A 'hermit' shell-dwelling lifestyle in a Cambrian priapulan worm

Yang, Xiao-yu[1], Smith, Martin R.[2], Yang, Jie[1], Li, Wei[1], Guo, Qing-hao[1], Li, Chun-li[1], Wang, Yu[1], Zhang, Xi-guang[1]*

1. Yunnan Key Laboratory for Palaeobiology and MEC International Joint Laboratory for Palaeoenvironment, Yunnan University, Kunming, 650091, China

2. Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK

* Corresponding author

The Cambrian 'explosion', c. 530 million years ago, marks a rapid diversification of the major animal lineages [1]. A concomitant increase in the complexity of ecosystems is believed to have accelerated this evolutionary radiation [2], but direct evidence of the ecological modes of Cambrian taxa is nevertheless scarce – even in exceptional Burgess Shale-type deposits [3]. New fossil material from the Cambrian (Stage 4) Guanshan biota in southern China reveals a consistent occurrence of the priapulan worm *?Eximipriapulus* [4] within the conical shells of hyoliths. This represents the first direct evidence of a 'hermiting' life strategy – the adoption of a different organism's exoskeleton – in phylum Priapulida, and within the Palaeozoic Era; it highlights the intense degree of convergent evolution during the Cambrian radiation. Hermiting behaviour has previously been linked with the escalation of predation pressure during the Mesozoic Marine Revolution [5]: this intensity of predation may also have characterised early Cambrian oceans.

Four specimens (YKLP 12430–12433) are tentatively attributed to *Eximipriapulus* [4] based on their size (approximate body width: 2–4 mm; exposed body length: 10–18 mm; Figure 1; Table S1); their gross morphology, including a papillate trunk (Figure 1D–F) with a tendency to bend close to the base of the introvert; the narrow width of their eversible pharynx relative to the introvert (Figure 1A, B, D, E, G, K); and their proboscis armature (Figure 1A–E, G–J), which comprises longitudinal rows of broad to equant triangular introvert scalids, grading to elongate spines anteriad (Figure 1A–E, G), and fine, quincuncially arranged pharyngeal teeth (Figure 1K).

The posterior portion of each worm is situated between the upper and lower surfaces of an otherwise empty shell (Figure 1) with an apertural width 1.3–1.6 times wider than the exposed anterior portion of the worm (Table S1). The shells resemble the conical shells (‘conchs’) of hyoliths in Burgess Shale-type deposits in shape (apical angle: 5–10°), size (c. 16–18 mm in preserved length; 5–7 mm in apertural width, excluding a possible lateral breach in YKLP 12431), presence of growth lines (Figure 1A, B, D, E, J, K), and preservation style; their longitudinal grooves (Figure 1A, B) and distinctive discoidal larval shell (Figure 1A, I) show a particular resemblance to the Chengjiang hyolith *Pedunculotheca* [6].

As the sampled horizons contain dozens of empty hyolith shells, but no other free-living ecdysozoan worms, we interpret the association as biological. Alongside the consistent co-occurrence, the correspondence in size suggests that the worms selected and dwelt within the shells, presumably for protection from predators, rather than, say, for temporary protection whilst moulting. An alternative possibility, that shells were used as temporary shelter from the hostile conditions of a burial event, is difficult to reconcile with the organisms’ orientation and incomplete withdrawal, the specificity to hyolith shells of a consistent relative size, the absence of *?Eximipriapulus* specimens that failed to find shelter, and the absence of sheltering behaviour in other taxa.

This first report of ‘hermiting’ in Priapulida expands the early ecological disparity of this important Cambrian group, and accentuates the magnitude of the ecological shift that separates the macroscopic, often epibenthic Cambrian representatives from the predominantly meiofaunal crown-group priapulans [1, 7].

Hermiting has evolved in a diverse range of lineages, including hermit crabs (Paguroidea), tanaid crustaceans, certain sipunculans, and fauveliopsid annelids; most of these taxa prefer gastropod shells, but in certain cases inhabit tubes and shells of polychaetes, scaphopods, and foraminifera. Hermiting taxa are often close relatives of lineages that manufacture their own tubes (e.g. the tanaid *Typhlotanais*; certain fauveliopsids [8]), consistent with the construction of tubes by secretion in Cambrian selkirkiid priapulans, and by agglutination in the Recent priapulan *Maccabeus*. Despite the wide phylogenetic distribution of this habit, hermiting clades are geologically young, and (notwithstanding inconclusive Cambrian trace fossils [9]) a hermit lifestyle has not been directly observed until the mid-Jurassic (c. 170 Ma), in concert with the ‘Mesozoic marine revolution’, a prominent escalation of predation pressure [5]. Whilst acknowledging that our conclusions rest on a relatively small number of specimens, the indication that this otherwise modern lifestyle evolved independently early in the Cambrian, together with the recent description of gregarious, commensal tube-sharing [10], would reinforce a growing sense that the earliest complex animal ecosystems were more contemporary in character than has traditionally been assumed – countering the view that predation intensity has increased monotonically through the Phanerozoic. Taken alongside the early Cambrian rise and subsequent decline of taxa with high metabolic activity [6], this contributes to an emerging picture [3,10] that the Cambrian explosion was characterized by highly complex, predator-heavy ecosystems.

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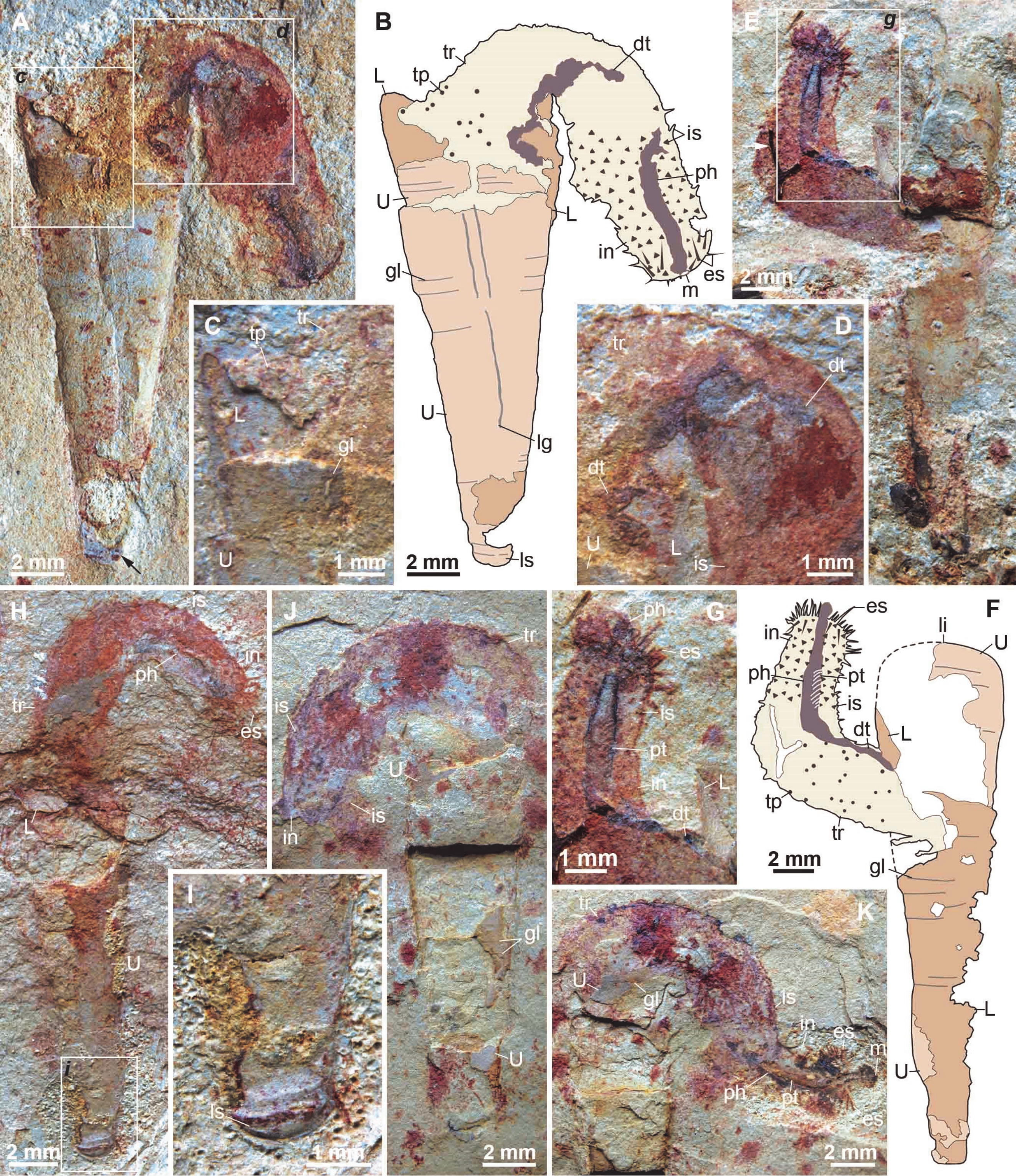
Figure Caption

Figure 1. Shell-dwelling behaviour in the Cambrian Stage 4 priapulan *?Eximipriapulus* sp. (A–D) YKLP12430, showing soft-part preservation within the worm’s trunk, situated between the upper and lower surfaces of the hyolith conical shell. (E–G) YKLP12431, with well-preserved pharyngeal armature; lateral emergence interpreted as evidence of breakage in original shell; black arrows denote modern plant roots on bedding surface. (H, I) YKLP 12432, showing larval shell of hyolith; (J, K) YKLP 12433, part (J) and counterpart (K). Abbreviations: dt, digestive tract; es, elongate spine; gl, growth lines; in, introvert; is, introvert scalid; L, lower shell surface; lg, longitudinal groove; li, ligula; ls, larval shell; m, mouth; ph, pharynx;

pt, pharyngeal teeth; tp, trunk papillae; tr; trunk; U, upper shell surface.



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