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Experimental taphonomy of velvet worms (Onychophora) and implications for the Cambrian "explosion, disparity and decimation" model

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Abstract: Experimental preservation of velvet worms (phylum Onychophora), a very rare but evolutionarily important group that has existed for more than 500 million years, showed that the absence of bucal parts, adhesive-expelling organs, gonopore, eyes, legs, claws, annulation and papillation in fossils may not represent absence in the living animals. In fossils, leg thickness and claw orientation can be unreliable. The experiments indicate that not only absence, but even presence of certain structures can simply be the result of tissue decomposition. Computer-aided photorealistic reconstructions of fossil onychophorans are presented. We recommend future researchers to conduct taphonomy experiments specially before analysing unusual fossils.

Key words: Taphonomy, Cambrian, Onychophora, evolution, model, fossil, photorealistic reconstruction.

Onychophoran worms are rare and most biologists have never seen them alive, but they are important because they have been considered "missing links" between annelids and arthropods as well as "living fossils" because their shape has not changed for 500 million years (Monge-Nájera 1995, Hou and Bergström 1997). Nevertheless, only four of the 130 known species have been studied in some detail (Monge-Nájera 1994b, 1995, 1999) and invertebrate textbooks are not only outdated but also fail to transmit our ignorance about the great mayority of species (Monge-Nájera 2001).

Except for mandibles, onychophoran bodies are soft and unlikely to fossilize, but special conditions led to the fossilitation of several specimens (Monge-Nájera and Hou 2000), mainly in Chengjiang (China) and Burgess Shale (Canada), where they were marine during the Cambrian (all known living species are terrestrial and their continental distribution has been studied paleobiogeographically, Monge-Nájera 1996).

A recent study indicated that Cambrian onychophoran communities did not differ as much as expected from a modern coastal tropical community. The proportion of the total invertebrate population represented by onychophorans and even ecological indices that mathematically measure biodiversity were similar in the Cambrian and present (Monge-Nájera and Hou 2000). Evidence suggests that onychophorans have been evolving as a separate group by more than 500 million years and that the modern concept of a Cambrian "explosion" reflects an artifact of fossilization, in agreement with what was believed nearly 200 years ago (Monge-Nájera and Hou 2000).

Experimental taphonomy of extant species has been found useful to interpret certain fossils for almost two centuries (see Briggs and Kear 1994, Orr *et al.* 1998 for recent studies). This paper complements Monge-Nájera and

Hou's (2000) paleoecological study by reporting on experimental decay of these rare animals and presents computer-aided photorealistic reconstructions of extinct onychophorans.

MATERIALS AND METHODS

To test the effect of compression and decay on onychophoran bodies five *Epiperipatus biolleyi* Bouvier, 1902 from Coronado, San José, Costa Rica (collected December 1992 and March 1993) were killed with an overdose of ethyl acetate (Monge-Nájera and Morera 1994) and placed in a 0.5 cm thick bed of marine mud (from the Punta Morales mudflat, Costa Rica, described by Vargas 1998 a,b, 1996) under a weight of 17 kg. This compression was used to simulate burial under a layer of sediment, as some believe was the case when the fossilized animals died (Conway Morris 1985, Hou *et al.* 1991). The pressure was enough to obtain a degree of flatening that in our opinion is similar to the one perceived in the fossils. Decay is very rapid in onychophorans, and for this reason three of the specimens were compressed 3.5 hr in mud and marine water and photographed. For comparison, the other two were left in mud with 70 % ethanol to prevent the action of decomposing microorganisms and photographed after 24 hr because no macroscopic indication of change had been noticed in that period.

A computer was used to produce photorealistic reconstructions of fossil onychophorans by applying standard functions of the software Photoshop 5.0 to photographic material of living onychophorans' skin texture, color and body shape.

RESULTS

In experimentally compressed onychophorans the general body shaped was preserved (Fig. 1) but mouth, mandibles, adhesive-expelling organs (that look like tip-less legs) and gonopore became invisible or indicated only by a spot (Fig. 1).

Mandibles were visible only in an individual that died with the mouth extruded. The eyes were always invisible. The leg tips and claws were lost in some cases. When visible, the claws sometimes turned toward the front or toward the rear of the animal, losing their natural position. Some legs look thicker or even thinner than they were in life and when appressed against the body became practically invisible in some cases (Fig. 1).

Sand grains and organic remains from the mud may give a false impression of organs (Fig. 1). The digestive tract was never visible (Fig. 1). The only visible difference between specimens that decayed naturally and those that were placed in alcohol was that when bacterial decomposition was allowed, annulation and papillation disappeared from several body parts and portions of skin were detached, giving some antennae a slightly branched appearance (Fig. 1).

The above results served as a basis, together with the senior author's direct experience with living onychophorans, to produce the photorealistic reconstructions of Cambrian onychophorans that appear in Fig. 2.

DISCUSSION

The experimental compression results suggest that in fossil onychophorans (both Cambrian and Carboniferous) the general shape can be reconstructed but that the absence of bucal parts, adhesive-expelling organs, gonopore, eyes, annulation, papillation, leg tips, claws and even whole legs, may not represent absence in the living animals. In the past, ways of feeding alien to onychophorans have been proposed because mandibles were not found (*e.g.* Robison 1985, Chen *et al.* 1995) but our results do not support those hypotheses.

Furthermore, in fossils, leg thickness and claw orientation may be unreliable and the branched antennae, interpreted as "grasping

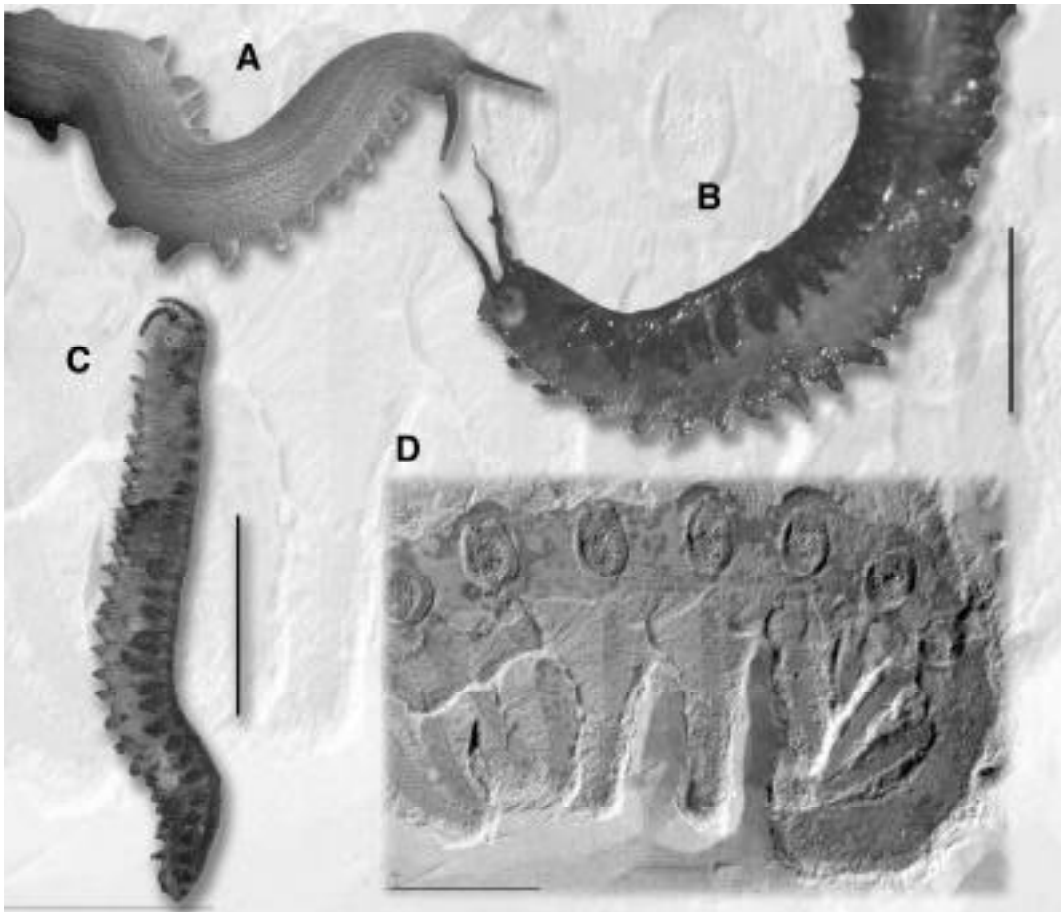

Fig. 1. Effects of experimental compression in the extant onychophoran *Epiperipatus biolleyi* and a Cambrian fossil of similar body posture. A. The living animal. B – C. Compressed dead *E. biolleyi*. D. *Microdyction sinicum* (fossil).

organs" in *Aysheaia* (review in Gould 1989) may also be post-mortem artifacts. The long papillae of *Onychodictyon* (Hou and Bergström 1995) could similarly be artifacts: more fossils are required to conclude that they were real.

Several reasons have been proposed to explain why longitudinal bands thought to represent the digestive tract vary their position in fossil onychophorans (Chen *et al*. 1995) but experience with dissection of extant species shows that this is normal for many internal organs because there are no mesenteries to hold them in a fixed position (J. Monge-Nájera personal observation).

Unidentified bands in fossil legs have been mentioned by Chen *et al.* (1995). We believe that they may represent the normal fluid-filled cavity of living onychophoran legs (Bouvier 1905). Neither these bands nor indication of the digestive tract were visible in the experimentally compressed specimens: apparently they must be formed as part of fossilization rather than during decay.

For centuries, science has been limited to drawings for the reconstruction of extinct species. Computer aided reconstructions became available at the end of the 20th century and have been extensively used to reconstruct dinosaurs in educational material but not in the

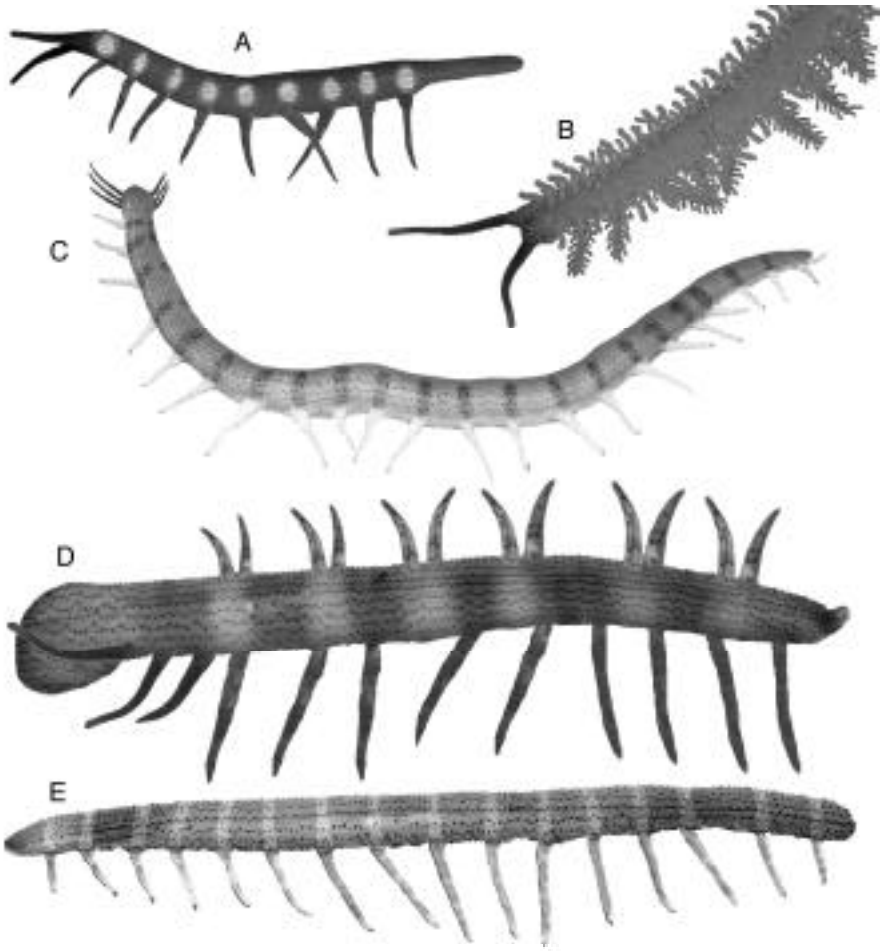

Fig. 2. Computer generated reconstructions of the fossil onychophorans. Despite their photorealistic appearance, these images are only the authors'interpretation of fossil impressions that have other possible interpretations. A: *Microdictyon sinicum*; B: *Onychodictyon ferox*; C: *Cardiodictyon catenulum*; D: *Hallucigenia fortis*; E: *Luolishania longicruris.*

primary scientific literature, despite the more satisfactory realism possible with computers. This may represent cultural inertia but another possible reason is that in contrast with photorealistic images, drawings are inmediately perceived as mere interpretations. If this is correct, we expect our use of photorealistic reconstructions to be controversial. However, we consider photorealism a superior method for the reconstruction of the organisms' appearance, which also is the goal of drawings. Photorealism appears valid to us as long as it is clearly stated that the images are reconstructions, as we have done here.

These experiments indicate that not only absence, but even presence of certain structures that may lead to the proposal of comprehensive evolutionary models such as the Cambrian "explosion, disparity and decimation" model (Gould 1989), can simply be the result of tissue decomposition. We recommend future researchers to conduct taphonomy experiments specially before analysing unusual fossils.

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RESUMEN

La preservación experimental de los gusanos "aterciopelados" u onicóforos (Phylum Onychophora), un grupo poco común pero evolutivamente importante que ha existido por más de 500 millones de años, mostró que la ausencia de partes bucales, glándulas secretoras de adhesivo, gonoporo, ojos, patas, garras, anulación cuticular y papilas en los fósiles, puede no representar la ausencia de tales órganos en los organismos vivos. No son confiables el grueso de las patas y la orientación de las garras (uñas), pues se modifican durante la preservación. Los experimentos indican que no sólo la ausencia, sino también la presencia de ciertas estructuras pueden ser simplemente resultado de la descomposición de los tejidos. Se presentan reconstrucciones fotorrealistas computarizadas de onicóforos fósiles. Para futuras investigaciones, recomendamos conducir experimentos tafonómicos previos al análisis del material preservado, especialmente antes de analizar fósiles poco comunes.

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