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A new hurdiid radiodont with a uniquely spinose carapace from the middle Cambrian Wheeler Formation of Utah, USA

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Radiodonts are non-biomineralized panarthropods emblematic of the lower Palaeozoic, whose taxonomy, morphology, and ecology have attracted considerable interest over the past two decades. Whereas the early Cambrian evolutionary history of the clade was dominated by anomalocaridids and amplectobeluids, the Miaolingian witnessed a major radiation of hurdiids, which became the most diverse and abundant radiodonts. Here we describe *Acanthopahvantia boardmani* gen. et sp. nov., the fifth hurdiid species reported from the Drumian (middle Cambrian) Wheeler Formation of the House Range, Utah. Although currently known from a single central carapace element, this new taxon exhibits a distinctive morphology combining a lanceolate outline, a robust anterior sagittal spine, and prominent spiniform lateral extensions. Phylogenetic analyses recover *A. boardmani* gen. et sp. nov. within Hurdiidae, in a clade with some (Bayesian inference) or all (parsimony) hurdiines. With its elongate outline and pronounced spinosity, the new taxon further expands the known morphological disparity of hurdiids.

Key words: Panarthropoda, Radiodonta, Hurdiidae, Wheeler Formation, Drumian, Cambrian, House Range, Utah.

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Introduction

Radiodonts, best known from the iconic genus *Anomalocaris*, are an extinct group of panarthropods that have become emblematic of the Cambrian Explosion. Documented in most Cambrian Konservat-Lagerstätten worldwide (e.g., Daley et al. 2013; Daley and Edgecombe 2014; Moysiuk and Caron 2019, 2025; Jiao et al. 2021; Pates et al. 2021; Paterson et al. 2023), and a few younger deposits (e.g., Van Roy et al. 2015; Pates et al. 2020; Potin et al. 2025), radiodonts have attracted considerable attention, with over 100 publications devoted to them over the last two decades. This sustained research effort has substantially expanded our knowledge of radiodont diversity, which now totals c. 40 species, and extended their stratigraphic (Cambrian Stage 3 to the Tremadocian, possibly the Emsian) and palaeogeographic (Avalonia, Baltica, Gondwana, Laurentia, North China, South China) ranges (e.g., Potin and Daley 2023). It has also revealed substantial morphological and ecological variation (e.g., Vinther et al. 2014; Van Roy et al. 2015; Lerosey-Aubril and Pates 2018; Liu et al. 2018, 2020; Moysiuk and Caron 2019, 2025; Caron and Moysiuk 2021; Potin and Daley 2023) and highlighted the significance of radiodonts for reconstructing early euarthropod evolution (e.g., Paterson et al. 2011, 2020; Cong et al. 2014; Ortega-Hernández 2015; Van Roy et al. 2015; Lerosey-Aubril and Ortega-Hernández 2022; Moysiuk and Caron 2021, 2022; Potin and Daley 2023). These discoveries have documented at least two major diversification pulses within the group: (i) an early Cambrian radiation that gave rise to all four radiodont families and was dominated by Anomalocarididae and Amplectobeluidae; and (ii) a Miaolingian radiation of Hurdiidae during which they became the dominant group and the only lineage to survive into the Furongian (Zhu et al. 2021; Potin and Daley 2023; Wu et al. 2024).

Following the re-description of the genus *Hurdia* (Daley et al. 2009, 2013) and the discovery that it forms a clade with genera such as *Peytoia* and *Stanleycaris* (Vinther et al. 2014), Lerosey-Aubril and Pates (2018) formally created the family Hurdiidae to encompass radiodonts with a large tripartite cephalic carapace, frontal appendages with long,

laminiform endites that do not alternate in length, and a tetraradially arranged oral cone. Subsequent discoveries have led to revisions of the family's diagnosis (Wu et al. 2022; Potin et al. 2023), yet its monophyly has been consistently recovered in phylogenetic analyses (Moysiuk and Caron 2019, 2021, 2022, 2025; Caron and Moysiuk 2021; Paterson et al. 2023; Zeng et al. 2023; Wu et al. 2024). Although the drivers of the Miaolingian diversification of hurdiids remain poorly understood, their remarkable morphological disparity is compatible with the hypothesis that this radiation was adaptive and involved the exploitation of an increasingly broad range of ecological niches.

Hurdiids are well represented in the middle Cambrian (Drumian) Wheeler Formation of the House Range of Utah. Known taxa include *Pahvantia hastata* (Robison and Richards 1981; Lerosey-Aubril and Pates 2018; Lerosey-Aubril et al. 2020a), *Peytoia nathorsti* (Conway Morris and Robison 1982; Pates et al. 2018), *Stanleycaris* sp. (Pates et al. 2017), and possibly *Buccaspinea cooperi* (Lerosey-Aubril et al. 2020a; Pates et al. 2021). Here we describe *Acanthopahvantia boardmani* gen. et sp. nov., the fifth hurdiid species reported from the Wheeler Formation in the House Range. Although currently known only from a single central carapace element, the new taxon exhibits a highly distinctive morphology, thereby expanding the known morphological disparity of Hurdiidae.

Institutional abbreviations.—KUMIP, Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, Lawrence, USA; MCZ.IP, Department of Invertebrate Paleontology, Museum of Comparative Zoology, Harvard University, Cambridge, USA; NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, Jiangsu, China.

Other abbreviations.—exs., exsagittal; sag., sagittal; tr., transverse.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:FB7A763C-22A1-47E9-B5FB-EE3E81C679D7.

Material and methods

MCZ.IP.206009 was collected by William E. Boardman (Delta, Utah, USA) from Drumian Wheeler Formation strata exposed at the U-Dig Quarry in the House Range, Utah. The specimen is housed in the Department of Invertebrate Paleontology of the Museum of Comparative Zoology, Harvard University. The Wheeler Formation of western Utah, composed predominantly of calcareous mudstone with subordinate limestone, varies in thickness from c. 140 m in the House Range to more than 300 m in the Drum Mountains (Brett et al. 2009; Foster and Gaines 2016). It unconformably overlies the Swasey Limestone and records the initial infilling of the fault-controlled House Range Embayment, which developed during the latest Wuliuan. In the House Range, its Drumian upper part (*Ptychagnostus atavus* Biozone) has yielded a diverse (c. 95 species) exceptionally preserved fossil assemblage dominated by panarthropods (c. 55 species), including radiodonts (e.g., Robison et al. 2015; Pates et al. 2017, 2018; Lerosey-Aubril and Pates 2018; Lerosey-Aubril and Skabelund 2018; Lerosey-Aubril et al. 2020a, b; Lerosey-Aubril and Ortega-Hernández 2026). Additional information on the Wheeler Formation in the House Range and its paleontological assemblages is provided by Robison et al. (2015), Foster and Gaines (2016), Lerosey-Aubril et al. (2020a), and references therein.

MCZ.IP.206009 was photographed under parallel-polarized light and cross-polarized light immersed in dilute ethanol using a Nikon D5500 DSLR fitted with a Nikon 40 mm DX Micro-Nikkor lens. Series of images were taken with manual focusing on different focal planes and subsequently stacked in Adobe Photoshop CS6. The same software was used to create the interpretative drawing and to produce the two figures.

The new taxon was added to the phylogenetic matrix of Wu et al. (2024), resulting in a dataset comprising 68 taxa and 208 morphological characters. This dataset was analysed through parsimony inference with TNT (Goloboff et al. 2008) using New Technology Search (Driven Search with Sectorial Search, Ratchet, Drift, and Tree fusing options activated) in standard settings under equal and implied weighting (Goloboff 1999; Nixon 1999). The analysis was set to find the minimum tree length 100 times and to collapse trees after each search, and all characters were treated as unordered. Additionally, we subjected the same dataset to a Bayesian inference analysis performed in MrBayes 3.2 using the Markov chain Monte Carlo (MCMC) model for discrete morphological characters (Lewis 2001; Ronquist et al. 2012). This analysis was run for 5 million generations with four chains, sampling every 1000 generations, and discarding the first 25% of samples as burn-in. Convergence was assessed in Tracer 1.7.2 (Rambaut et al. 2018), with all effective sample size values exceeding 200. Note that the recently described hurdiid *Mosura fentoni* (Moysiuk and Caron 2025) was not added to our phylogenetic analysis, as its unique trunk morphology would have required substantial modifications to the matrix of Wu et al. (2024), which were unnecessary for assessing the position of the new taxon within Hurdiidae.

The terminology used in this contribution follows Lerosey-Aubril and Pates (2018), Lerosey-Aubril et al. (2020a), and Pates et al. (2021).

Systematic palaeontology

Superphylum Panarthropoda Nielsen, 1995
Order Radiodonta Collins, 1996
Family Hurdiidae Lerosey-Aubril & Pates, 2018

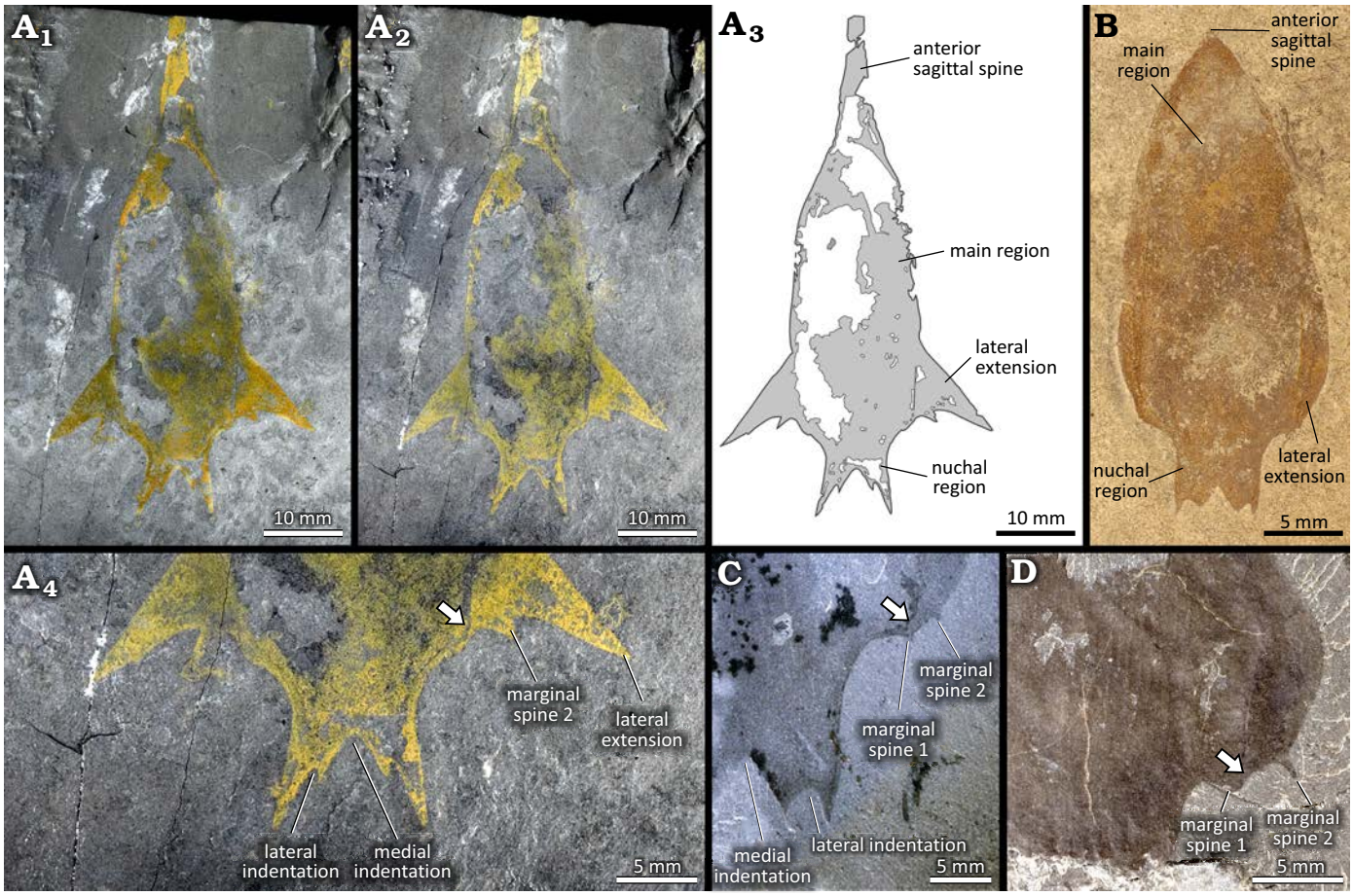


Fig. 1. Hurdiid radiodonts from the Drumian, middle Cambrian. **A**. *Acanthopahvantia boardmani* gen et sp. nov. from the Wheeler Formation, U-Dig Quarry, House Range, Utah. Holotype (MCZ.IP.206009), general view of specimen photographed wet using cross-polarized (A_1) and parallel-polarized (A_2) illumination; interpretative drawing (A_3); detailed view of the posterior third of the central carapace element (A_4), showing the tri-indented margin of the nuchal region and the spiniform lateral extensions; note the abaxial position of the marginal spine relative to the boundary between the main region and the lateral extension (arrow), hence its identification as marginal spine 2, by comparison with the condition in species of *Pahvantia* and *Cordaticaris*. **B**. *Pahvantia hastata* Robison & Richards, 1981, from the Wheeler Formation, U-Dig Quarry, House Range, Utah. Holotype (KUMIP134878), central carapace element in general view. **C**. *Pahvantia hastata* Robison & Richards, 1981, from the Marjum Formation, unknown locality, House Range, Utah. UMNH.IP6101, central carapace element, detailed view of the posterior margin of the left lateral extension (mirrored); note that one marginal spine is aligned with the boundary between the main region and the lateral extension (arrow), whereas the other is located abaxial to this boundary in a position similar to the sole preserved in MCZ.IP.206009. **D**. *Cordaticaris striatus* Sun et al., 2020a, from the Zhangxia Formation, Shandong Province, North China. NIGPAS 173111, central carapace element, detailed view of the posterior margin of the right lateral extension (arrow); note that the positions of the two marginal spines relative to the boundary between the main region and the lateral extension are similar to those in *P. hastata*.

Subfamily Hurdiinae Lerosey-Aubril & Pates, 2018

Remarks.—The new species belongs to the subfamily Hurdiinae recently defined by Moysiuk and Caron (2025). The authorship of this subfamily is credited to Lerosey-Aubril and Pates (2018) as per ICZN Article 36 (Joseph Moysiuk, personal communication 2026).

Genus *Acanthopahvantia* nov.

Zoobank LCID: urn:lsid:zoobank.org:act:4ABBD946-5653-4D24-992C-4033B0F47F1F.

Type species: *Acanthopahvantia boardmani* sp. nov., monotypic, see below.

Etymology: From the Greek *akantha*, spine, thorn; and *Pahvantia*, referring to its gross similarity to the genus *Pahvantia* while highlighting its much more pronounced spinosity.

Diagnosis.—As for monotypic type species.

Remarks.—The assignment of *Acanthopahvantia* gen. nov. to the radiodont family Hurdiidae and subfamily Hurdiinae is supported by the general organization of the central element of the cephalic carapace. The carapace element comprises a main region that extends anteriorly into a sagittal spine, a pair of lateral extensions, and a narrowed nuchal region separated from the main region by a marked posterolateral constriction corresponding to ocular notches (Fig. 1A). This overall morphology resembles that of the central carapace element of *Pahvantia* Robison & Richards, 1981 (Fig. 1B, C), a hurdiid genus known from the Wheeler Formation of the House Range and Drum mountains (Robison and Richards 1981; Lerosey-Aubril and Pates 2018; Lerosey-Aubril et al. 2020a) and from the slightly younger Marjum Formation of the House Range (Pates et al. 2021). However, *Acanthopahvantia* gen. nov. differs markedly from *Pahvantia* in several con-

spicuous features: (i) a much longer and more robust anterior sagittal spine; (ii) prominent spiniform lateral extensions rather than the narrow lateral lappets of *Pahvantia*; and (iii) a proportionally longer nuchal region, with more deeply incised lateral and median indentations (Fig. 1A–C).

The occurrence of both genera in the Wheeler strata at the U-Dig Quarry raises the possibility that these morphological differences reflect ontogenetic variation or sexual dimorphism within *Pahvantia hastata* Robison & Richards, 1981, the only described species of *Pahvantia*. We consider both hypotheses unlikely for three reasons. First, comparison of the main region indicates that MCZ.IP.206009 falls within the documented size range of the central carapace element of *P. hastata*, whose morphology appears to change only subtly throughout ontogeny (Pates et al. 2021). Second, *P. hastata* is relatively common in the Wheeler Formation of the House Range, being represented by over 20 central carapace elements (Pates et al. 2021 and unpublished data), whereas *Acanthopahvantia* gen. nov. is currently known only from the holotype of its type species, despite decades of collecting at the U-Dig Quarry and nearby Wheeler localities. Although sex ratios can vary substantially in arthropods, this marked disparity in abundance may weigh against interpreting the two forms as sexual morphs of a single species. Third, the morphological differences between the two taxa are conspicuous, readily recognizable, and substantially greater than any intraspecific variation documented to date in radiodonts (Fig. 1A–C). These observations support the interpretation of *Acanthopahvantia* as a distinct genus similar to, but clearly separable from, *Pahvantia*.

Acanthopahvantia gen. nov. shares the presence of a sagittal spine with the Burgess Shale *Hurdia* Walcott, 1912 (Daley et al. 2009, 2013) but otherwise differs from it in possessing a well-defined nuchal region with a deeply multi-indented posterior margin, spiniform lateral extensions, and a lanceolate, rather than broadly to narrowly triangular, outline of the central carapace element.

Acanthopahvantia gen. nov. resembles *Cambroraster* Moysiuk & Caron, 2019, *Cordaticaris* Sun et al., 2020a (Fig. 1D), and *Titanokorys* Caron & Moysiuk, 2021, in the pronounced development of the nuchal region (Moysiuk and Caron 2019; Liu et al. 2020; Sun et al. 2020a, b; Caron and Moysiuk 2021), but differs from these genera in the complex indentation pattern of its posterior margin (entire or with a single median indentation in the latter three taxa) and in the lanceolate, rather than horseshoe-shaped (*Cambroraster* and *Titanokorys*) or spade-shaped (*Cordaticaris*), outline of the central carapace element. *Acanthopahvantia* gen. nov. also possesses a robust anterior sagittal spine, whereas the anterior margin of the central carapace element in *Cambroraster* is rounded.

Lastly, the presence of spiniform lateral extensions in *Acanthopahvantia* gen. nov., each bearing a posterior marginal spine, is uniquely shared with *Zhenghecaris* Vannier et al., 2006 (Zeng et al. 2018). However, the two genera are readily distinguished by the overall shape of the central carapace element (lanceolate versus subquadrate) and by the presence of an anterior sagittal spine in *Acanthopahvantia* gen. nov., a feature absent in *Zhenghecaris*.

Acanthopahvantia boardmani sp. nov.

Fig. 1A.

Zoobank LCID: urn:lsid:zoobank.org:act:B76EB562-058B-4588-931E-BD50BC06FC32.

Etymology: In honour of William E. Boardman (Delta, Utah, USA), the collector of the holotype and currently only known specimen.

Type material: Holotype, MCZ.IP.206009 (part only), an isolated central element of a cephalic carapace.

Type locality: The U-Dig Quarry (GPS: 39.354792, -113.278643), House Range, Utah, USA.

Type horizon: Drumian part (*Ptychagnostus atavus* Agnostoid Biozone) of the Wuliuan–Drumian Wheeler Formation, middle Cambrian.

Material.—The holotype only.

Diagnosis.—Hurdiid radiodont exhibiting the following unique combination of characters. Central carapace element lanceolate (length/width ratio > 2) exhibiting: a robust anterosagittal spine at least c. one-fourth of the total element length; lateral extensions forming large posterolaterally projecting spines, each bearing a single small spine on the posterior margin; and a strong posterolateral constriction separating the main region from the nuchal region, the latter with three deep marginal indentations.

Description.—MCZ.IP.206009 (Fig. 1A) measures 63 mm in length (from the tip of the anterior sagittal spine to the posteriormost part of the nuchal region) and 34 mm in maximum width (tr., including the lateral extensions). The main region is elongate, c. 2.2 times longer (sag.) than wide (tr.), and accounts for c. 0.6 times the total fossil length (sag.); its lateral margins diverge slightly anteriorly along the posterior two-fifths, then increasingly converge anteriorly, giving the region an ogival outline (Fig. $1A_1$–A_3). The incomplete anterior sagittal spine accounts for c. one-fourth of the total fossil length (sag.); it has a particularly broad base, c. one-third of the width of the main region (tr.), and tapers only gently anteriorly, suggesting that the spine may originally have been up to twice its preserved length (Fig. $1A_1$–A_3). The nuchal region accounts for c. 0.15 times the total fossil length (sag.) and is less than two-thirds of the maximum width (tr.) of the main region (Fig. $1A_1$–A_3); it resembles a pair of acute spines owing to its deeply tri-indented posterior margin, in which the median indentation is noticeably wider (tr.) and deeper (sag.) than the two lateral indentations (Fig. $1A_4$). The posterolateral extensions arise from the posterior fourth (exs.) of the main region and form robust, posterolaterally directed spines slightly longer than wide, each bearing a short secondary spine along its posterior margin; the boundary between the right posterolateral extension and the main region is marked by a dark line (Fig. 1A).

Stratigraphic and geographic range.—Type locality and horizon only.

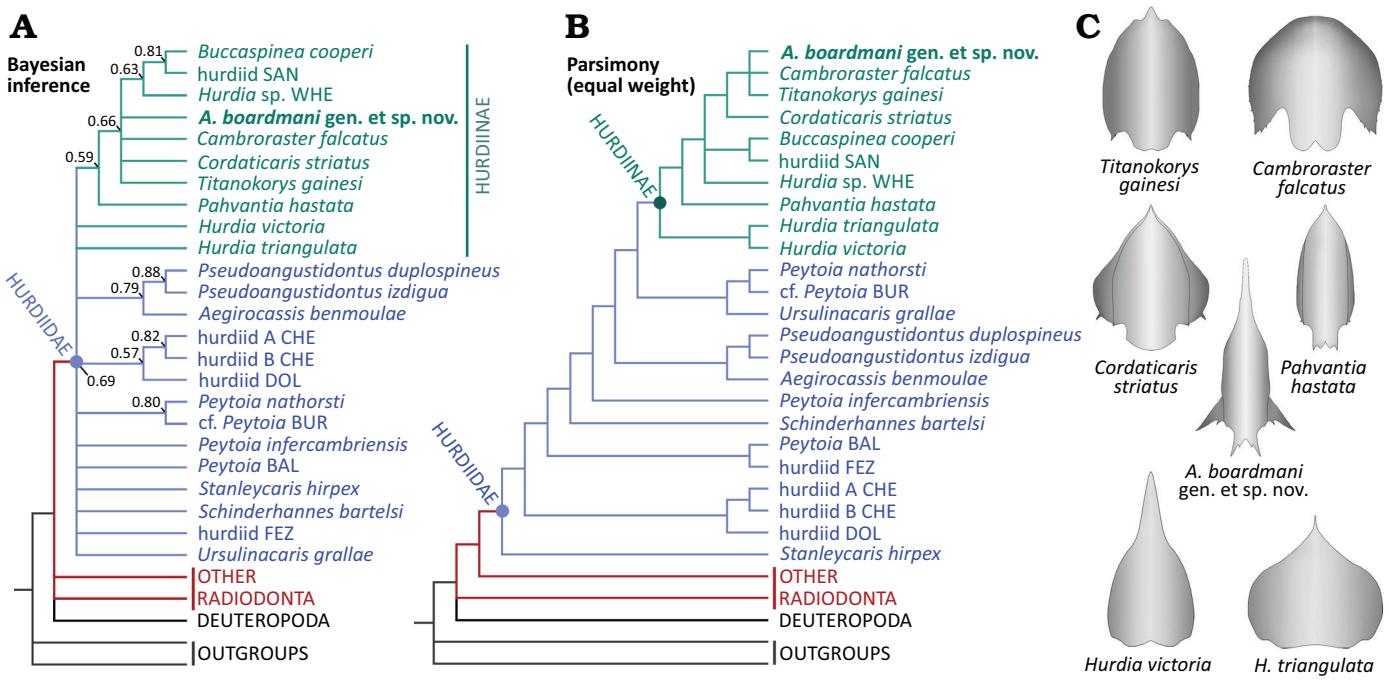


Fig. 2. Phylogeny and morphological disparity of hurdiid radiodonts. **A**, **B**. Phylogenetic position of *Acanthopahvantia boardmani* gen. et sp. nov., shown in simplified topologies of the strict consensus trees recovered from Bayesian inference (**A**) and equally weighted parsimony (**B**) analyses of the dataset of Wu et al. (2024) following the addition of the new taxon. **C**. Morphological disparity of the central carapace element in hurdiines; *Acanthopahvantia boardmani* gen. et sp. nov. uniquely combines a particularly elongate morphology with prominent spiniform lateral extensions. The grey gradient conveys three-dimensionality, with darker shades indicating greater distance from the viewer. Abbreviations: *Ac.*, *Acanthopahvantia*; BAL, Balang Formation; BUR, Burgess Shale Formation; CHE, Chengjiang Biota; DOL, Dol-cyn-afon Formation; FEZ, Fezouata Biota; SAN, Sandu Formation;WHE, Wheeler Formation.

Phylogenetic analysis

The Bayesian inference analysis recovers Hurdiidae as monophyletic, albeit poorly resolved, and comprising a monophyletic group composed of *Acanthopahvantia boardmani* gen. et sp. nov. and all the members of the Hurdiinae, except the two formally described species of the type genus *Hurdia* (Fig. 2A). The latter species form a polytomy with this monophyletic grouping of hurdiines and non-hurdiine hurdiids. This lack of resolution within Hurdiidae prevents us from assessing the monophyly of Hurdiinae using Bayesian inference. A similar topology was recovered in the Bayesian inference analysis of Wu et al. (2024, SOM 1: fig. S1, Supplementary Online Material available at http://app.pan.pl/SOM/app71-LeroseyAubril_OrtegaHernandez_SOM.pdf).

Acanthopahvantia boardmani gen. et sp. nov. forms a clade with *Cambroraster falcatus* and *Titanokorys gainesi* in all strict consensus trees recovered under the various parsimony settings (equal weighting, Fig. 2B; implied weighting with k = 1–10). This grouping reflects the shared presence of well-developed posterolateral extensions. In all recovered topologies, this clade is nested within a monophyletic Hurdiinae, itself nested within a monophyletic Hurdiidae.

Both phylogenetic analyses provide strong support for the familial and subfamilial assignments of the new taxon proposed herein.

Discussion

Acanthopahvantia boardmani gen. et sp. nov. represents the eleventh radiodont species reported from the middle Cambrian strata of Utah's West Desert to date (Pates et al. 2021). Hurdiids dominate the radiodont assemblages recovered from this region (Pates et al. 2021), except in the Weeks Formation, where the assemblage comprises only two anomalocaridid species (Lerosey-Aubril et al. 2014). *Pahvantia hastata* is known from the largest number of specimens in the Wheeler Formation (Robison and Richards 1981; Lerosey-Aubril and Pates 2018; Lerosey-Aubril et al. 2020a; Pates et al. 2021), but these consist almost exclusively of isolated central carapace elements (see Lerosey-Aubril and Pates 2018 for the rare known frontal appendage), leaving most of the anatomy of this taxon unknown. The three other hurdiids reported from western Utah, *Buccaspinea cooperi*, *Peytoia nathorsti*, and *Stanleycaris* sp., are all known from body parts other than central carapace elements (Conway Morris and Robison 1982; Briggs and Robison 1984; Pates et al. 2017, 2018, 2021; Lerosey-Aubril et al. 2020a). Although *A. boardmani* gen. et sp. nov. can readily be distinguished from *P. nathorsti* and *Stanleycaris* sp. based on cephalic carapace morphologies documented from other deposits (Collins 1996, his "*Laggania cambria*"; Moysiuk and Caron 2022), its possible assignment to *B. cooperi* cannot be ruled out entirely. *Buccaspinea cooperi* was described from an articulated specimen lacking all cephalic carapace elements, discovered at the Gray Marjum

locality of the Marjum Formation (e.g., Lerosey-Aubril et al. 2024; not Kells Knolls, as erroneously reported by Pates et al. 2021). Its occurrence in the Wheeler Formation of the House Range remains uncertain, being supported only by a frontal appendage tentatively referred to this species (Pates et al. 2021). We therefore consider that the current uncertainties surrounding the anatomy and stratigraphic distribution of *B. cooperi* should not preclude the establishment of a new hurdiid species from the Wheeler Formation.

The predominance of hurdiids in the middle Cambrian radiodont assemblages of Utah, reinforced by the description of *Acanthopahvantia boardmani* gen. et sp. nov., reflects a broader evolutionary trend within the clade's history. Following a rapid diversification that began around the Cambrian Series 2/Miaolingian boundary, hurdiids replaced anomalocaridids and amplectobeluids as the dominant radiodonts (Zhu et al. 2021; Wu et al. 2022, 2024), a pattern that persisted until the extinction of the clade. The unique morphology of the central carapace element of *Acanthopahvantia boardmani* gen. et sp. nov. combines features otherwise distributed among several hurdiine genera, further expanding the known disparity of hurdiid cephalic carapaces (Fig. 2B; Caron and Moysiuk 2021). This discovery adds to the growing evidence that the Miaolingian taxonomic diversification of hurdiids was accompanied by increasing morphological disparity, a pattern consistent with, although not in itself proof of, an adaptive radiation involving the exploitation of an increasingly broad range of ecological niches. Such ecological differentiation might explain the recurrent coexistence of multiple hurdiid taxa within Cambrian and Ordovician Konservat-Lagerstätten.

Conclusions

The description of *Acanthopahvantia boardmani* gen. et sp. nov. increases the documented diversity of Hurdiidae in the Drumian Wheeler Formation and further highlights western Utah as one of the world's richest records of middle Cambrian radiodont evolution. The co-occurrence of several hurdiids in the Burgess Shale and Wheeler formations suggests that their diversity in other prominent Miaolingian deposits, such as the Marjum Formation in the USA and the Zhangxia Formation in North China, may be underestimated. Continued collecting efforts in these and other fossil Lagerstätten will likely reveal additional hurdiid taxa, further refining our understanding of the timing, pace, and extent of the early radiation of these carapace-bearing radiodonts.

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Authors' contributions

RL-A and JO-H designed the project; RL-A prepared and photographed the specimen, made anatomical interpretation with inputs from JO-H, run the phylogenetic analyses, and prepared the figures; RL-A led manuscript writing and both authors contributed to editing the manuscript.

Editor: Andrzej Kaim

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