



Comment on “*Aysheasia prolata* from the Utah Wheeler Formation (Drumian, Cambrian) is a frontal appendage of the radiodontan *Stanleycaris*” by Stephen Pates, Allison C. Daley, and Javier Ortega-Hernández

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Pates et al. (2017) and Pates and Daley (2017) reinterpreted a number of presumable xenusians (lobopodians) and described some new fossils from various Cambrian Lagerstätten as radiodontan (anomalocaridid) frontal appendages. The authors suggested that some features including overall length of a specimen, a number of tentative podomeres, a number of ventral blades (spines) and dorsal spines, their morphology, and an angle between the dorsal and ventral surfaces (θ) of a specimen provide enough information for a fairly good morphological description and a relevant systematic interpretation of stem group ecdysozoans. The case of xenusian *Mureropodia apae* from the lower Cambrian Valdemiedes Formation of Murero, northeastern Spain (Gámez Vintaned et al. 2011), which Pates and Daley (2017) identified as radiodontan *Caryosyntrips* cf. *camurus*, does not verify a plausibility of such a reductive approach.

First of all, Pates and Daley (2017: 466) suggested that *Mureropodia* had 6 podomeres the faint boundaries of which are visible on its dorsal surface under low angle light. Despite of the study of this specimen with different methods, no such boundaries have been documented. It remains uncertain which structures Pates and Daley (2017) have taken for the podomere boundaries because the authors have not indicated them on their figure of the specimen. These can be either repeatable transverse terraces of the matrix which continue across the specimen (as well as beyond its boundaries) or imprints of possible muscle fibres. There are several terraces indeed on the sample surface but they are not restricted to the fossil itself while a number of identical fibre imprints transecting the entire body is over a hundred. Secondly, Pates and Daley (2017) assumed that *Mureropodia* had to have dorsal spines which were absent due to incomplete preservation of its dorsal surface. Again, the boundaries of both dorsal and ventral surfaces of the specimen are expressed identically except for the presence of ventral lobopods (“spines”) and appendicules.

Thirdly, the authors ignored a wide array of features observable in *Mureropodia* (Gámez Vintaned et al. 2011). Among these features are: (i) a dermomuscular sac of circular and longitudinal muscular systems being preserved as multiple imprints of muscle fibres similar by arrangement to those of xenusians

Paucipodia inermis and *Tritonychnus phanerosarkus* from the Yu’anshan Formation, South China (Hou et al. 2004; Zhang et al. 2016) and *Pambdelurion whittingtoni* from Sirius Passet, North Greenland (Young and Vinther 2017); (ii) a filament-like antenniform frontal appendage similar to those occurring in the head part of xenusian *Hallucigenia sparsa* from the Burgess Shale, western Canada (Smith and Caron 2015); and (iii) possible proboscis retractors which were not described from other xenusians yet but took the same position in the body of palaeoscolecidans which is different from the position of an intestine (Zhuravlev et al. 2011). Palaeoscolecidans are stem group introvert-bearing cycloneuralians comprising a sister group of xenusians (Harvey et al. 2010; Zhuravlev et al. 2011; Liu et al. 2014). In turn, the presence of both antenniform filament and retractors reveals that anterior part of *Mureropodia* is rather a proboscis than “a distorted distal end of the appendage”. None of these features were observed in frontal appendages of radiodontans. Also, some ventral “spines” of *Mureropodia* are terminated with a few minute curved claws and show transverse telescopic structures and muscle bundles associated to them (Gámez Vintaned et al. 2011: figs. 12.4f, 12.9b, c) indicative of lobopods but not of radiodontan ventral endites bearing stiff auxiliary spines. The auxiliary spines are an order larger than lobopodian claws and are not restricted to the distal end (Pates et al. 2017: figs. 2, 3A₂). Similar lobopodian claws are shown by Pates et al. 2017 on their fig. 3D which has an incorrect caption “*Stanleycaris hirpex*” instead of *Aysheasia pedunculata*.

Furthermore, neither an absence of body annulations, nor stubby lobopods, nor the proboscis itself do exclude *Mureropodia* from a large array of highly morphologically variable lower to middle Palaeozoic xenusians which possess similar features (Dzik and Krumbiegel 1989; Liu et al. 2011; Ou et al. 2011; Smith and Caron 2015). As to the θ values of 11–17°, which is another important character of radiodontan frontal appendages according to Pates et al. (2017) and Pates and Daley (2017), it is a common feature as among other incompletely preserved xenusians (e.g., *Jianshanopodia decora* in Liu et al. 2006), which were not ascribed to radiodontans yet, as well as in a number of sponges, cancelloriids, and hyoliths of conical shape in any Cambrian Lagerstätte. Some of these fossils

also bear sharply pointed and distally curved marginal spines and due to their robust stature are even more similar to all the putative radiodontan appendages being described as *Caryosyntrips durus* and *C. serratus* from the Langston and Wheeler formations of the Great Basin, USA by Pates and Daley (2017: figs. 3E, 4C, 5). Both these fossils have straight margins and faint “podomere boundaries” and are triangular at outlines, thus, being obviously different from genuine radiodontan frontal appendages which are curved dorsally, bear pivot-hinged ventral endites, and are subdivided into distinct podomeres articulated by arthrodial membranes (Daley and Budd 2010; Daley and Edgecombe 2014; Cong et al. 2017). This is a very viable difference because such radiodontan appendages serving for prey capture were flexible structures with pivotal joints. Without alike biomechanics the specimens listed above hardly can be used in a similar way to radiodontans. In addition, radiodontan frontal appendages are never preserved as dorso-ventral compressions with blades unfolded in butterfly-like pattern (cf. Pates and Daley 2017: fig. 4C).

In summary, of all the new-old finds of Pates et al. (2017) and Pates and Daley (2017), only *Aysheia prolata* from the Wheeler Formation can be accepted as a radiodontan frontal appendage by the presence of curved podomeres, ventral blades, and dorsal spines. The only problem is that it cannot be attributed to *Stanleycaris* Caron et al. (2010) because its description has been published as a supplement available in an online version and, thus, does not satisfy the ICZN requirements as electronic publications have been accepted after 2011 (ICZN 2012). Currently, *Stanleycaris* is a nomen nudum.

References

- Caron, J.-B., Gaines, R.R., Mángano, M.G., Streng, M., and Daley, A.C. 2010. A new Burgess Shale-type assemblage from the “thin” Stephen Formation of the southern Canadian Rockies. *Geology* 38: 811–814.
- Cong, P., Daley, A.C., Edgecombe, G.D., and Hou, X. 2017. The functional head of the Cambrian radiodontan (stem-group Euarthropoda) *Amplectobelua symbrachiata*. *BMC Evolutionary Biology* 17: 208.
- Daley, A.C. and Budd, G.E. 2010. New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* 53: 721–738.
- Daley, A.C. and Edgecombe, G.D. 2014. Morphology of *Anomalocaris canadensis* from the Burgess Shale. *Journal of Paleontology* 88: 68–91.
- Dzik, J. and Krumbiegel, G. 1989. The oldest “onychophoran” *Xenusion*: A link connecting phyla? *Lethaia* 22: 169–181.
- Gámez Vintaned, J.A., Liñán, E., and Zhuravlev, A.Y. 2011. A new early Cambrian lobopod-bearing animal (Murero, Spain) and the problem of the ecdysozoan early diversification. In: P. Pontarotti (ed.), *Evolutionary Biology—Concepts, Biodiversity, Macroevolution and Genome Evolution*, 193–219. Springer, Berlin.
- Harvey, T.H.P., Dong, X., and Donoghue, P.C.J. 2010. Are palaeoscolecid ancestral ecdysozoans? *Evolution & Development* 12: 177–200.
- Hou, X., Ma, X., Zhao, J., and Bergström, J. 2004. The lobopodian *Paucipodia inermis* from the Lower Cambrian Chengjiang fauna, Yunnan, China. *Lethaia* 37: 235–244.
- ICZN (International Commission on Zoological Nomenclature) 2012. Amendment of Articles 8, 9, 10, 21 and 78 of the *International Code of Zoological Nomenclature* to expand and refine methods of publication. *Bulletin of Zoological Nomenclature* 69: 161–169.
- Liu, J., Shu, D., Han, J., Zhang, Z.F., and Zhang, X.L. 2006. A large xenusiid lobopod with complex appendages from the Chengjiang Lagerstätte (Lower Cambrian, China). *Acta Palaeontologica Polonica* 51: 215–222.
- Liu, J., Steiner, M., Dunlop, J.A., Keupp, H., Shu, D., Ou, Q., Han, J., Zhang, Z., and Zhang, X. 2011. An armoured Cambrian lobopodian from China with arthropod-like appendages. *Nature* 470: 526–530.
- Liu, Y., Xiao, S., Shao, T., Broce, J., and Zhang, H. 2014. The oldest known priapulid-like scolidoforan animal and its implications for the early evolution of cycloneuralians and ecdysozoans. *Evolution & Development* 16: 155–165.
- Ou, Q., Liu, J., Shu, D., Han, J., Zhang, Z., Wan, X., and Lei, Q. 2011. A rare onychophoran-like lobopodian from the Lower Cambrian Chengjiang Lagerstätte, southwestern China, and its phylogenetic implications. *Journal of Paleontology* 85: 587–594.
- Pates, S. and Daley, A.C. 2017. *Caryosyntrips*: a radiodontan from the Cambrian of Spain, USA and Canada. *Papers in Palaeontology* 3: 461–470.
- Pates, S., Daley, A.C., and Ortega-Hernández, J. 2017. *Aysheia prolata* from the Utah Wheeler Formation (Drumian, Cambrian) is a frontal appendage of the radiodontan *Stanleycaris*. *Acta Palaeontologica Polonica* 62: 619–625.
- Smith, M.R. and Caron, J.-B. 2015. *Hallucigenia*’s head and the pharyngeal armature of early ecdysozoans. *Nature* 523: 75–78.
- Young, F.J. and Vinther, J. 2017. Onychophoran-like myoanatomy of the Cambrian gilled lobopodian *Pambdelurion whittingtoni*. *Palaeontology* 60: 27–54.
- Zhang, X., Smith, M.R., Yang, J., and Hou, J. 2016. Onychophoran-like musculature in a phosphatized Cambrian lobopodian. *Biological Letters* 12: 20160492.
- Zhuravlev, A.Y., Gámez Vintaned, J.A., and Liñán E. 2011. The Palaeoscolecida and the evolution of the Ecdysozoa. *Palaeontographica Canadiana* 31: 177–204.

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