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A middle Cambrian arthropod with chelicerae and proto-book gills

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SUPPLEMENTARY DISCUSSION

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Systematic palaeontology

Superphylum **Panarthropoda** Nielsen, 1995
Phylum **Euarthropoda** Lankester, 1904
Clade **Cenocondyla** Aria, 2019

Clade **Panchelicerata**, nom. nov.

Derivation of name. From the subphylum Chelicerata Heymons, 1901 and the Greek *πᾶν*, meaning "all, every," for this clade encompasses chelicerates and their stem lineage.

Definition. Total-group Chelicerata excluding Artiopoda (under an Arachnomorpha scenario, see e.g. Aria and Caron 2017b).

Tentative diagnosis. Cenocondylans with the following characters: ground pattern of seven-segmented prosoma, trunk appendages with reduced or vestigial endopods.

Remark. The definition takes precedence over the diagnosis. The current diagnostic characters are based on Aria and Caron (2017b). Their validity depends both on the phylogenetic position of sea spiders and on the morpho-anatomy of other possible non-fossil taxa part of the stem lineage.

Subphylum **Chelicerata** Heymons, 1901

Family **Mollisoniidae** Simonetta and Delle Cave, 1975

Type genus. *Mollisonia* Walcott, 1912.

Other included genera. *Thelxiope* Simonetta and Delle Cave, 1975; *Corcorania* Jell, 1980; possibly *Urokodia* Hou *et al.* 1989.

Remarks. *Mollisonia*, *Thelxiope* and *Corcorania* can be clearly diagnosed by the presence of the following characters: broad, helmet-like head shield bearing wide eye notches; anterior portion of trunk bearing seven free segments extending into short pleurae; posterior trunk segments fused unto a pygidium. *Urokodia* Hou *et al.* 1989 shows notable difference in trunk segment number, but other exoskeletal characteristics (e.g. non-tapering and narrow trunk, cephalon and pygidium of similar size and shape) are strikingly similar to *Mollisonia*, and especially *M. gracilis* (Zhang *et al.* 2002a). A more detailed taxonomic investigation accompanied by a cladistic analysis of these taxa will be required to clarify their affinities. Simonetta and Delle Cave (1975) also erected the order Mollisoniida, but it is uncertain how its diagnosis would differ from Mollisoniidae, or if it is at all needed.

Genus ***Mollisonia*** Walcott, 1912

Type species. *Mollisonia symmetrica* Walcott, 1912 (=*Mollisonia*? *rara* Walcott, 1912).

Other included species. *Mollisonia gracilis* Walcott, 1912 (=*Houghtonites gracilis* Raymond, 1931); *Mollisonia sinica* Zhang *et al.*, 2002; *Mollisonia plenovenatrix* sp. nov.

Diagnosis (emended from Zhang *et al.* 2002). Mollisoniids with the following characters: body 18-segmented (cephalic tagma: 7, trunk: 11, including pygidium: 4), subrectangular in dorsal view and subquadrate in transverse section; head shield with broad ocular notches accommodating large ovoid eyes innervated by three optic neuropils; chelicerae inserted at an inter-ocular position; first three pairs of post-cheliceral appendages are walking legs with differentiated podomeres; posterior three pairs of cephalic limbs bearing gnathobasipods; trunk organized into seven articulating segments and a pygidium formed by the fusion of four posteriormost segments, all bearing limbs; pleurae short and leaf-like; trunk appendages with reduced or absent endopods, and exopods composed of several overlapping lobes, with main, large lobe bearing short lamellae; pygidium subhexagonal, bearing four pairs of marginal spines; segmental boundaries visible in pygidium as paired ridges connected to the marginal spines; pygidium subequal to 1.3 times longer than cephalon.

Remarks: "*Houghtonites*" Raymond, 1931 is here synonymized with *Mollisonia* given that the diagnostic characters of this new genus were derived from an upside-down interpretation of MCZ 1811. Raymond indeed erected the genus *Houghtonites* based on differences in the morphology of the head, but the cephalic spines he described belong in fact to the pygidium (Extended Data Fig. 4). *Houghtonites* is therefore invalid and *M. gracilis* should be upheld. A more comprehensive taxonomic work about the genus *Mollisonia* and its different species will be subject of a different study.

Mollisonia plenovenatrix Aria and Caron, sp. nov.
Figs. 1-2, Extended Data Figs. 1-3
LSID: urn:lsid:zoobank.org:pub:6E2217D1-88C3-4CC7-85B7-F2C8E3477CAA

= *Mollisonia symmetrica* Caron *et al.*, 2014, fig. 3p, q

Etymology. From the Latin *plenus*, meaning "full, plump," owing to the fuller appearance of this species compared to its slenderer relatives; and *venatrix*, meaning "huntress," owing to its presumed predatory life habit.

Material. Holotype ROMIP 65264; Paratypes ROMIP 62978, 65262, 65263, 65266 and 45 additional specimens: 63828.1, 63828.2, 65015, 65265, 65267-65268.1, 65268.2, 65269, 65275-65300, 65303-65312. Most specimens were collected *in-situ* from a ca. five-meter-thick quarry interval (See SI Table).

Occurrence. Cambrian Series 3, Wuliuan Stage, ca. 508 Mya; Marble Canyon (Burgess Shale), Kootenay National Park, British Columbia.

Diagnosis. Compact body aspect in lateral view; cephalic shield bearing short, acute sub-genal spines; well-developed paired dorsal spines on trunk.

Description. *Habitus*. Body size ca. 2.5cm; body 18-segmented (cephalic tagma: 7, trunk: 11, including pygidium: 4), subrectangular in dorsal view and subquadrate in transverse section; pygidium subequal to 1.3 times longer than cephalon.

Eyes. Lateral eyes large (between 1/4th and 1/3rd of cephalic length), elliptical, protruding under the cephalic eye notches, borne by very reduced attachment stalks. Lateral eyes innerved by three contiguous optic neuropils; distalmost neuropil rounded, diameter ca. 1/3 of eye great axis length; medial neuropil ovoid, reaching eye attachment point; third and proximalmost neuropil rounded and similar to distalmost neuropil in size, located within body next to eye insertion. No median eyes.

Cephalon. Head shield formed by the fusion of tergites 1-7, ca. 1/5 of body length, with broad ocular notches over half of length, and well-developed lateral expansions covering the sides of the head; sub-postero-lateral cephalic margins bearing short, acute genal spines; postero-lateral margins smooth; occipital angle ca. 90 degrees in lateral view.

Mouth. Seemingly located very anteriorly, at the level of lateral eye insertion.

Cephalic appendages. Seven pairs of developed cephalic appendages. Pair of short chelicerae (ch) projecting at an anteriormost position, between lateral eyes; insertion possibly para-oral; seemingly composed of an enlarged basal podomere bearing a finger and a small opposing, free finger. Following three pairs of post-cheliceral appendages (c2-c4) heptopodomerous walking legs with differentiated podomeres, ending in sharp, elongate claws; c2 and c4 about the same size, ca. 55% cephalic length; c3 substantially longer, about 80% of cephalic length; podomeres 1 and 2 quadrate, podomeres 3 to 5 (counting proximo-distally) slightly elongate, rectangular in lateral aspect; podomere 6 elongate and tapering distalward, trapezoidal to sub-triangular in shape; in c4, podomere 6 also much longer, ca. twice the length of podomere 5, giving the appendage a distinct lance-like shape; all three pairs inserted up to about midline of cephalic length and projecting ventro-laterally. Posterior three pairs of cephalic limbs biramous; major part of appendages made of well-developed gnathobasipods with toothed, protruding masticatory margins inserted within the posterior half of the cephalic length and projecting antero-medially between c2-c4, reaching

the mouth; small endopods with at least a terminal claw and four short podomeres associated with the gnathobasipods, probably attaching on their proximal sides; presence of small exopods with short podomeres and setose termination, and whose insertion point is unclear; all associated rami mostly concealed under the cephalic shield and projecting medially towards the post-oral area.

Trunk. Trunk organized into seven homonomous articulating segments and a pygidium formed by the fusion of four posteriormost segments, all bearing limbs; free segments bearing short and leaf-like pleurae; segments 2-7 bearing paired sub-triangular dorsal projections. Pygidium subhexagonal, bearing four pairs of marginal spines; first and second pairs short and produced close to each other, past the pygidial mid-length; third pair longer, inserted posteriormost; fourth pair shorter, inserted posteriormost at the same level as the third pair, mesially; pairs 2, 3 and 4 associated with cuticular ridges running posteriad along part of the pygidial length, and which are likely remainders of segmental boundaries; posteriormost segment enclosed between 4th pair of spines; three pairs of dorsal spines similar to those of free segments present on pygidial segments 1, 2 and 3.

Trunk appendages. Appendages on all trunk segments homonomous, and of equal size on trunk segments 1-7; tapering in pygidial segments; formed by large exopods composed of a main rounded lobe bearing thin marginal lamellae and two additional, smaller overlapping lobes, so as to form a complex of flat superimposed circular lobes; first overlapping lobe inserted towards the base of the main lobe, second overlapping lobe inserted slightly above first overlapping lobe; base of whole appendage unknown; endopods reduced or absent.

Gut. Intestinal tract large (ca. 1/3 of body diameter) from about cephalic segment 4 to penultimate pygidial segment. Anus likely located within posteriormost pygidial segment.

Remarks. *M. plenovenatrix* sp. nov. mainly differs from *M. symmetrica* and *M. gracilis* in its stout body aspect and sub-genal spines. The dorsal cuticular projections also seem much more developed than in these other species. Two morphs may be present in our samples, possibly distinguished by the differential development of the dorsal spines. As mentioned above, a more detailed taxonomic investigation will be the subject of a future study.

Additional comments

The redescriptions of *Sanctacaris uncata* (Legg 2014) and *Habelia optata* (Aria and Caron 2017b), which linked the morpho-anatomy of these taxa to that of the early "xiphosurans" *Offacolus kingi* (Sutton *et al.* 2002) and *Dibasterium durgae* (Briggs *et al.* 2012), helped to constrain a "panchelicerate" clade and to draw the stem lineage directly leading to Euchelicerata (sensu Weygoldt and Paulus 1979). The genus *Mollisonia* not only strongly supports these conclusions, but closes the gap between the stem and the crown euchelicerates, shedding light on the origin of several key morphological features characteristic of this group, and showing that early euarthropods with notched head shields and a combination of megacheiran and trilobite-like characters gave rise to chelicerates.

Morphology of fossil and living euchelicerates would predict the plesiomorphic chelicera/chelifore to be composed of three podomeres (Sharma *et al.* 2012). The chelicerae of *Mollisonia*, seemingly

composed of only a peduncle and an articulating claw, do not readily fit this evolutionary pattern, although a few additional podomeres could be concealed taphonomically. It certainly shows, however, that the long multipodomerous chelicerae of *Offacolus* and *Dibasterium* are either an error of interpretation of the three-dimensional models or an autapomorphic condition of these taxa. Chelicerae are also preserved in *Mollisonia gracilis* MCZ 1811 (Extended Data Fig. 4; "*Houghtonites*" Raymond is invalid; see above), but their poor preservation, which makes them look like short antennules, also does not permit a podomere count.

The very anterior, inter-ocular position of the chelicerae also raises the question of the homology of these appendages. A suite of developmental studies have identified chelicerae as belonging to the deutocerebral part of the brain (Telford and Thomas 1998; Mittmann and Scholtz 2003), homologous to mandibulate antennules, a view still contested by some, based on internal morphology (Bitsch and Bitsch 2007), which would see chelicerae as tritocerebral and the deutocerebrum reduced in chelicerates. With respect to other early euarthropods, *Mollisonia*'s chelicerae are not directly comparable structurally or topologically with either the artiopodan antennules or the megacheiran "great appendages." Unexpectedly, they are more similar to the inter-ocular appendage-like protrusions known in *Canadaspis*, which would have a protocerebral origin if hymenocarine antennules are deutocerebral (Briggs 1978; Aria and Caron 2017a; Vannier *et al.* 2018). This would also explain developmental results finding the chelifores of sea spiders to have a protocerebral origin (Maxmen *et al.* 2005). Under the hypothesis of a universally deutocerebral frontalmost appendage, including the megacheiran "great appendage" (Scholtz and Edgecombe 2006), however, the morpho-anatomy of *Mollisonia* supports at least the view that a direct evolution of "great appendages" into chelicerae is unlikely (Aria and Caron 2017b). Because they are small and robust, *Mollisonia*'s chelicerae are already close to the derived condition of xiphosuran and a large number of arachnids, in which these appendages are specialized for manipulation and dissection, rather than the catching of prey (as would be the case for "great appendages"). For these reasons, and given their topology, it seems more plausible that chelicerae originated from more antennular, and thus, sensorial, appendages.

The seven-segmented (or 'octasomitic') head of *Mollisonia* is consistent with previous findings that this tagmatic configuration is plesiomorphic for eucheliceratе (Moore *et al.* 2005; Sutton, *et al.* 2002; Aria and Caron 2017b). The fact that the seventh appendage pair had a fully differentiated gnathobasipod shows that the integration of this segment from the prosoma was accompanied by a complete cephalization. The three pairs of uniramous walking legs are a significant feature, as they represent the first documented step towards the modification of the head as an ambulatory tagma in eucheliceratе, in combination with the reduction of endopods in the trunk—already initiated in habeliids (Aria and Caron 2017b). The retention of anterior cephalic exopods in xiphosurans may mean either that this adaptation remained developmentally labile before the evolution of eurypterids and chasmataspidids, or that xiphosurans are in fact monophyletic, which would conflict with most recent analyses of merostome phylogeny (Lamsdell *et al.* 2015). Our phylogeny favours here the former hypothesis (Fig. 4). The combination of the chelicerae with these three differentiated pairs of uniramous walking legs also corresponds to what would be the ancestral euarthropod tagma, as represented by megacheirans (Chen *et al.* 2004; Haug *et al.* 2012b; Aria *et al.* 2015). It is therefore possible that the early formation of the eucheliceratе head was built upon a drastic expansion of this ground pattern (Aria and Caron 2017b), and retained some of its developmental program, occasionally expressed anatomically.

The trunk limbs of *Mollisonia* are atypical (Fig. 3c). They constitute a deviation from the single posterior lobes described in *Habelia* (Aria and Caron 2017b), while lacking the multi-lamelate structure characteristic of more derived taxa and the operculum regarded as synapomorphy of Euchelicerata (Dunlop 1997; Aria and Caron 2017b). As such, we think that *Mollisonia*'s exopods are an ancestral form of book gills, assembled from a megacheiran-like exopod and two additional lobate exites. This condition would explain for the first time the direct correspondence between the exopods of early euarthropods and the respiratory system of a euarthropod crown group. There is a likely relationship between these tri-lobate exopods and the tripartite exopods of sidneyiids (Stein 2013), emeraldellids (Stein and Selden 2012) and certain trilobites (Zeng *et al.* 2017), which further implies that xenopodans and trilobites did possess active exopodial respiration.

It is also remarkable that *Mollisonia* possess an "artiopodan-like" pygidium. Although this does not, in itself, corroborate the monophyly of Arachnomorpha—this could be an inherited trait from more basal taxa—it does emphasize the close evolutionary history of artiopodan and chelicerates while also supporting the pygidial origin of the limulid thoracetron. The first segment of the pygidium is still somewhat associated with the anterior free tergites, as can be seen from partially disarticulated specimens (Fig. 1e, Extended Data Fig. 2h). This can sometimes give the appearance of an eighth free trunk segment.

The number of trunk segments in *Mollisonia* is therefore 7+4=11. The seventh cephalic / prosomal pair of appendages is arguably integrated originally from the trunk (Aria and Caron 2017b), implying a ground pattern of 12 trunk segments. This trunk configuration is the same as that of cheiromorphs and a number of artiopodans, and phylogenetic proximity strongly suggests that it was inherited from a common ancestor; however, as discussed in the case of habeliidans (Aria and Caron 2017b), this is at odds with cephalic anatomy, involving four segments in cheiromorphs but six (strictly) in habeliidans and *Mollisonia*. This punctualistic pattern seems to find its origin in the plasticity of head tagma length across artiopodans (Lerosey-Aubril *et al.* 2017; Moysiuk and Caron 2019), although it remains developmentally unexplained. It should be noted that, with the same calculation, *Habelia optata* would have an ancestral trunk of 13 segments (1+12), hence an additional segment compared to *Mollisonia* (and Sanctacarididae [the statement "We maintain the family Sanctacarididae erected by Legg and Pates, since 10 trunk segments and a spatulate telson remain diagnostic of *Sanctacaris uncata*, *Utahcaris orion* and *Wisangocaris barbarahardyae*" in Aria and Caron 2017b was an error and should read "11 trunk segments"]). If the alignment of head tagmata is correct, then this supernumerary segment in *Habelia* must have belonged to the trunk.

While optic neuropil remains were identified in other Burgess Shale arthropods (Ortega-Hernandez 2015; Vannier, *et al.* 2018), *Mollisonia plenovenatrix* provides clear evidence of their shape and number for the first time in this Lagerstätte. The presence of three nested optic neuropils stands in contrast to the two neuropils known to innervate extant chelicerate (e.g. Lehmann *et al.* 2016; Lehmann and Melzer 2018, 2013), while fitting with the putative derived condition of pancrustaceans, and especially malacostracans (Strausfeld *et al.* 2016). This condition is also, interestingly, similar to that of *Fuxianhuia* (Ma *et al.* 2012). Although the phylogenetic position of *Fuxianhuia* is debated (Edgecombe 2017), current views place it either as a very basal euarthropod or as a basal mandibulate. In light of the brain morphology of the stem euchelicerate

Mollisonia, this implies that a complex eye innervation made of three optic neuropils is likely ancestral in euarthropods, and convergently simplified in arachnids, myriapods and certain pancrustaceans, thereby emphasizing the importance of visual development in Cambrian environments. There is thus probably also no need to invoke a reduction of primary cone pigment cells at the origin of Euarthropoda (Strausfeld, *et al.* 2016).

The exact phylogenetic origin of Chelicerata still depends on the problematic phylogenetic position of pycnogonids, which is a historical and seemingly intractable issue for this group (Weygoldt and Paulus 1979; Dunlop 2010; Rota-Stabelli *et al.* 2011; Giribet 2018). This, in turn, questions whether chelicerae may have been present in taxa ancestral to *Mollisonia*, considering that the chelate nature of frontalmost appendages in habeliidans remains uncertain (Aria and Caron 2017b). Early larval stages of an upper Cambrian fossil (Waloszek and Dunlop 2002) and an Ordovician species (Rudkin *et al.* 2013) suggest, however, that the pycnogonid cephalon has gone through phases of dramatic segmental reductions, with an original condition of at least five segments, and, consequently, that an ancestral four-segmented head tagma (as coded in our phylogeny), including the first walking leg, may be an incorrect interpretation (Dunlop and Lamsdell 2016). In light of this evidence, a ground pattern of six or seven segments may also be possible, and pycnogonids may therefore lie much more crownward than their "simplified" morpho-anatomy suggests. Such an alternative phylogenetic placement has been found in recent years, although it appears to have been driven by non-cephalic characters (Garwood and Dunlop 2014; Garwood *et al.* 2017). Here, we found Pycnogonida to be basalmost within Panchelicerata, but with relatively low support (Extended Data Fig. 6). Excluding pycnogonids from the analysis alters neither the overall panchelicerate topology nor the placement of *Mollisonia* as sister-taxon to Euchelicerata (Fig. 4a, Extended Data Fig. 6).

We know that *Mollisonia* likely had a global distribution in Cambrian warm seas, since the genus has been found in Utah (Robison 1991; Briggs *et al.* 2008) and China (Zhang *et al.* 2002b) as well as the Burgess Shale. The genus has also been reported from the Fezouata biota in Morocco (Van Roy *et al.* 2015), extending its longevity into at least the Early Ordovician. In addition, a number of other taxa from various Lagerstätten and so far described based only on exoskeletons are arguably related to *Mollisonia*. This includes *Thelxiope* Simonetta and Delle Cave from the Burgess Shale (Simonetta and Delle Cave 1975) and Fezouata (Van Roy *et al.* 2010; Van Roy, *et al.* 2015) biotas. *Thelxiope* has a helmet-like cephalic shield with wide eye notches, seven free thoracic segments and a pygidium, but also an elongate telson and very well-developed dorsal spines, not unlike *Habelia*. It is not clear whether the species from Fezouata is more closely related to *Mollisonia* or *Thelxiope*. Another Early Ordovician taxon, *Corcorania trispinosa* Jell (Jell 1980), shows clear mollisoniid characteristics, viz. broad head shield with wide eye notches, seven free segments in the trunk, and a pygidium, but also atypical development of lateral spines in the cephalon and pygidium. Isolated appendages appear to correspond to cephalic gnathobases with particularly well-developed marginal teeth (fig. 3A-C in the same paper). *Urokodia* Hou et al. from the early Cambrian of South China displays a habitus very similar to *M. gracilis*, with narrow and straight trunk, and cephalon of similar size and shape to the pygidium, but also, surprisingly, a much longer trunk composed of 14 or 15 free segments (Zhang, *et al.* 2002a). Although the systematics and phylogenetic affinities of these taxa remain to be investigated in detail, there is little doubt that, in light of this study, they show that stem euchelicerates were well diversified during the Cambrian and Ordovician.

Character list

Character headings refer to the original publication by [ACX], where X is the corresponding number for that character in Aria and Caron (2017a). Remarks are not carried over here if no change was made. Characters either new since Aria and Caron (2017a), or which have gone through substantial change in overall coding or definition are marked with an asterisk. Some other small corrections were applied to the original matrix but are not reported here in detail.

GENERAL CHARACTERS

[1] Limbs [AC1]
0. Absent
1. Present

[2] External cuticular segmentation [AC2]
0. Absent
1. Present

[3] Type of body segmentation [AC3]
0. Sclerotized
1. Arthrodized (=tergal)

[4] Calcified cuticle [AC4]
0. Absent
1. Present

[5] Visual surface with calcified lenses, bounded by circumocular suture
0. Absent
1. Present

Remark: See Mayers *et al.* (2018, ch. 12).

[6] Holometaboly [AC6]
0. Absent
1. Present

LOBOPODIAN CHARACTERS

[7] External anteriorization restricted to a single pair of frontalmost appendages [AC7]
0. Absent
1. Present

[8] Lobopodous limbs [AC8]
0. Absent
1. Present

[9] Type of main lobopodous trunk limb [AC9]

0. Short, conical, subequal or shorter than trunk width
1. Elongated, slender, longer than trunk width

[10] Flap-like lateral limbs [AC10]
0. Absent
1. Present

[11] Nodes/tubercles/dermal papillae [AC11]
0. Absent
1. Present

[12] Differentiation at limb insertion [AC12]
0. Absent
1. Present

[13] Dorso-lateral sclerites above limb insertion [AC13]
0. Absent
1. Present

[14] Median spine above limb insertions [AC14]
0. Absent
1. Present

[15] Lobopod tip (main trunk limb) [AC15]
0. Double claw
1. Juxtaposed series of claws
2. Pad

[16] Posterior-most single claws [AC16]
0. Absent
1. Present

[17] Posterior claws pointing anteriad [AC17]
0. Absent
1. Present

VISUAL ORGANS

[18] Ocelli as primary ocular units [AC18]
0. Absent
1. Present

[19] Median eyes [AC19]
0. Absent
1. Present

[20] Number of median eyes [AC20]

0. 2
1. 3
2. 4

[21] Rhabdomeric lateral eye [AC21]
0. Very reduced or absent
1. Present and well developed

[22] Type of lateral eyes [AC22]*
0. Few and simple lenses with cup-shaped retina
1. Faceted (compound)
2. Stemmata

[23] Type of corneagenous cells [AC23]
0. Many
1. Two

[24] Tetraconate condition [AC24]
0. Absent
1. Present

[25] Number of nested optic neuropils [AC25]
0. 1
1. 2
2. 3

[26] Multi-layered rhabdomeres [AC26]
0. Absent
1. Present

[27] Star-shaped rhabdomeres [AC26]
0. Absent
1. Present

[28] Lateral compound eye topology [AC27]*
0. Projecting laterally beneath the head shield or through a notch
1. Projecting dorsally and embedded within the shield
2. Projecting latero-ventrally close to the medial axis, possibly accommodated with bulges in shield

Remark: See Mayers *et al.* (2018, ch. 11).

[29] Ophthalmic ridges [AC28]
0. Absent
1. Present

[30] Lateral eyes pedunculate [AC29]
0. Absent
1. Present

[31] Peduncular lobes [AC67]
0. Absent
1. Present

Remark: See Vannier *et al.* (2018) for a discussion of that character.

[32] Pedunculate eyes large and ovate, part of a prominent ocular segment projecting anteriad [AC30]
0. Absent
1. Present

HEAD AND CEPHALIC CHARACTERS

[33] Somital head (as tagma I) defined by series of appendages and/or external segmentation [AC31]
0. Absent (only anteriormost defines head)
1. Present

[34] Somites defining anteriormost tagma* [AC31]
0. 4
1. 5
2. 6
3. 7
4. 8

Remark: Habeliidans and relevant synziphosurines are coded for octasomitic heads following Aria and Caron (2017b).

[35] Tergite of the ocular (protocerebral) somite [AC127]*
0. Absent
1. Present

Remark: We consider here that the chelicerate epistome is homologous to other types of frontal sclerites among euarthropods.

[36] Tergite of the ocular (protocerebral) somite, type [AC128]
0. Rounded
1. Sub-triangular

[37] Supernumerary frontal sclerite attached to the ocular tergite [AC128]
0. Absent
1. Present

Remark: This character codes for the so-called epipharyngeal sclerite attached to the epistome in some chelicerates.

[38] Tergal sclerotization of the post-ocular somite [AC33]
0. Absent
1. Present

[39] Tergal sclerotization type [AC34]
0. Tergites with posterior expansion over at least some trunk segments (carapace)
1. Tergites with limited expansion, cephalic tergites all fused and articulating or connecting with first trunk segment (shield)

[40] Carapace type [AC35]
0. Bivalved
1. Plate

[41] Bivalved carapace type*
0. Type I: Sub-straight cross-section, covering body dorsally
1. Type II: Convex cross-section, enveloping body laterally

[42] Shape of carapacal valves*
0. Symmetrical respective to sagittal axis, ventral margins tight ('*Isoxys* type')
1. Asymmetrical respective to sagittal axis, antero-ventral margin tight, postero-ventral margin ample ('*Canadaspis* type')
2. Symmetrical respective to sagittal axis, ventral margins ample ('*Branchiocaris* type')
3. Variable (ostracods)

[43] Ventral closure of carapace*
0. Absent
1. Present

Remark: 'Odaraiids' (*Odaraia* and *Nereocaris*) are characterized by carapacal valves that fully enclose the body, with ventral margins extensively covering the underside of the body. We recognize a similar condition in ostracods.

[44] Type II bivalved configuration [AC36]*
0. Unfused along most of dorsal margin
1. Fused along most of dorsal margin

Remark: Among hymenocarines, we consider that *Odaraia* and *Waptia* present an extensive fusion of the valves with effacement of the median fold.

[45] Covering of the type II bivalved carapace (when body fully extended antero-posteriorly) [AC37]
0. At least two thirds of body length
1. Cephalothorax

[46] Frontal and lateral extensions of cephalic shield*
0. Limited; tergites not raised or expanding laterally
1. Distinct and well-developed; shield forms anterior and/or lateral extensions

[47] Articulation of posterior margin of shield with first trunk segment [AC39]
0. Tergal overlap
1. Occipital closure

[48] Segmental impression in shield [AC40]
0. Absent
1. Present

[49] Occipital lobe [AC41]
0. Absent
1. Present

[50] Pair of occipital carinae [AC42]
0. Absent
1. Present

[51] Anterior reduction of segments and/or appendages [AC43]
0. Absent
1. Present

[52] Compaction of the cephalic unit [AC44]
0. Absent
1. Present

[53] Cephalic doublure [AC45]
0. Absent
1. Present

[54] Cephalic kinesis [AC46]
0. Absent
1. Present

[55] Well-developed pair of genal spines on cephalic shield
0. Absent
1. Present

[56] Cephalic shield overlapping first trunk sternite, pair of trunk appendages, or trunk caeca
0. Absent
1. Overlap of sixth body somite
2. Overlap of eighth body somite

Remark: See Mayers *et al.* (2018, ch. 22). This is a multistate character without corresponding sovereign (or primary) character because states 1 and 2 are unlikely to have a common origin.

[57] Dorsal facial sutures
0. Absent
1. Present

BRAIN CHARACTERS

[58] Ganglia of post-oral cephalic appendages fused into single nerve mass [AC47]
0. Absent
1. Present

[59] Trunk ganglia individually expressed*
0. Absent
1. Present

Remark: Generalized from Wang *et al.* (2018), ch. 146.

[60] Contiguity of the first two post-protocerebral ganglia [AC48]
0. Absent
1. Present

[61] Fan-shaped body in brain [AC49]
0. Absent
1. Present

[62] Position of midline neuropil [AC50]
0. Superficial to protocerebrum
1. Embedded within protocerebral matrix

[63] Olfactory lobes linked to a lateral component of protocerebrum by olfactory globular tract [AC51]
0. Absent
1. Present

[64] Deutocerebral olfactory lobe with glomeruli [AC52]
0. Absent
1. Present

[65] Lateral eyes pedunculated [AC53]
0. Absent
1. Present

STERNITES (CEPHALON)

[66] Sternites [AC54]

0. Absent
1. Present

[67] Endosternum (or endosternite) [AC55]
0. Absent
1. Present

[68] Labrum*
0. Absent
1. Present

Remark: Characters describing the hypostome-labrum complex have been reorganized and expanded compared to Aria and Caron (2017a). Here, we code the labrum as a common feature shared by all euarthropods, which arguably originates from the protocerebral somite (Scholtz and Edgecombe 2006). Classically, in mandibulates, the "labrum" covers the mouth and such pre-oral structure generally takes two forms: the typical fleshy protrusion of oligostracans, anostracans and other crustaceans, and the sclerotic plates encountered in myriapods, malacostracans and hexapods—which are commonly designated as either "epistome-labrum" or "clypeo-labrum" depending on the group of interest. Pre-labral sclerites in mandibulates are often distinct from the labrum *per se* and are usually closely associated with the insertion of the antennules. For this reason, the pre-labral sclerite is sometimes referred to as the "hypostome," a common term from the pre-oral sclerite used among extinct euarthropods, especially trilobites and their allies. Such a terminology has been used for instance for Cephalocarida (Olesen *et al.* 2011) but arguably applies to all other crustaceans, including copepods (Schram 1986), leptostracans (Olesen and Walossek 2000) and stomatopods (Haug *et al.* 2012a). Herein (chars. 62-64), we therefore harmonize the terms "epistome," "clypeus" and "hypostome" under the same concept of "hypostome."

[69] Labrum expression and location*
0. Expressed frontally
1. Expressed as a postero-ventral structure separate from frontalmost organs

Remark: This character fundamentally distinguishes the anteriormost chelicerate "epistome-labrum" from ventral structures characteristic of Mandibulata. Hymenocarines and ostracods are considered to belong to the first group (see Vannier *et al.*, 2018).

[70] External inter-ocular sensory organs [AC68]*
0. Absent
1. Present

Remark: Ortega-Hernández and Budd (2016) have discussed their views on the analogous nature of sensory organs and paired inter-ocular projections in panarthropods. Our aim here is to test local cases of homology, and we therefore code this character as present when known. We do however make a distinction for the limb-like inter-ocular features of *Canadaspis* and remipedes (see char. 86).

[71] Type of ventral labrum* [AC58]

0. Single fleshy protrusion
1. Plate with underlying soft tissues

[72] Labral plate, type*
0. Bilobate lip with partial fusion to the hypostome
1. Free bilobate or wide lip
2. Expanded subtriangular or subrectangular lip

Remark: This character codes for variations in labral shape amongst mandibulates. Most crustaceans possess state 2, whereas myriapods possess state 0. State 1 is derived and found in pterygotes.

[73] Hypostome [AC56]*
0. Absent
1. Present

Remark: The hypostome is here defined on the basis of the artiopodan hypostome, that is, as a pre-oral sclerotic structure associated with the insertion of the anteriormost appendages.

[74] Hypostome attachment [AC57]*
0. Conterminant
1. Natant

[75] Hypostome accommodating antennules and extensively covering the mouth [AC59]
0. Absent
1. Present

Remark: This is a character mostly discriminating the typical artiopodan hypostome.

[76] Mandibulate labium [AC60]
0. Absent
1. Present

[77] Chelicerate labium*
0. Absent
1. Present

Remark: The chelicerate labium is a ventral sclerite (sternapophysis) apparently associated with the palpal somite and forming the posterior border of the stomodaeum. We follow Wang *et al.* (2018) in coding the labium as absent in Pedipalpi but otherwise code state 1 for pseudoscorpions and solifuges after Schultz (2007).

[78] Sternites externally developed within segments 2–4 [AC61]
0. Absent
1. Present

[79] Fusion of sternites within segments 2–4 [AC62]
0. Absent
1. Present

[80] Metastoma [AC63]*
0. Absent
1. Present

Remark: The metastoma is a modified sternite of the first opisthosomal segment in euchelicerates—typically, in eurypterids (Dunlop 1997). We also code this character for scorpions (sternum) and harvestmen (aculi genitales) (Dunlop and Lamsdell 2016).

[81] Coxosternite [AC64]
0. Absent
1. Present

[82] Single main maxilliped [AC163]
0. Absent
1. Present

[83] Head has tendention to form a hypostomal bridge [AC65]
0. Absent
1. Present

[84] First opisthosomal tergite triangular
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 109. Only applies to the total-group Chelicerata given that the homology of this somite requires a prosoma.

[85] Genital operculum overlaps sternite of third opisthosomal segment
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 123. Only applies to the total-group Chelicerata given that the homology of this somite requires a prosoma.

FRONTALMOST APPENDAGES

[86] Frontalmost limb-like projections
0. Absent
1. Present

Remark: This character codes specifically for the appendicular outgrowths present between the eyes of *Canadaspis*, and comparable ones in remipedes. Their nature and homology with other known cephalic features remain uncertain.

[87] Arthrodization of first axial appendage [AC66]
0. Absent
1. Present

[88] Size of frontalmost appendage [AC74]
0. Long, multipodomerous; > 6 podomeres
1. Short; ≤ 6 podomeres

[89] Well-developed ventral spinose outgrowths on frontalmost appendage [AC76]
0. Absent
1. Present

[90] Ventral spinose outgrowths forming elongate rami on frontalmost appendage [AC69]
0. Absent
1. Present

[91] Rami of branching frontalmost appendage originating from different podomeres [AC70]
0. Absent
1. Present

[92] Short and ramified frontalmost appendage ending in a raptorial device made of three to four elongate spines*
0. Absent
1. Present

Remark: This is a potential apomorphy of Megacheira.

[93] Spine morphology of megacheiran appendage*
0. Thin, ca. 10 times as long as thin (base width) or more
1. Thick, ca. 7 times as long as thin (base width) or less

[94] Multichelate device type on megacheiran appendage*
0. Made of four spines (‘yohoiid type’)
1. Made of three spines (‘leanchoiliid type’)

[95] Podomere number of articulating basis of megacheiran appendage*
0. Single elongate podomere
1. Two short podomeres

[96] Single-podomere basis of megacheiran appendage, type*
0. Slender
1. Stout

Remark: *Fortiforceps* and apparently also *Parapeytoia* possess a stouter basal podomere compared to other megacheirans with yohoiid type of “great appendages.”

[97] Shape of peduncular podomere for yohoiid great appendages*
0. Sub-cylindrical
1. Chalice-shaped

[98] Thickness of peduncular podomere for yohoiid great appendages*
0. Slender
1. Stout

Remark: *Yohoia* and *Jianfengia* have slenderer peduncles compared to other megacheirans. A *Yohoia* morph was reported (Haug *et al.* 2012b) to have stouter 'great appendages,' but appears less common—it may also be a different species than *Yohoia tenuis*.

[99] Ramified frontalmost appendage with flagellate extensions [AC71]
0. Absent
1. Present

[100] Short frontalmost appendage with first and second podomere forming an elbowed articulation*
0. Absent
1. Present

Remark: Typical of non-leanchoiliid megacheirans and some chelicerates, see Haug *et al.* (2012b) and Wang *et al.* (2018), ch. 37.

[101] Frontalmost appendage a chelicera, i.e. chelate or subchelate with only two opposing faces [AC72]
0. Absent
1. Present

[102] Orientation of closure of terminal podomere (apotele) on chelicera*
0. Ventral
1. Dorsal
2. Lateral

Remark: See Wang *et al.* (2018), ch. 40.

[103] Cheliceral fang*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 41.

[104] Number of cheliceral podomeres*
0. Three
1. Two

Remark: See Wang *et al.* (2018), ch. 35.

[105] Cheliceral serrula*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 53.

[106] Orientation of first axial appendage [AC73]
0. Ventro-frontal
1. Dorsal

[107] Arthrodized frontalmost appendage, multipodomerous type [AC75]
0. Robust, thick branch
1. Long antennular

[108] Type of inner (ventral) spinose outgrowths on frontalmost appendage [AC77]
0. Sub-equal length or tapering gradually along entire margin
1. Elongate mid-margin

[109] Secondary spines on ventral spinose outgrowths of frontalmost appendage [AC78]
0. Absent
1. Present

[110] Dorsal spinose outgrowths on podomeres of arthrodized frontalmost appendage [AC79]
0. Absent
1. Present

OTHER CEPHALIC LIMBS

[111] Maximum podomere number in head (tagma I) [AC90]*
0. 7
1. <7
2. >7

Remark: When endopods are differentiated and vary from one somite to the other, this character takes into account the endopod with the highest number of podomeres.

[112] Punctual subdivision of endopod podomeres from an heptopodomeran limb*
0. Absent
1. Basi- and telofemur
2. Basi- and telotarsus

Remark: See Wang *et al.* (2018), chs. 88 and 93. This multistate has no sovereign character because states 1 and 2 do not necessarily have a common origin.

[113] All cephalic endopods posterior to frontalmost appendage pair well-developed (seven-segmented or more) [AC81]*
0. Absent
1. Present

Remark: Taking the heptopodomeran condition as a reference for the ground pattern (see Aria *et al.* 2015), endopods are considered reduced here when the podomere count is below seven. Sometimes an exact podomere count has not been possible so far (e.g. in the first post-antennular limb of leanchoiliids) and the modified state is occasionally extrapolated from a substantial reduction of the appendage in size.

[114] Endopod of second appendage pair [AC82]
0. Developed
1. Reduced

[115] Endopod of third appendage pair [AC83]
0. Developed
1. Reduced

[116] Endopod of fourth appendage pair [AC84]
0. Developed
1. Reduced

[117] Exopod of fourth appendage pair [AC112]*
0. Developed
1. Reduced

[118] Endopod of fifth appendage pair [AC85]
0. Developed
1. Reduced

[119] Exopods of fifth appendage pair*
0. Developed
1. Reduced

[120] Exopods on cephalic appendages posterior to fifth pair*
0. Absent
1. Present

[121] Exopod of cephalic appendages excluding two anteriormost pairs, type [AC102]
0. Stenopodous, podomeres > 4
1. Annulate
2. Short, few podomeres (≤ 4)

Remark: See Mayers *et al.* (2018).

[122] Subdivision of short cephalic exopod, type
0. Bipartite
1. Tripartite

Remark: See Mayers *et al.* (2018).

[123] Stenopodous exopod, type [AC103]
0. Antenniform with elongate podomeres
1. Short and stout, ending in setal brush (underdeveloped claw)

[124] Partial detachment of exopods from main limb branch in head tagma*
0. Absent
1. Present

Remark: This character expresses the peculiar condition of habeliidans, *Offacolus* and *Dibasterium*, in which the cephalic exopods preserve as partially dissociated from their main biramous branch (Aria and Caron 2017b). The exact attachment remains unknown.

[125] Some cephalic endopods are walking limbs [AC86]
0. Absent
1. Present

[126] Repeated appendage morphology in tagma I [AC87]
0. Absent
1. Present

[127] Dichotomy in appendage morphology between tagma I and tagma II [AC88]
0. Absent
1. Present

[128] Proximo-distal differentiation of endopod podomeres in head (tagma I) [AC89]
0. Absent
1. Present

[129] Arthrodized post-antennular appendage expressed [AC91]
0. Absent
1. Present

[130] Post-antennular appendage differentiated [AC92]
0. Absent
1. Present

[131] Chelate or sub-chelate termination of post-antennular appendage [AC93]*
0. Absent
1. Present

[132] Plane of motion of chelate or sub-chelate post-antennular appendage*
0. Sub-vertical, leg-like
1. Horizontal

Remark: See Wang *et al.* (2018), ch. 62.

[133] Ramification of post-antennular appendage [AC95]
0. Uniramous
1. Biramous

[134] Developed endites on endopod of post-antennular appendage [AC96]
0. Absent
1. Present

[135] Endopod of post-antennular appendage annulate or flagellate [AC97]
0. Absent
1. Present

[136] Coxa on post-antennular appendage [AC99]
0. Absent
1. Present

[137] Exopod of post-antennular appendage, type [AC100]
0. Stenopodous
1. Annulate
2. Short, lobate

[138] Endopod of third cephalic appendage very thin and elongate, filament-like*
0. Absent
1. Present

Remark: This condition is sometimes called "antenniform" in chelicerates (e.g. Dunlop and Lamsdell 2016). We differentiate the chelicerate condition from the annulate condition, that is, with podomeres extremely thin and elongate, as opposed to being very short and numerous.

[139] Enditic outgrowths on cephalic endopods excluding two anteriormost pairs [AC104]
0. Absent
1. Present

[140] Endopod of third cephalic appendage chelate or subchelate [AC105]
0. Absent
1. Present

[141] Third cephalic appendage with a well-developed, toothed gnathobase [AC106]
0. Absent
1. Present

[142] Third cephalic appendage a mandible [AC107]
0. Absent
1. Present

[143] Mandibular palp [AC107]
0. Non-developed
1. Developed

[144] Mandible with three-segmented palp, appressed on the ventral side of the head, curving inward [AC94]*
0. Absent
1. Present

Remark: This characterizes the endopod of the fuxianhuiid mandible.

[145] Telognathic mandible [AC108]
0. Absent
1. Present

[146] Mandibular gnathal edge [AC109]
0. Consisting of molar and incisor process
1. Only ellipsoid pars molaris present
2. Row of parallel teeth
3. Shovel with terminal teeth
4. Group of paired teeth and hair pad

[147] Mandibular lamellate combs [AC110]
0. Absent
1. Present

[148] Hypopharynx [AC111]
0. Absent
1. Present

[149] Modified endopod/palp on fourth cephalic appendage [AC113]
0. Absent
1. Present

Remark: This character implies the modification of the appendage basis as a mouthpart and the reduction of the endopod of the fourth appendage pair (char. 90), whereby the complete reduction of the endopod is coded “0”.

[150] Modified endopod/palp on fourth cephalic appendage, type [AC114]*
0. Reduced, vestigial, undeveloped
1. Well developed

[151] Post-mandibular plate formed by the fusion of the maxilla and the intermaxillary sternum [AC115]
0. Absent
1. Present

[152] Cephalic appendages 4 and 5 ending with chelate termination [AC116]
0. Absent
1. Present

[153] Fifth cephalic appendage, differentiation type [AC117]
0. Integrated to gnathal plate (labium)
1. Reduced, enditic

[154] Fifth cephalic appendage vestigial [AC118]
0. Absent
1. Present

[155] Fifth cephalic appendage with developed palp [AC119]
0. Absent
1. Present

Remark: Same requirements for coding as for char. 121, but with respect to fifth cephalic pair.

[156] Internalization of mouthparts [AC120]
0. Absent
1. Present

[157] Oral cone [AC121]
0. Absent
1. Present

[158] Atrium oris [AC122]
0. Absent
1. Present

MOUTH AND STOMODAEAL AREA

[159] Mouth opening [AC123]
0. Frontal
1. Ventral

[160] Ventral mouth opening, type
0. Antero-ventral
1. Postero-ventral

[161] Type of circumoral structures [AC124]*

0. Toothed lips
1. Lamellae
2. Ring of plates
3. Mouth surrounded by arthrodized limbs

[162] Circumoral structures sclerotized [AC125]*
0. Absent
1. Present

[163] Proboscis [AC126]
0. Absent
1. Present

ALIMENTARY TRACT AND OTHER INTERNAL CHARACTERS

[164] Large and well-differentiated stomach [AC129]
0. Absent
1. Present

[165] Stomach in a frontal position [AC131]
0. Absent
1. Present

[166] Stomach—additional pouch (crop) [AC132]
0. Absent
1. Present

[167] Secondary organs connected to the central digestive duct [AC132]
0. Absent
1. Present

[168] Secondary digestive organs serially repeated along the post-cephalic portion of the gut [AC133]
0. Absent
1. Present

[169] Shape of post-cephalic secondary digestive structures [AC134]
0. Reniform
1. Bulgy triangles
2. Caeca

[170] Striations on post-cephalic secondary digestive structures [AC135]
0. Absent
1. Present

[171] Branching of post-cephalic secondary digestive structures [AC136]
0. Absent

1. Present

[172] Differentiation of cephalic secondary digestive structures (compared to trunk) [AC137]
0. Absent
1. Present

[173] Ramification of cephalic secondary digestive structures [AC138]
0. Absent
1. Present

[174] Branching of cephalic secondary digestive structures [AC139]
0. Absent
1. Present

[175] Peritrophic membrane [AC140]
0. Absent
1. Present

[176] Metameric ganglia on nerve cord [AC141]
0. Absent
1. Present

[177] Metanephridia with sacculus containing podocytes [AC142]
0. Absent
1. Present

[178] Segmental invaginations of neuroectoderm giving rise to ventral organs [AC143]
0. Absent
1. Present

[179] Malpighian tubules*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 164, for coding in arachnids.

[180] Coxal glands opening at base of prosomal leg 1*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 166. Only applies to Euchelicerata.

[181] Distodorsal insertion of posterior transpatellar muscle*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 190. Muscle data in chelicerates carry some obvious conflicts, both internally and with other parts of the anatomy. We selected those characters based on musculature that provide information on major internal arachnid subdivisions (aside from the extensive evidence supporting the monophyly of Arachnida and Pedipalpi, methodologically enforced in our analysis) but do not assume spurious configurations, such as a polyphyletic Tetrapulmonata. We also kept the information to the homologous insertions of the muscles and did not assume losses as having common origins in case of multistates. Only applies to Euchelicerata.

[182] Ventral insertion of the anterior transpatellar muscle*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 192. Only applies to Euchelicerata.

[183] Ventral insertion of the anterior patellotibial muscle on tibia*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 193. Only applies to Euchelicerata.

[184] Posterior patellotibial muscle*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 194. Only applies to Euchelicerata.

[185] 9x2 +3 microtubule arrangement in euchelicerate sperm axoneme*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 218. Only applies to Euchelicerata.

[186] Iso/telolecithal euchelicerate eggs*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 226. Only applies to Euchelicerata.

TRUNK

[187] Fusion of trunk tergites
0. Absent
1. Present

Remark: See Mayers *et al.* (2018, ch. 2).

[188] Fusion of trunk tergites, type
0. Partial—some segments still freely articulate
1. Complete—all trunk tergites show some degree of fusion

Remark: See Mayers *et al.* (2018, ch. 3).

[189] Degree of effacement of tergite boundaries on fused trunk portion
0. Low—pleurae outstanding, at least laterally
1. High—pleurae margins fused, at least laterally
2. Tergo-pleurae individualized and arthrodial membranes sometimes visible, but with no tergite overlap

Remark: See Mayers *et al.* (2018, ch. 5). State 2 is added here to reflect the condition of most terrestrial euarthropods. Certain chelicerates (Haptopoda, Uropygi) have fused trunks but retain overlapping tergites.

[190] Distinct pygidium [AC209]
0. Absent
1. Present

Remark: See Mayers *et al.* (2018, ch. 7).

[191] Thorax [AC144]
0. Absent
1. Present

[192] Number of thoracic somites [AC145]
0. 11+
1. 4/5
2. 7/9
3. 3

[193] Abdomen [AC146]
0. Absent
1. Present

[194] Post-abdomen
0. Absent
1. Present

Remark: A post-abdomen is defined here by the differentiation of limbless tergo-pleurae posterior to an abdomen.

[195] Multisegmentation (trunk somites ≥ 20) [AC149]
0. Absent
1. Present

[196] Number of core trunk segments (non multisegmented taxa) [AC147]*
0. 15-19
1. 10-14
2. 9
3. 7-8
4. <7

[197] Seventh appendage integrated into the prosoma [AC148]*
0. Absent
1. Present

Remark: This character only applies to Chelicerata and their stem groups (see also char. 32).

[198] Tergite of eighth somite (counting the ocular somite as the first) drastically reduced as a "microtergite"*
0. Absent
1. Present

Remark: See Dunlop and Lamsdell (2016) for a review of this character across chelicerates.

[199] Constriction of eighth somite (segment seven) into a pedicel*
0. Absent
1. Present

Remark: A widespread arachnid character (see e.g. Dunlop and Lamsdell (2016)).

[200] Post-cephalic appendages covered by sclerotic plates (opercula)*
0. Absent
1. Present

Remark: Used as an apomorphy of Euchelicerata (Dunlop and Lamsdell 2016; Aria and Caron 2017b), although it mostly applies to merostomes and tetrapulmonates.

[201] Tergo-sternal decoupling [AC150]
0. Absent
1. Present

[202] Tergo-sternal decoupling, type [AC151]
0. Polypody
1. Polypody and "polysternity"
2. "Polytergity" (autapomorphy of symphylan myriapods)

[203] Pleurae [AC152]
0. Reduced or fused
1. Developed

[204] Tergo-pleural rings [AC153]*
0. Absent
1. Present

[205] Pleural orientation [AC154]
0. Horizontal
1. Around body

[206] Pleural length [AC155]
0. Short, i.e. equal or inferior to body diameter
1. Long, i.e. exceeding body diameter

[207] Articulating ridge [AC156]
0. Absent
1. Present

[208] Articulating ridge, type [AC157]
0. Single
1. Antero-posterior

[209] Transverse stipital muscle [AC158]
0. Absent
1. Present

TRUNK APPENDAGES AND GENERAL APPENDICULAR CHARACTERS

[210] Limb arthrodization in trunk [AC181]
0. Absent
1. Present

[211] Proximo-distal differentiation of endopod podomeres in tagma II [AC159]
0. Absent
1. Present

[212] Podomere number in endopods of tagma II [AC160]
0. 7
1. <7
2. >7

[213] Maxillipeds [AC161]
0. Absent
1. Present

[214] Tergites of maxilliped segments fused to head shield [AC162]
0. Absent
1. Present

[215] Maxilliped pairs*
0. Single main pair
1. Several pairs

[216] Slit sensilla [AC164]
0. Absent
1. Present

[217] Trichobothria*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 139.

[218] Basis (basipod) [AC165]
0. Absent
1. Present

[219] Basipod formed of at least two elements [AC166]
0. Absent
1. Present

[220] Basipod multi-segmented [AC167]
0. Absent
1. Present

[221] Multiple endites on basipod [AC168]
0. Absent
1. Present

[222] Proximalmost endite on basipod [AC169]
0. Absent
1. Present

[223] Coxa as entire pre-basal podomere [AC170]
0. Absent
1. Present

[224] Precoxa as whole pre-coxal podomere [AC171]
0. Absent
1. Present

[225] Pleurites formed by several sclerotic elements surrounding limb insertion [AC172]
0. Absent
1. Present

[226] Arrangement of pleurites [AC173]
0. Outer/proximal and distal/inner sets
1. Multiple sclerotic pieces

[227] Gnathobases (= heavily-sclerotized and toothed masticatory basipods) on any body limb [AC174]
0. Absent
1. Present

[228] One or more gnathobase(s) reduced in tagma I [AC175]
0. Absent
1. Present

[229] Secondary appendicular outgrowths on trunk [AC176]
0. Absent
1. Present

[230] Secondary appendicular outgrowths on trunk, type [AC177]
0. Lobopodous
1. Sclerotized

[231] Distal oblanceolate lamellae on exopod
0. Absent
1. Present

[232] Proximal lamellae (gills) with appendicular affinity in trunk [AC178]
0. Absent
1. Present

[233] Proximal lamellae (gills) present on trunk somites 10 to 13*
0. Absent
1. Present

Remark: Generalized from Wang *et al.* (2018), ch. 152, to all relevant arthropods.

[234] Book gills made of a series of broad, overlapping lamellae*
0. Absent
1. Present

Remark: This character codes for the gill form generally characteristic of euchelicerates, worded to also include variations with fewer lamellae than those known in merostomes.

[235] Proximal lamellae internalized [AC179]
0. Absent
1. Present

[236] Trunk exopod posterior to head tagma, type [AC182]*
0. Reduced, vestigial
1. Annulate
2. Short, few podomeres (≤ 4)
3. Phyllopodous

[237] Short trunk exopod, type
0. Single lobe
1. Bipartite
2. Tripartite

[238] Trunk endopod reduced posterior to head tagma [AC180]
0. Absent
1. Present

[239] Endopod strongly developed in thorax (or anterior trunk if thorax undifferentiated) [AC183]
0. Absent
1. Present

[240] Phyllopodous-type limbs anywhere on body [AC184]
0. Absent
1. Present

[241] Terminal endopods stenopodous [AC185]
0. Absent
1. Present

[242] Identical morphology of endopod and exopod rami on pleopods/post-thorax [AC186]
0. Absent
1. Present

[243] Annulation of at least one pair of exopods [AC187]
0. Absent
1. Present

[244] Epipod [AC191]
0. Absent
1. Present

[245] Endites as latero-distal projections on endopod podomeres [AC192]
0. Absent
1. Present

[246] Pusher legs with paddle tips [AC193]

0. Absent
1. Present

[247] Developed endites on endopod podomeres in trunk (tagma II and III) [AC194]
0. Absent
1. Present

[248] Paired spines on endopod podomeres [AC195]
0. Absent
1. Present

[249] Short spines on endopod podomeres [AC196]
0. Absent
1. Present

[250] Multiple setae on endopod podomeres [AC197]
0. Absent
1. Present

[251] Complex articulation between basipod and first endopod podomere involving surnumerary sclerites*
0. Absent
1. Present

Remark: Generalized from Wang *et al.* (2018), ch. 87. Mandibulate pleurites are not considered here.

[252] Bicondylar femoropatellal articulation*
0. Absent
1. Present

Remark: See Wang *et al.* (2018), ch. 89. Only applicable to euchelicerates.

[253] Patellotibial articulation*
0. Monocondylar
1. Hinge
2. Bicondylar

Remark: See Wang *et al.* (2018), ch. 90. Only applicable to euchelicerates.

[254] Main limb tip along body [AC199]
0. Pad
1. Juxtaposed claws
2. Trident of claws
3. Chelate or sub-chelate
4. Double claw

5. Multiple spines
6. Single claw

[255] Coxal vesicles*
0. Absent
1. Present

Remark: So-called “sternal pores” in euthycarcinoids have been reinterpreted by Edgecombe and Morgan (1999) as probable homologs to the coxal vesicles of certain terrestrial mandibulates, including Symphyla and Diplopoda. We follow this view here.

POSTERIOR TERMINATION

[256] Sclerotization of termination [AC200]
0. Absent
1. Present

[257] Telson developed [AC201]
0. Absent
1. Present

[258] Telson type [AC202]
0. Spine
1. Plate / Spatula

[259] Flagellate extension of telson*
0. Absent
1. Present

[260] Anus location [AC203]
0. Terminal somite
1. Base of telson

[261] Caudal rami [AC204]
0. Absent
1. Present

[262] Caudal rami, type [AC208]
0. Spinose
1. Annulate
2. Subdivided
3. Rounded
4. Flap

[263] Additional caudal processes [AC205]
0. Absent
1. Present

[264] Furca [AC206]
0. Absent
1. Present

[265] Uropods sensu stricto [AC207]
0. Absent
1. Present

[266] Axial elevation of pygidium [AC211]
0. Absent
1. Present

[267] Pygidial ornamentation [AC212]
0. Smooth
1. Spinose

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