

# Current Biology

## A 425-Million-Year-Old Silurian Pentastomid Parasitic on Ostracods

### Highlights

- A 425-million-year-old pentastomid is the first adult example from the fossil record
- It is the only known fossil pentastomid preserved with its host
- Uniquely among pentastomids, some specimens are attached to the host externally
- Living pentastomids may have originated as ectoparasites on marine invertebrates

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### In Brief

Most Recent pentastomids are parasitic on vertebrates. Siveter et al. describe a 425-million-year-old pentastomid—the first fossil adult examples and the only known fossil pentastomid preserved with its (ostracod) host, including, uniquely, some specimens attached externally. Pentastomids may have originated as ectoparasites on marine invertebrates.

# A 425-Million-Year-Old Silurian Pentastomid Parasitic on Ostracods

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## SUMMARY

Pentastomids (tongue worms) are worm-like arthropods known today from ~140 species [1]. All but four are parasitic on vertebrates. Their life cycle typically involves larval development in an intermediate host followed by maturation in the respiratory tract of a definitive terrestrial host. Fossil pentastomids are exceedingly rare and are known only from isolated juveniles [2–6]. The identity of the possible hosts of fossil pentastomids and the origin of their lifestyle have generated much debate. A new, exceptionally preserved species, described based on adults from 425-million-year-old marine rocks, is the only known fossil pentastomid associated with a host, in this case a species of ostracod crustacean. The pentastomids are preserved near eggs within the ostracod and also, uniquely for any fossil or living pentastomid, are attached externally to the host. This discovery affirms the origin of pentastomids as ectoparasitic on marine invertebrates. The terrestrialization of pentastomids may have occurred in parallel with the vertebrate invasion of land.

## RESULTS

There are ~140 living pentastomid species. All but four, which infest insects, are obligate parasites in fish or tetrapods, particularly reptiles but also including humans [1]. Although direct development can occur in a single host, the life cycle of pentastomids normally involves larval development and molting in an intermediate host followed by maturation (adults 1–16 cm long) in the respiratory tract of a definitive host, typically a terrestrial tetrapod [2]. Fossil pentastomid species are exceedingly rare and are based only on isolated juveniles, of Cambrian or Ordovician age [2–6]. Here we document a new, exceptionally preserved fossil pentastomid species based on adults associated with a host, which in this case is a marine ostracod crustacean from Silurian-age rocks.

*Invavita piratica* is a new pentastomid genus and species provisionally assigned to the order Cephalobaenida. It is based on

adult specimens from the marine mid-Silurian Herefordshire Lagerstätte (about 425 million years before present [7, 8]), England, and is preserved in association with the ostracod crustacean *Nymphetelina graviga* Siveter et al., 2007 [9]. The name of the pentastomid alludes to its parasitic lifestyle and marine habitat (“invasor,” intruder, plus “avitus,” ancient; “piratica,” piracy). All of the specimens are preserved in carbonate nodules and reconstructed as virtual fossils through physical-optical tomography [10, 11].

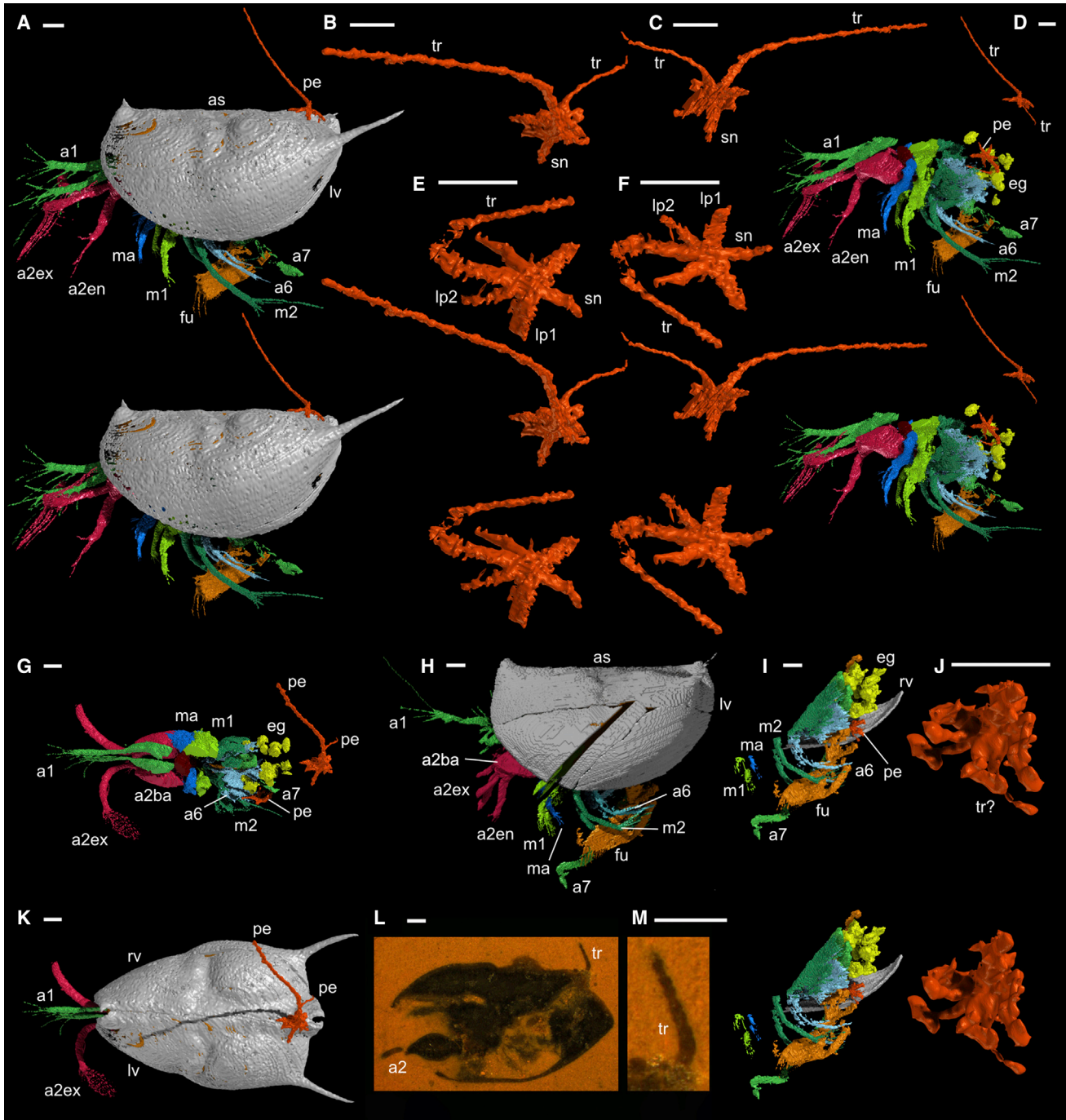
## Material

The material is registered at Oxford University Museum of Natural History (OUMNH). The holotype specimen (OUMNH C.29677; Figures 1D–1G) is preserved within the domicilium of a specimen of the ostracod *Nymphetelina graviga* (OUMNH C.29678), adjacent to tiny globular to elongate structures interpreted as the eggs of the ostracod host. Two other pentastomid specimens (OUMNH C.29679 and OUMNH C.29680) are attached, with the head of one overlapping that of the other, to the external surface of the carapace of the same ostracod specimen, a unique position for any fossil or living pentastomid (Figures 1A–1D, 1G, and 1K). A further pentastomid (OUMNH C.29681; Figures 1I and 1J) occurs within the domicilium of the holotype of *N. graviga* (OUMNH C.29600; Figures 1H and 1I).

## Description

The head of the holotype (Figures 1E and 1F) is slightly convex dorsally and weakly concave ventrally and bears five similar-shaped, elongate, gradually tapering projections each ~0.34 mm long. The projection aligned with the axis of the trunk is interpreted as the snout. The other four projections represent two limb pairs extending laterally at about 45° to the axis of the body. The head is 0.15 mm long excluding the snout. The long, slender trunk tapers gradually from its junction with the head to an acute tip (Figures 1E and 1F). It is ~1.6 mm long and 0.13 mm at its widest point and is preserved flexed through ~130° at about one-third of its length.

The presumed snout of OUMNH C.29679 is ~0.35 mm long; its limbs are less well preserved, especially the posterior pair, which are difficult to distinguish from the underlying head region and limbs of OUMNH C.29680 (Figures 1B–1D, 1G, and 1K). The trunk of OUMNH C.29679 is 3.3 mm long, 0.12 mm at its widest



**Figure 1. The Pentastomid *Invavita piratica* in Association with the Ostracod *Nymphetelina gravidia***

(A–G and K–M) *I. piratica* (OUMNH C.29677, C.29679, C.29680) attached to *N. gravidia* (OUMNH C.29678).

(A) Left lateral view of *N. gravidia* with *I. piratica* (OUMNH C.29679, C.29680) attached posterodorsally.

(B and C) “Dorsal” and “ventral” views of overlapping *I. piratica* specimens OUMNH C.29679 and C.29680.

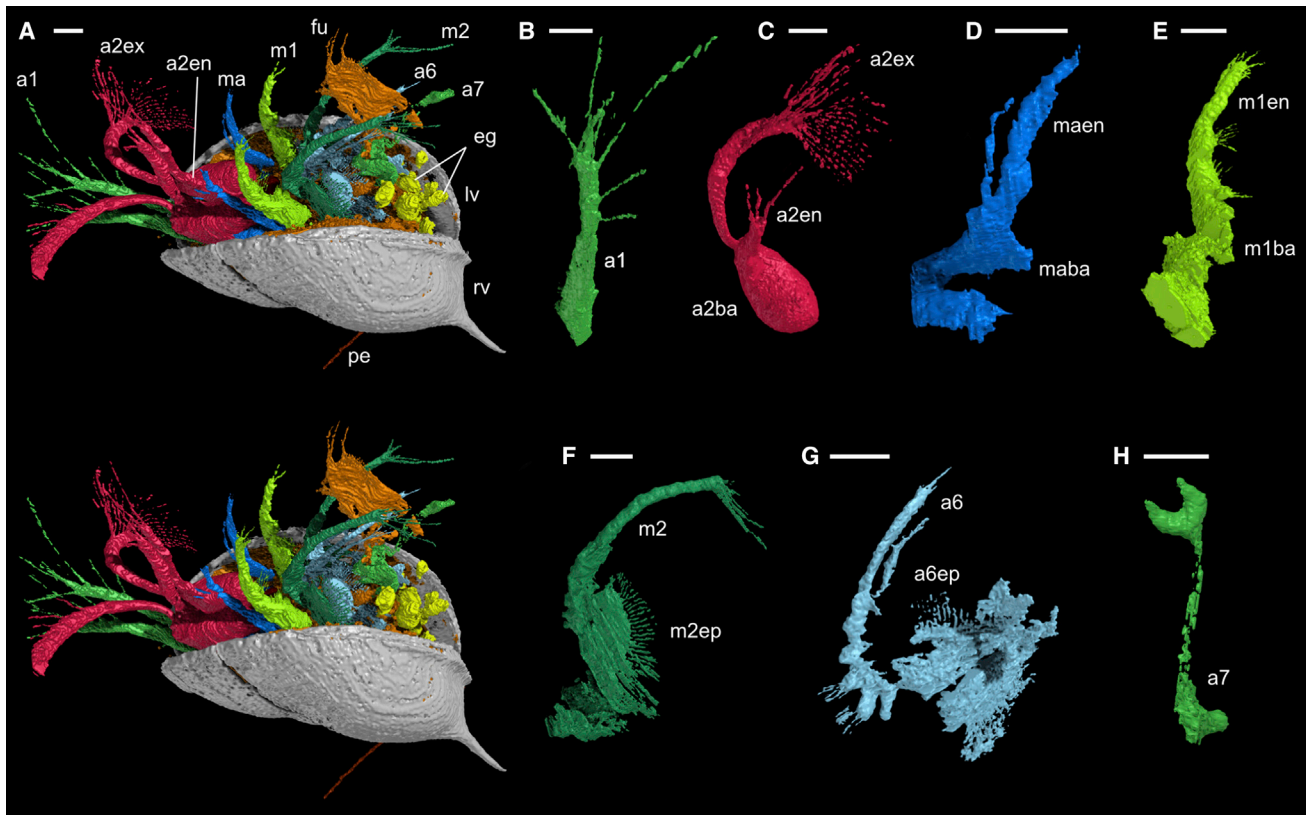
(D) Left lateral view of *N. gravidia*, with valves and unidentifiable material removed, showing two specimens of *I. piratica* posterodorsally (OUMNH C.29679, C.29680) and one internally adjacent to eggs (holotype, OUMNH C.29677).

(E and F) “Dorsal” and “ventral” views of holotype of *I. piratica*.

(G and K) Dorsal views of *N. gravidia* with valves removed and present, respectively, showing *I. piratica* specimens OUMNH C.29679 and C.29680 attached posterodorsally.

(L and M) *I. piratica* attached to *N. gravidia* in rock prior to serial grinding (i.e., section along primary split of the rock), showing the complete specimen and a detail of *I. piratica* (OUMNH C.29679) on the external surface of carapace.

(legend continued on next page)



**Figure 2. The Limbs of the Ostracod *Nymphetelina gravaida*, Specimen OUMNH C.29678**

(A) Right ventral oblique view, stereo-pair, of *N. gravaida* with the pentastomid *I. piratica* (OUMNH C.29679) attached posterodorsally.

(B–H) Appendages of *N. gravaida*, oblique posterior approximately medial views: left first antenna (B), left second antenna (C), left mandible (D), mirror image of right first maxilla (left limb is less well preserved) (E), mirror image of right second maxilla (left limb is less well preserved) (F), left sixth appendage (G), and left seventh appendage (H).

Images are “virtual” fossils. All scale bars are 0.5 mm. Abbreviations are as in Figure 1.

point, and is gently curved at  $\sim 0.5$  mm from the head (Figures 1B–1D, 1G, and 1K). Closely spaced undulations in the trunk outline, each  $\sim 0.10$  mm long, are interpreted as annulations (Figure 1M). The trunk of OUMNH C.29680 is 1.0 mm long, 0.75 mm at its widest point, and is gently curved overall with a sharp flexure at the tip (Figures 1B–1D, 1G, and 1K). None of the pentastomid specimens preserves evidence of the mouth, anus, or details of the limbs such as possible podomeres and claws.

Specimen OUMNH C.29681 preserves six or possibly seven narrow, elongate, bent, and crumpled projections (Figures 1I and 1J) and is interpreted as a poorly preserved pentastomid. One projection is  $\sim 0.33$  mm long, and the longest projection,  $\sim 0.40$  mm long, is interpreted as the remains of the trunk. The six (?) other projections may represent taphonomic distortion of five head protuberances of a single specimen rather than more than one individual.

### The Limbs of *Nymphetelina gravaida*

The specimen of the myodocopid ostracod *N. gravaida* (OUMNH C.29678; Figures 2A–2H) that contains the pentastomid holotype preserves new details of the ostracod appendages that are not evident in the holotype [9]. The first appendage bears two long, fine, subparallel setae distally in addition to the four long, fine terminal/subterminal setae (Figures 2A and 2B). The gently curved distal part of the exopod of the second antenna (clearly evident in the left limb) bears an array of long, fine setae—about 7 on the outer edge and 15 shorter ones forming a terminal splay (Figures 2A and 2C). This arrangement is remarkably similar to that in the same appendage in Recent cylindroleberid myodocopes, in which a long proximal podomere is succeeded by podomeres 2–8, each with a seta, and podomere 9 bearing multiple setae. The exopod of the mandible of *N. gravaida* (well preserved in the left limb) is slender, gently curved, and about two-thirds

(H–J) Specimen of *I. piratica* (OUMNH C.29681) associated with the holotype of *N. gravaida* (OUMNH C.29600) showing left lateral view of *N. gravaida* (H), *I. piratica* in the posteroventral part of the domicilium (left valve and unidentifiable material removed) (I), and *I. piratica* (J).

(A)–(K) are “virtual” fossils. (L) and (M) are photographs. (A)–(F), (I), and (J) are stereo-pairs. All scale bars represent 0.5 mm. The following abbreviations are used: a1, first antenna; a2ba, a2en, and a2ex, basipod, endopod, and exopod of second antenna; a6, sixth appendage; a6ep, epipod of sixth appendage; a7, seventh appendage; as, adductorial sulcus; eg, eggs; fu, furca; hd, head of pentastomid; la, labrum; lv, left valve; lp1, first limb pair; lp2, second limb pair; m1, first maxilla; m1ba and m1en, basipod and endopod of first maxilla; m2, second maxilla; m2ep, epipod of second maxilla; ma, mandible; pe, pentastomid; rv, right valve; sn, snout of pentastomid; tr, trunk of pentastomid.

the length and one-quarter the width of the endopod (Figures 2A and 2D). The endites of the limb stem of the first maxilla are finely setose; the proximal part of the slender ramus (presumed endopod) bears multiple setae on its inner edge and on its distal extremity (Figures 2A and 2E). The curved outer margin of the epipod of the second maxilla (clearly evident in the right limb) bears a row of more than 25 tiny slender setae (Figures 2A and 2F). The basal part of the long, slender, gently curved ramus of the sixth limb bears at least three well-developed, adaxially projecting setose endites, distal to which an elongate seta-bearing structure projects from and extends parallel to the main ramus (Figure 2G). The curved outer margin of the epipod of the sixth limb bears a row of at least 15 tiny, slender setae (Figure 2G). The tip of the vermiform seventh limb (only the left limb is preserved; Figure 2A and 2H) has a well-developed V-shaped indentation like that in many Recent cylindroleberid myodocopes, but the fossil shows no evidence of the bristles and spines present along the margin of the indentation as occurs in living forms.

This new evidence confirms the myodocopid affinity of *Nymphatolina*. The additional details of the appendages emphasize their similarity to those of living forms and the remarkable stasis in the morphological evolution of the group [9].

## DISCUSSION

*Invavita piratica* shares the principal features of the head and trunk tagmata of Pentastomida: a short head region with five projections comprising two pairs of limbs and a forward axial structure (which bears the mouth centrally in living forms), and an annulated vermiform trunk. *I. piratica* is most similar in its general anatomy to the order Cephalobaenida, as represented by the monotypic *Cephalobaena*, of the living pentastomid groups [1, 12–14]. *I. piratica*, like *Cephalobaena tetrapoda*, has elongate finger-like cephalic limbs, a snout at the presumed position of the mouth, and an annulated trunk. It differs from other fossil and Recent pentastomids in the symmetrical star-like arrangement of the projections on the head. The lack of preservation of finer morphological details of the head, limbs, and trunk (e.g., tagmosis) precludes further taxonomic resolution. In tentatively assigning *I. piratica* to the Cephalobaenida, we posit that a crown-group pentastomid may have been present in the Silurian. It is likely that sequence data will be necessary to resolve the debate on the phylogenetic position of pentastomids [15, 16], which are currently regarded either as derived from the euarthropod stem lineage or as closely related to the branchiuran crustaceans (fish lice) (e.g., [2, 4–6, 17–21]).

Reports of parasitic associations of animals through the Phanerozoic fossil record are rare [22–24]. Previous records of fossil pentastomids are exceedingly rare and are based exclusively on larval forms preserved by replication in calcium phosphate (“Orsten”-type preservation) in late Cambrian to earliest Ordovician deposits [2–6]. This discovery of an adult pentastomid in the Silurian Herefordshire Lagerstätte identifies for the first time the host of a fossil pentastomid and shows that the group exhibits remarkable evolutionary stasis in gross morphology [4]. Only four of the ~140 known species of living pentastomids parasitize non-vertebrates, and in each case,

the (intermediate) host is an insect—a scarabaeid beetle and three cockroach species [1]. In contrast to Recent pentastomids, the host of *I. piratica* is a marine crustacean. Arthropods were previously suggested as potential hosts for fossil pentastomids, but in view of the rarity of these parasites in living arthropods, vertebrates such as conodonts were considered more likely candidates [4].

The three unequivocal specimens of *I. piratica* range from over 1 mm to almost 4 mm in length, and the limbs are well developed, unlike those of the older fossil pentastomids, especially the “hammer-head” and “round-head” types, which are interpreted as larvae [2–4]. Thus, the size and morphology of the *I. piratica* specimens supports their interpretation as adults, the first described from the fossil record. The size difference between the three specimens of *I. piratica* (OUMNH C.29679 is larger than both OUMNH C.29680 and the holotype OUMNH C.29677) might reflect sexual dimorphism: the females of living pentastomids are typically much larger than males [2, 25]. In harboring an adult pentastomid, the marine ostracod *N. gravis* is unique among living and fossil arthropods in serving as the definitive host. The rare examples of living insects infected by pentastomids represent intermediate stages in the life cycle of the parasite [1]. It is possible that *I. piratica* was transferred to vertebrates such as conodonts and fish when they consumed ostracods. Fish do not harbor adult pentastomids today but are common intermediate hosts for forms that parasitize a wide range of terrestrial reptiles [1].

Living pentastomids are exclusively endoparasitic, feeding on blood and other tissues in various parts of the gut-respiratory system (e.g., lungs, air sacs, and nasal and oral cavities) of the host [25]. The holotype of *I. piratica* and the poorly preserved pentastomid specimen OUMNH C.29681 are attached inside the domicilium of their respective ostracod hosts (Figures 1D and 1I). Gills occur in this position in other, similarly large myodocopid ostracods [26] such as the co-occurring *Colymbosathan* [27]. Gills may have been present in *N. gravis* but are not preserved due to their delicate nature and susceptibility to decay: a posterior lamella of unidentified nature was noted in the holotype [9]. The pentastomids in *N. gravis* are attached next to the eggs, a possible alternative source of nutrients. Various crustaceans, including isopods and copepods, are frequently recorded as ectoparasites within the domicilium of living ostracods, especially myodocopes [28, 29]. The only other unequivocal case of parasitism in a fossil ostracod, however, is the occurrence of ciliates preserved in apatite within Triassic myodocopes scavenging on an ammonoid [30]. An analog to the parasitism of *I. piratica* on the Silurian ostracod *N. gravis* is provided by the isopod *Onisocryptus ovalis*, which attaches to females of the living myodocopid ostracod *Vargula hilgendorffii* near the heart and feeds on the brooded eggs [28].

It has been suggested that Cambrian-Ordovician pentastomids lived in the gill chambers of their unknown hosts [5] or were ectoparasitic to mesoparasitic with a possible free-living phase [2, 4]. This last possibility is directly supported by the attachment of two specimens of *I. piratica* (OUMNH C.20679 and C.20680) ‘one above the other’ to the external surface of the carapace of *N. gravis* (Figures 1A–1D, 1G, and 1K). These two individuals might represent a stage in the life cycle of *I. piratica*, discovered here for the first time in any fossil or living

pentastomid, before it migrated into the domicilium of the ostracod. Such a scenario suggests that *I. piratica* had some type of locomotory ability (Cambrian-Ordovician larval pentastomids may have crawled [4]). This ectoparasitic association suggests that, unlike extant pentastomids, all of which are transmitted passively when eaten [31], the Silurian pentastomid may have actively sought attachment to a host. Such external parasitism may have preceded the evolution of endoparasitism universal in living pentastomids. The biota of the Herefordshire Lagerstätte lived in marine waters at possibly 100–200 m depth [7, 8]. The discovery of an adult pentastomid parasitic on an ostracod in this environment shows that the life cycle of these parasitic arthropods evolved in a marine setting [4, 5] and was retained when pentastomids moved onto land in the gut-respiratory system of tetrapods. The timing of the terrestrialization of pentastomids is unknown but may have occurred with the mid-to late-Palaeozoic vertebrate invasion of land.

## EXPERIMENTAL PROCEDURES

Serial grinding, at 20  $\mu\text{m}$  intervals, of specimens preserved in carbonate nodules was followed by digital reconstruction of the morphology [10, 11] to produce virtual fossils. Some material of *Nymphatolina gravida* was lost to saw cuts in processing. Interpretation of the virtual fossils was facilitated by on-screen variable magnification, unlimited rotation, virtual dissection, and stereoscopic viewing using the SPIERS software suite, and by stereo-viewing hard-copy images.

## ACCESSION NUMBERS

Virtual models of two *Invavita/Nymphatolina* specimens in VAXML format [11] have been deposited with FigShare (<http://figshare.com>). DOIs and URLs for these datasets are <http://dx.doi.org/10.6084/m9.figshare.1246902> and <http://figshare.com/s/e80abfcc70c011e4b6b806ec4b8d1f61> (OUMNH C.29600 and OUMNH C.29681) and <http://dx.doi.org/10.6084/m9.figshare.1246901> and <http://figshare.com/s/d8e487f870c011e49f4506ec4b8d1f61> (OUMNH C.29677–C.29680). The raw datasets are curated at the Oxford University Museum of Natural History.

## AUTHOR CONTRIBUTIONS

David J. Siveter, Derek E.G. Briggs, Derek J. Siveter, and Mark D. Sutton carried out fieldwork. Mark D. Sutton reconstructed the specimens. David J. Siveter wrote the manuscript with scientific and editorial input from all authors.

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