwise) (2), pectinate (3).
17. Number of elements in first circlet of pharyngeal armature (base of zone III): first circlet of numerous elements (more than 10) (0), first circlet of 10 elements (1), first circlet of 5 elements (2).
18. Number of proximal, pentagonal circlets in zone III of the proboscis: none (0), five (1), six (2), seven (3).
19. Width of zone III relative to zone II: zone III less than twice the width of zone II (0), zone III equal to or greater than twice the width of zone II (1).

20. Width of the distal portion of zone III: distal zone III parallel to proximal zone III or tapering gradually (0), distal zone III expanded into a bulb (1).
21. Eversibility of zone III: zone III completely eversible (0), zone III completely eversible, but eversible beyond the proximal teeth (1), zone III normally eversible only as far as the proximal teeth (2).
22. All zone III elements of approximately equal size (0), zone III elements decreasing regularly in size from the posterior to the anterior (anteriormost elements less than half the size of the posteriormost) (1).
23. Surface of trunk cuticle: smooth and unannulated (0), annulated (1).
24. Number of trunk annuli: 7-11 (0), 30-50 (1), 90-120 (2), 160 or more (3).
25. Trunk spines, fine spines, or setae: absent (0), present (1).
26. Trunk papillae: absent (0), present (1).
27. Trunk sclerites: absent (0), present (1). Although *Louisella* exhibits patterns of trunk tubercles comparable to the palaeoscolecids, it is far from certain that these are mineralised; originally mineralised and tissues (and those presumably heavily cuticularised) are usually preserved in relief in the Burgess Shale and in Burgess Shale-type preservation.
28. Trunk tumuli: absent (0), present (1).
29. Trunk tubuli: absent (0), present (1).
30. Flosculi, N-flosculi or sensory spots: absent (0), present (1).
31. Posterior hooks: absent (0), present (1).
32. Posterior ring papillae: absent (0), present (1).
33. Eversible bursa: absent (0), present (1).
34. Position of the anus: anus terminal, whether within a bursa or otherwise (0), anus in posterolateral or posteroventral surface of the abdomen (1).
35. Posterior tubuli or setae: absent (0), present (1).
36. Caudal appendage(s): absent (0), present (1).
37. Division of caudal appendage(s) or tail: undivided (0), pseudosegmented (1)
38. Caudal appendage vesiculae: absent (0), present (1).
39. Polythyridium: absent (0), present (1).
40. Nucleation of "peritoneal" membrane: membrane without nuclei or simply with amoebocytes in association with the surface (0), membrane containing scattered nuclei (1).
41. Developmental mode: direct (0), biphasic (1).
42. Loricata stage: absent (0), present (1).
43. Cuticle containing collagen: absent (0), present (1). *Palaeoscolex* is coded present on the basis of the presence of cross-helicoil fibres underpinning the cuticle of *Gamoscolex*, a taxon that differs from *Palaeoscolex* only on the basis of cuticular plate ornamentation. The position and arrangement of the fibres is entirely consistent with the cuticular collagen of nematomorphs and nematodes.
44. Moulting cuticle: absent (0), present (1).
45. Scalids (non-specific and *sensu lato*, including both scalids and presumed scalid derivatives): absent (0), present (1).
46. Extent of scalid cuticularization: scalid composed exclusively of cuticle (0), cuticle limited to a thin outer covering (1). Schmidt-Rhaesa³ has demonstrated that, in comparison to the scalids of Scalidophora (Kinorhyncha+Loricifera+Priapulida), the scalids of nematoids (Nematoda+Nematomorpha) are composed exclusively of cuticle. The collapse and folding of the scalids in *Markuelia* indicates that they are hollow structures and, thus, not wholly composed of cuticle.
47. Terminal mouth: absent (0), present (1).
48. Mouth cone: absent (0), present (1). The eversible (though not necessarily inversible) upstanding anterior limit of the pharynx, its presence in *Markuelia* is inferred by comparison of the mouth to the mouth cone of priapulids (e.g. Lemburg⁹, fig. 1B) which is structurally very similar.
49. Non-inversible mouth cone: absent (0), present (1).
50. Division of the body into a distinct proboscis and abdomen in juvenile/larva: absent (0), present (1).
51. Division of the body into a distinct proboscis and abdomen in adult: absent (0), present (1).
52. Introvert: absent (0), present (1).
53. Helicoil collagen in cuticle: absent (0), present (1).

54. Hexaradial arrangement of armature: absent (0), present (1). Characters 51 and 52 are distinguished, rather than reduced to a single binary character, because although it is possible to resolve that *Markuelia* does not possess hexaradial armature, it is not possible to determine whether or not they exhibit a pentaradial arrangement of armature.
55. Circum-oral structures: absent (0), present (1).
56. Circular body musculature: absent (0), present (1). Circular body musculature is present in all taxa of nemathelminthe grade except nematodes and nematomorphs, and its absence has been considered both secondary and a synapomorphy of Nematoida³.
57. Ventral nerve cord unpaired throughout its length: absent (0), present (1). Living priapulids possess unpaired ventral nerve cords, while gastrotrichs, onychophorans and loriciferans possess ventral nerve cords that are paired throughout their length, and the ventral nerve cords of nematomorphs and nematodes divide at points along their length^{3,7}; the situation in kinorhynchs is unresolved (paired according to ref⁸, unpaired according to ref⁹). The condition in *Ottoia* is common to extant priapulids¹⁰.
58. Ventral nerve cords merge caudally: absent (0), present (1).
59. Dorsal nerve cord unpaired: absent (0), present (1).
60. Cloaca in both sexes: absent (0), present (1).
61. Protonephridia: absent (0), present (1). Protonephridia are considered an apomorphy of the Bilateria¹¹ and are present in gastrotrichs, kinorhynchs, loriciferans and extant priapulids, but absent, presumably secondarily, from onychophorans, nematodes and nematomorphs.
62. Protonephridia flow into the gonoduct and/or are integrated into the gonad (= urogenital system): absent (0), present (1). Lemburg⁴ recognised this as a synapomorphy of loriciferans and extant priapulids.
63. Urogenital system attached to the body wall by a ligament: absent (0), present (1). Lemburg⁴ recognised this as a synapomorphy of loriciferans and extant priapulids.
64. Spermatozoa with a flagellum: absent (0), present (1). The presence of a flagellum in spermatozoa is a metazoan symplesiomorphy, but a flagellum is lacking from the spermatozoa of nematodes and nematomorphs³.
65. Locomotory cilia: absent (0), present (1). The presence of locomotory cilia is a symplesiomorphy of the clade, lost in onychophorans, nematodes, nematomorphs, kinorhynchs, loriciferans, and extant priapulids⁵.
66. Endocuticle containing chitin: absent (0), present (1).
67. Circumpharyngeal brain: absent (0), present (1).
68. Brain with anterior-posterior sequence of pericarya – neuropil – pericarya: absent (0), present (1). Lemburg⁴ recognised this as a synapomorphy of Introverta (Nematoda+Nematomorpha+Kinorhyncha+Loricifera+Priapulida).
69. Apical part of the brain composed only of Perikarya (rather than as a sequence of pericarya – neuropil - perikarya): absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of (extant) Eupriapulida.
70. Two rings of introvert retractors attached through the collar-shaped brain: absent (0), present (1). Proposed by Nielsen⁵ as a synapomorphy of kinorhynchs, loriciferans and extant priapulids.
71. High aspect ratio of body length to width in adult: absent (0), present (1).
72. Zone I armature arranged in rows aligned diagonal to the anterior-posterior axis of the animal: absent (0), present (1).
73. Lorica of the larvae dorso-ventrally flattened (at least in older stages), with 6 lateral plates in-folded accordion-like: absent (0), present (1).
74. Cuticle of the lorica thickened in dorsal and ventral plates (at least) with sculpture of 4-6 longitudinal rows of narrow, rectangular fields: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of (extant) Eupriapulida.
75. Single dorso-median caudal appendage: absent (0), present (1).
76. Pharyngeal nervous system comprised of numerous tooth ganglia connected by a diagonal nerve net: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of (extant) Priapulida.
77. Larvae with six long pharynx retractor muscles: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of (extant) Priapulida.
78. Voluminous primary body cavity: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of (extant) Priapulida.

79. Movement by peristaltic movement of the pharynx/introvert: absent (0), present (1).
80. Adult with pectinate pharyngeal scales: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of Tubiluchidae (*Tubiluchus+Meiopriapululus*).
81. Cone-like protusible pharynx: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of Tubiluchidae (*Tubiluchus+Meiopriapululus*).
82. Introvert 30-50% of body length: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of Megaintroverta (*Priapulopsis+Acanthopriapululus+Priapululus*).
83. Teeth of second circle of the larvae with very small median denticle: absent (0), present (1). Lemburg⁴ recognises the presence of this character as a synapomorphy of Megaintroverta (*Priapulopsis+Acanthopriapululus+Priapululus*).
84. Basal cuticular layer of the adult containing chitin: absent (0), present (1).
85. Pharyngeal lumina: round (0), triradiate (1).
86. Paired, lateral, locomotary appendages: absent (0), present (1).
87. Anterior branched frontal appendages: absent (0), present (1).

Coding strategy

We have adopted a contingent coding strategy wherever applicable. Contingent coding overcomes the limitations of other schemes of character design, such as multistate and strict binary coding, in dealing with inapplicable characters¹²⁻¹³, which is of particular concern in this analysis. Contingent coding has a couple of drawbacks. One is that it requires much more careful analysis of *a posteriori* character changes across trees because inapplicable character states will, nevertheless, be assigned a (meaningless) state by the analysis. Second, we have encountered artificially lower bootstrap and Bremer support indices in contrast with other coding strategies. Third, contingent coding violates the assumption of character independence in cladistic analysis, although in this case the limitation is of more theoretical than practical significance. Given the analytical benefits, these drawbacks, once recognised and controlled for, are of little significance.

Search techniques

Cladistic analyses were carried out using PAUP* 4.0b10¹⁴; branch and bound analyses were undertaken on small partitions of the dataset while heuristic searches (100 replicate random sequence addition with 10 trees retained at each step; steepest descent search option on) were utilised in analysis of larger partitions, and the complete dataset, because of computational limitations. Character evolution was resolved using PAUP* 4.0b10 and MacClade 4.05¹⁵. All characters were unweighted and unordered in the preliminary analyses of the dataset. Gastrotricha was used as an outgroup (notionally designated paraphyletic for PAUP analyses) to root trees. Bremer support values were calculated for each of the nodes using TreeRot 2c¹⁶, and bootstrap values were calculated using PAUP* 4.0b10 (1,000,000 'fast' heuristic search option); these values are presented on the node to which they relate.

In all instances, results from primary unweighted analyses were subjected to *a posteriori* reweighting, where characters are weighted in proportion to their performance in the primary analysis, as measured by the rescaled consistency index. Thus, characters exhibiting a relatively high degree of fit to the tree(s) derived from the primary analysis (and assumed, therefore, to carry more phylogenetic information than those with poor fit) are assigned a relatively high weight; characters exhibiting poor fit to the original tree(s) are assigned a relatively low weight, or even no weight at all. The purpose of a *a posteriori* reweighting is to test for character consistency and character support in the original tree(s), derived from unweighted analysis. If a dataset includes many characters that are a poor fit to the original tree(s), reweighting assigns low or no weight to many characters, and subsequent analysis is likely to increase, rather than decrease the number of competing trees¹⁷; this contrasts with the conventional assumption that a *a posteriori* reweighting is a method for choosing between multiple most-parsimonious trees (e.g. ref¹⁸). Thus, it has been argued¹⁹⁻²⁰ that parsimony analysis requires a *a posteriori* reweighting to achieve self-consistent results, even if the primary, unweighted, analysis produced a single optimal tree. Indeed, it has been contended²¹ that unweighted analyses can be considered only a preliminary and crude estimate of the relative value of the data.

Results and experimental analysis of the dataset

The objective of the analysis was to determine the phylogenetic position of *Markuelia*, not a means to resolve the interrelationships of extant ecdysozoans/introvertans. Thus, an initial analysis included

only extant taxa to determine whether, in the absence of fossil taxa, the resulting hypothesis of relationships concurs with contemporary hypotheses based on comparable datasets. Branch and bound analysis of the dataset yielded a single most parsimonious tree (Fig. Supp1) at 125 steps (Clex [consistency index excluding uninformative characters] 0.7672; RI [retention index] 0.8200; RC [rescaled consistency index] 0.6429) in which all nodes show high statistical support. Two rounds of a *posteriori* reweighting yielded a single tree with the same topology (85.88333 steps; Clex 0.9346; RI 0.9530; RC 0.0.8972).

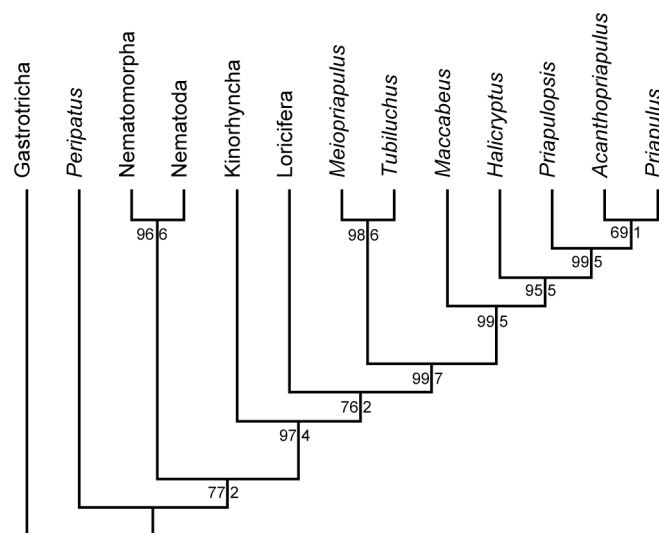


Figure Supp1: Most-parsimonious tree derived from analysis of extant taxa alone. Numeric values to the left and right of each branch are bootstrap and Bremer support values, respectively.

This topology indicates that arthropods and nematoids are successive sister-taxa to Scalidophora; this is common to most analyses based on morphological data^{2,4,22,23} (but not ref²⁴), but contrasts with recent molecular analyses which resolved nematoids and arthropods as sister-taxa^{22,25-28} (but not ref²³); different total evidence analyses contrast in the same way (refs^{23,27} versus refs^{22,24}) in all instances the result is closer to that derived from morphological data, rather than molecular data, alone. The curious topology recently proposed by Nielsen²⁹ resolves nematodes as the sister taxon to priapulids, a hypothesis that is incompatible with existing topologies based on morphological and molecular data alike. The main argument in favour of Nielsen's hypothesis is that it provides for a gradational reduction in segmentation/annulation in the lineage of common ancestors subtending successive sister taxa Annelida> Arthropoda> Kinorhyncha> Priapulida> Nematoda. However, this scenario is complicated by polymorphic character states in Nematoda and by the selectively excluded taxa Loricifera and Nematomorpha. It is further complicated by a consideration of fossil taxa.

Inclusion of *Markuelia* into this analysis resolves its phylogenetic position unequivocally as a sister-taxon to Scalidophora (Fig. Supp2; 127 steps; Clex 0.7542; RI 0.8165; RC 0.6300). Thus, equivocation over arthropod-nematoid-scalidophoran interrelationships is not germane to the affinity of *Markuelia*. All branches are well supported by bootstrap and most are well supported by Bremer Support. The least well supported branch subtends *Markuelia* plus all other scalidophorans, but this topology is fully supported by a *posteriori* reweighting (86.58333 steps; Clex 0.9289; RC 0.9500; RC 0.8894)

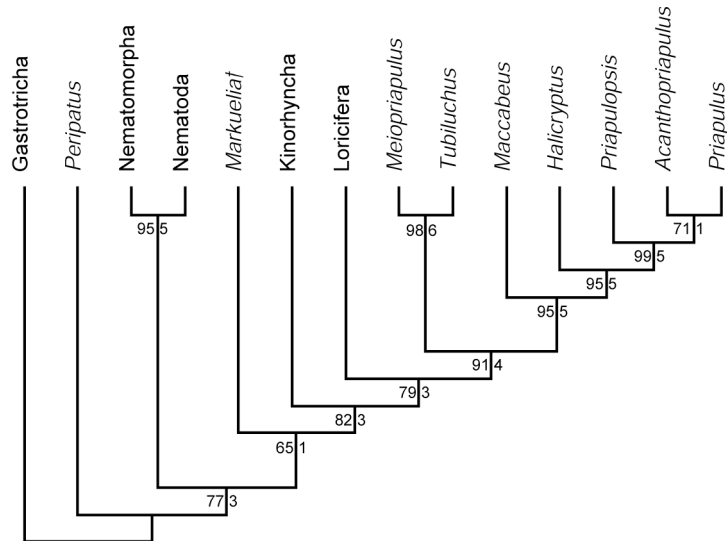


Figure Supp2: Most parsimonious tree derived from analysis of extant taxa and *Markuelia hunanensis*. Numeric values to the left and right of each branch are bootstrap and Bremer support values, respectively. † denotes extinct taxon.

Analysis of all taxa using the heuristic search option yields three equally most parsimonious trees that differ in the relative relationships of *Markuelia* and two Burgess Shale taxa, *Ancalagon* and *Fieldia*, the strict consensus of which leaves their relative relationships unresolved (176 steps; Clex 0.6199; RI 0.7601; RC 0.4794). Few of the branches are supported by bootstrap (an artefact of the coding strategy), although many are well supported by Bremer Support. Successive rounds of *a posteriori* reweighting yields a single most parsimonious tree that is compatible with one of the three competing trees derived from the primary, unweighted analysis (Fig. Supp3; Clex 0.8152; RI 0.8963; RC 0.7402).

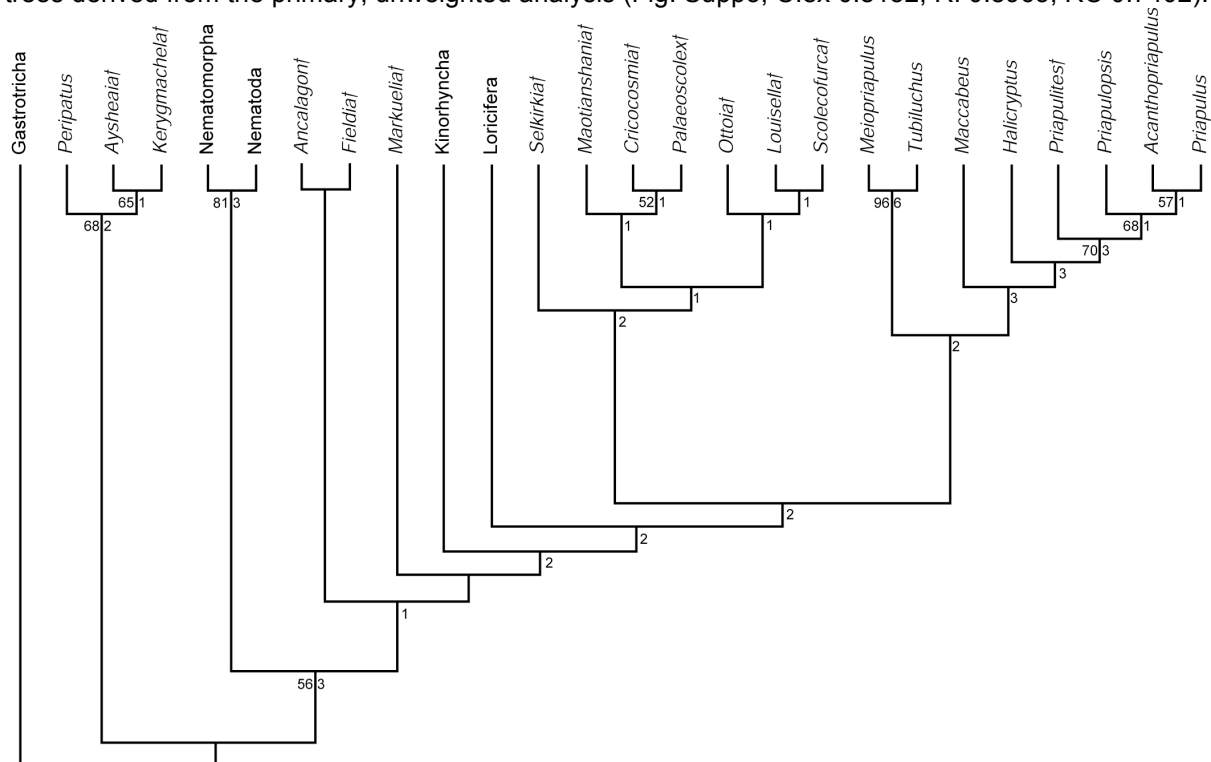


Figure Supp3: Most parsimonious tree derived from analysis of all taxa. Numeric values to the left and right of each branch are bootstrap and Bremer support values, respectively. † denotes extinct taxon.

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Data matrix

† denotes extinct taxon; - denotes inapplicable; ? denotes missing data or unknown; & denotes polymorphic character

Acanthopriapulus	111113100?????????02?11010000010101110111011110111-011100011110111110011111100111000
Ancalagont	0-10120000-11400100020131000000000000--0?????1?1?0?11?01????????????????1??-????000??00
Cricocosmiat	??1??2000????111?010012001010100000--0?????1?1??11??1????????????????1??-????00??00
Fieldiat	??1??2?000-11100000?00-100000000000--0?????1?1?0?11??1????????????????11??-????000??00
Halicryptus	111115100101322122102112100000010110--01110111110111-011100011110111110011-111100001000
Louisellat	10101000010131110011001-11?000001000--0?????1?1?0?11?01????????????????11??-????000??00
Maccabeus	111112&7100111262122&3002012000001100110--00110111110111-011100011110111110011-111100001000
Maotianshaniat	11101?00?13??0?000112001000100000--0?????1?1?0?11?01????????????????11??-????00??00
Meiopriapulus	11111820011127330000100-100111100000--10000111110?11-0111000111101110100---1-11110-1000
Ottoiat	111012200101351&2200110112000000101000--0?????1?1?0?11?01?10?????????????01??-??1?000??00
Palaeoscolex†	??1?????0????111????00013001010100000--0?????1?1?1?0?11101????????????????1??-????000??00
Priapulites†	111113010?????????02?11000000000101000?????1?1?0?11?01????????????????00??1?1?01??00
Priapulopsis	111114110111332111102111010100010101010111011110111-0111000111101111100110111100111000
Priapulus	111113110111322123102111010000010101110111011110111-011100011110111110011111100111000
Scolecofurcat	??1?0?000-13111?011?01000000000?000--0?????1?1??1?0?0????????????????????-????000??00
Selkirkiat	10101120010122220000010-010000000000--0?????1?1?0?11?01????????????????1??-????000??00
Tubiluchus	11111600011128330000100-100111000101001011011110111-0111000111101110100000111111001000
Kinorhyncha	1110190010-119111000200-100001000000--0000011111111-0110?00100101111101---0000000-10&100
Loricifera	11101900111119011010100-000001000000--0011011111111-011000011110111110100-000000001100
Markuelia hunanensis†	??1??1000?????????????12100000100000--?00??1111?1?1?01????????????????11---????00-??00
Nematomorpha	0-1-01300?????????????0&13110000100100--0?10111010-10111100111000001111010---00000000000
Nematoda	0-1-01300?????????????0&13100000000&1000--0?00111010-000&10&11100111000001111010---0000000-0100
Aysheaiat	-----111100000000?0--0?????0-10-000?-1????????????????1-??-????00-??11
Peripatus	-----1?110000000100--0?00010-00-000--1100?000010100-01----000000--1110
Kerygmachelat	-----13110000000?01--0?????0-10-000?-?1????????????????1-??0??00-??11
Gastrotricha	-----0-100000000000--0?00000-10-000--01000010011000--0----000000---100