

# A New Ichnospecies of *Arthropycus* from the Upper Cambrian-Lower Tremadocian of Northwest Argentina: Implications for the Arthropycid Lineage and Potential in Ichnostratigraphy

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A new ichnospecies of *Arthropycus* Hall 1852, *A. minimus*, is described from Upper Cambrian-Lower Tremadocian, shallow-marine strata of northwest Argentina. This new ichnospecies consists of small, long, regularly annulated hypichnial elements displaying subcircular to squarish cross-section and a ventral median groove. Side branches are occasionally present, but palmate, fan-like structures and scribbling patterns are absent. We adopt a relatively narrow diagnosis of *Arthropycus*, suggesting that roughly annulated, cylindrical structures should not be included in this ichnogenus, unless other diagnostic features (i.e., squarish cross-section, median groove, zipper-like annulations) are also present. *Arthropycus* is a common ichnotaxon in Ordovician-Silurian shallow-marine siliciclastic environments. Post-Paleozoic occurrences are removed from *Arthropycus*. *Arthropycus* has been proposed as a biostratigraphic index fossil in Ordovician-Silurian rocks. The presence of *A. minimus* in the Santa Rosita Formation of northwest Argentina indicates that *Arthropycus* ranges at least from the Upper Cambrian-Lower Tremadocian with probable representatives in the Lower Cambrian and, therefore, its biostratigraphic utility is extended. *Arthropycus minimus* represents the first Cambrian occurrence exhibiting not only fine, diagnostic morphologic features, but also the classical *Arthropycus* behavioral pattern in dense monoichnospecific assemblages. The exploratory behavioral pattern displayed by *A. minimus* is simpler than that of the younger ichnospecies, particularly *A. brogniartii*, *A. alleghaniensis*, and *A. lateralis*. This is consistent with the basal position of *A. minimus* within the arthropycid lineage.

**Keywords** *Arthropycus*; ichnostratigraphy; Paleozoic; Cambrian-Ordovician; shallow marine; Argentina

## INTRODUCTION

Considerable attention has been focused recently on the ichnogenus *Arthropycus*, particularly its behavioral pattern, biologic affinities (i.e., worm vs. arthropod producers), and biostratigraphic significance (e.g., Seilacher, 2000; Fernandes et al., 2000; Neto de Carvalho et al., 2002, 2003; Rindsberg and Martin, 2003; Baldwin and Strother, 2004). *Arthropycus* Hall 1852 is a distinctive trace fossil composed of dominantly horizontal structures with a secondary teichinoid component, characterized by conspicuously regular annulations, cylindrical to squarish cross-section and a ventral median groove (Häntzschel, 1975; Fernandes et al., 2000; Seilacher, 2000). *Arthropycus*, the type ichnogenus of the ichnofamily Arthropycidae (see Seilacher, 2000; Rindsberg and Martin, 2003), is a feeding structure (foodichnion) well known in Ordovician and Silurian shallow-water quartzites.

Outside the usual size range of this ichnotaxon, tiny structures found in Upper Cambrian-Lower Tremadocian deposits of the Santa Rosita Formation in northwest Argentina (Fig. 1) otherwise fit *Arthropycus* morphologically and in terms of constructional and feeding program, and are, therefore, included as a new ichnospecies, *A. minimus*. Further re-evaluation and ichnotaxonomic discussion of *Arthropycus* are presented, exploring constraints in ichnostratigraphic utility. Also, the implications for the arthropycid lineage and ichnostratigraphic potential of the new ichnospecies *Arthropycus minimus* are outlined based

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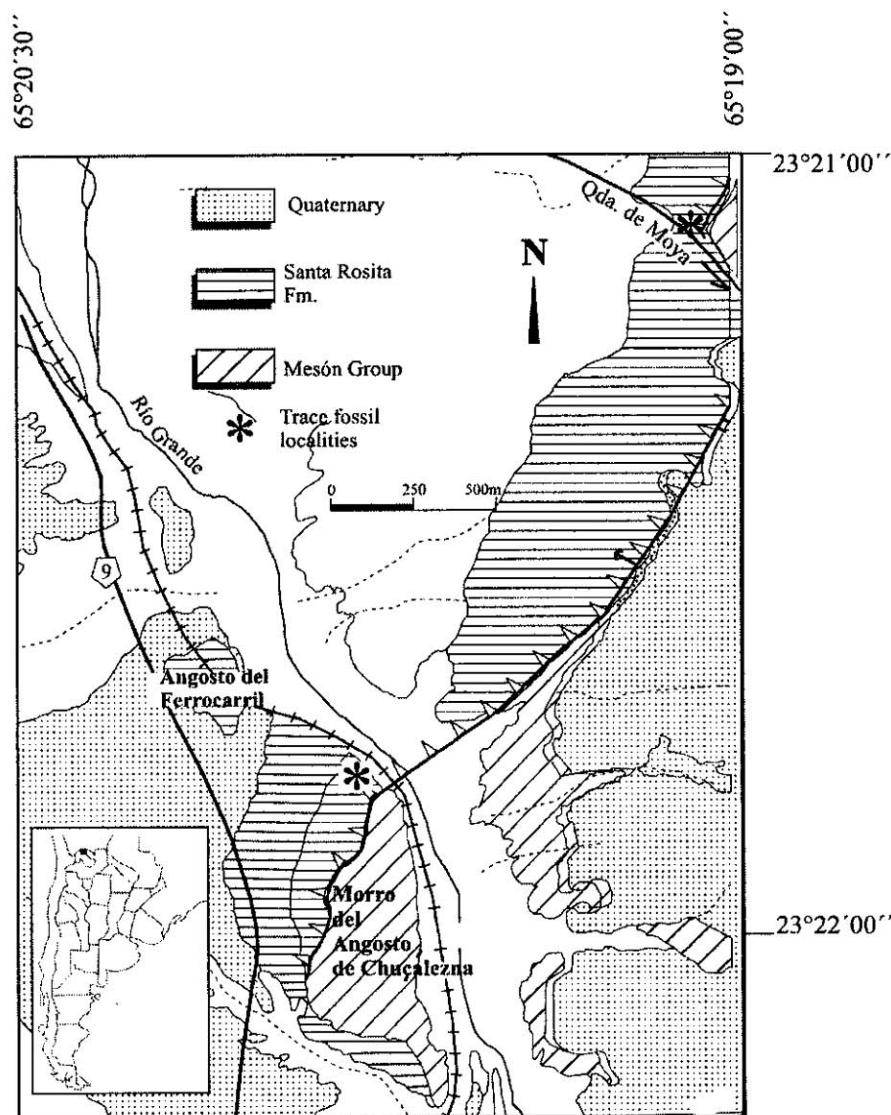


FIG. 1. Location map of the trace-fossil localities (modified from Mángano et al., 2002).

on its precise stratigraphic position in siliciclastic deposits of northwest Argentina.

#### STRATIGRAPHIC AND DEPOSITIONAL SETTING

The Santa Rosita Formation (Upper Cambrian-Tremadocian) is the lowermost unit of the Santa Victoria Group in Cordillera Oriental of northwest Argentina. This formation overlies the Cambrian Mesón Group and conformably underlies the Arenigian Acoite Formation (Turner, 1960). The Santa Rosita Formation is in turn divided, from base to top, into five members: Tilcara, Casa Colorada, Alfarcito, Rupasca, and Humacha members (Moya, 1988; Buatois and Mángano, 2003). The Santa Rosita Formation reflects a complex sedimentary history, including a wide range of depositional environments, such as fluvial, tide-dominated estuarine, and wave-dominated shallow marine

(Moya, 1988, 1999; Buatois and Mángano, 2003; Mángano and Buatois, 2003a, b).

The specimens of *Arthropycus minimus* were found in outcrops of the Santa Rosita Formation at Quebrada de Moya and Angosto del Morro de Chucalezna, close to the Rio Grande, along Quebrada de Humahuaca, Cordillera Oriental, Jujuy Province, northwest Argentina (Fig. 1). *Arthropycus minimus* is present in the lowermost fine-grained interval of the Alfarcito Member, which is made up of mudstone and thinly interbedded rippled sandstone that pass upwards into regularly interbedded mudstone and hummocky cross-stratified sandstone. The deposits represent a major transgressive-regressive cycle that records deposition in wave-dominated, open marine setting, mostly ranging from lower offshore to upper offshore and offshore transition environments (Mángano et al., 2002; Buatois and Mángano, 2003).

The late Cambrian age of these strata in this area is suggested by acritarchs (Rubinstein et al., 2003). However, the presence of the brachiopod *Nanorthis calderensis* Benedetto in the upper coarse-grained interval of the Alfarcito Member indicates an early Tremadocian age (Juan L. Benedetto, personal communication). This is consistent with paleontologic information from coeval strata in adjacent areas where integrated stratigraphic and biostratigraphic studies have been undertaken (e.g., Zeballo et al., 2003).

*Arthropycus minimus* occurs at the base of thin (1.0–2.5 cm), light gray, laterally extensive, erosively based, very fine-grained silty sandstone beds with parallel lamination, combined-flow ripple cross-lamination and symmetrical to near-symmetrical ripples with rounded tops. These sandstone layers are interbedded with parallel laminated, yellowish green and dark gray mudstone. Ripple amplitude is 0.3–1.0 cm; wavelength is 1.5–20 cm. Micro-hummocky cross-stratification and planar lamination are present in some of the thin sandstone beds. Gutter casts are relatively common. Small load casts and tool marks are present on the bases of some sandstone beds. The sandstone/mudstone ratios in this facies are low to rarely moderate (1:10 to 1:2). These deposits are included in the Facies J (mudstone and combined-flow rippled sandstone facies) of Buatois and Mángano (2003).

Although not commonly associated with *A. minimus*, other biogenic structures present in this facies include *Archaeonassa fossulata* Fenton and Fenton, *Arthraria antiquata* Billings, *Bergaueria* aff. *hemispherica*, *Cruziana problematica* (Schindewolf), *C. semiplicata* Salter, *Cruziana* sp., *Dimorphichnus* cf. *quadridens*, *Diplichnites* sp., *Gyrolithes* sp., *Gyrophylites* sp., *Monomorphichnus multilineatus* Alpert, *Palaeophycus striatus* Hall, *P. tubularis* Hall, *Phycodes* sp., *Planolites reinecki* Książkiewicz, *Rusophycus carbonarius* Dawson, *R. moyensis* Mángano et al., and *Skolithos linearis* Haldeman (Mángano et al., 2002, in press; Mángano and Buatois, 2003c). Poorly preserved specimens of *Rusophycus moyensis* locally occur associated with *A. minimus*.

This facies mostly records sediment fall-out in a low energy setting, although the presence of thin, interbedded, erosive-based sandstone layers records event deposition (Buatois and Mángano, 2003). The presence of micro-hummocky cross-stratification, combined-flow ripple cross-lamination, symmetrical to near-symmetrical ripples and gutter casts indicates deposition from storm flows and the sandstone beds are, therefore, interpreted as distal tempestites. This facies records alternating background suspension fall-out and distal storm deposition above storm wave base, more precisely in an upper offshore environment (Fig. 2) (Buatois and Mángano, 2003).

## SYSTEMATIC ICHNOLOGY

### Ichnogenus *Arthropycus* Hall 1852

#### *Arthropycus minimus* n. sp.

Figs. 3A–F, 4A–B

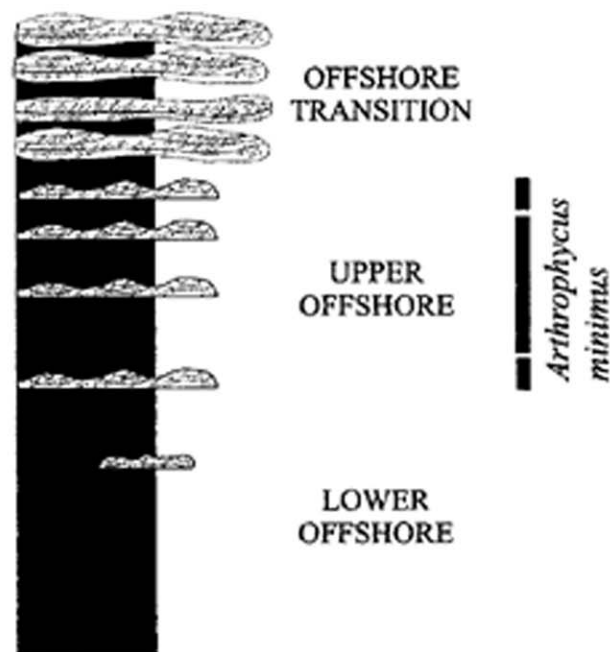


FIG. 2. Idealized wave-dominated parasequence of the lower interval of the Alfarcito Member (Santa Rosita Formation), showing paleoenvironmental distribution of *Arthropycus minimus*.

? 1984 *Arthropycus alleghaniensis* Liñán, Pl. 2, Fig. 5

? 1996 *Arthropycus strictus* Paczeńska, Pl. X, Fig. 3

2003a *Arthropycus* Mángano and Buatois, p. 37

2003b *Arthropycus* sp. Mángano and Buatois, p. 175

2003c *Arthropycus* sp. Mángano and Buatois, Pl. I, Figs. 4, 5

2003 *Arthropycus* cf. *alleghaniensis* (*lapses calami*) Aceñolaza and Aceñolaza, Fig. 20

**Material:** More than 30 specimens in PILs 13212, 13213 (two slabs, a and b), 13214, 13215 (partim), 14946 (three slabs), 14947 (two slabs), 14948, 14949, 14950, 14602 and 14603. A possible epichnial preservation is present in PIL 15187. Specimens are housed in the invertebrate paleontology collection of the Instituto Miguel Lillo, Universidad Nacional de Tucumán.

**Holotype:** 13213a. Specimens in the other slabs are regarded as paratypes.

**Occurrence:** Santa Rosita Formation (Alfarcito Member), Quebrada de Moya and Angosto del Morro de Chuculezna sections, Cordillera Oriental, Jujuy Province, Argentina.

**Diagnosis:** Narrow (width typically millimetric), long, regularly annulated hypichnial structures displaying intergrading subcircular to squarish cross-section and a ventral median groove, resulting in a bilobate aspect. Individual elements straight or gently curved. Side branches occasionally present, typically emerging at acute angle. Palmate, fan-like structures and scribbling patterns absent.

**Description:** Small (1.8–4.8 mm wide), long, relatively shallow hypichnial ridges, unbranched or with few side branches, typically running straight or smoothly curving along bedding planes for long distances (up to 20 cm). Structures

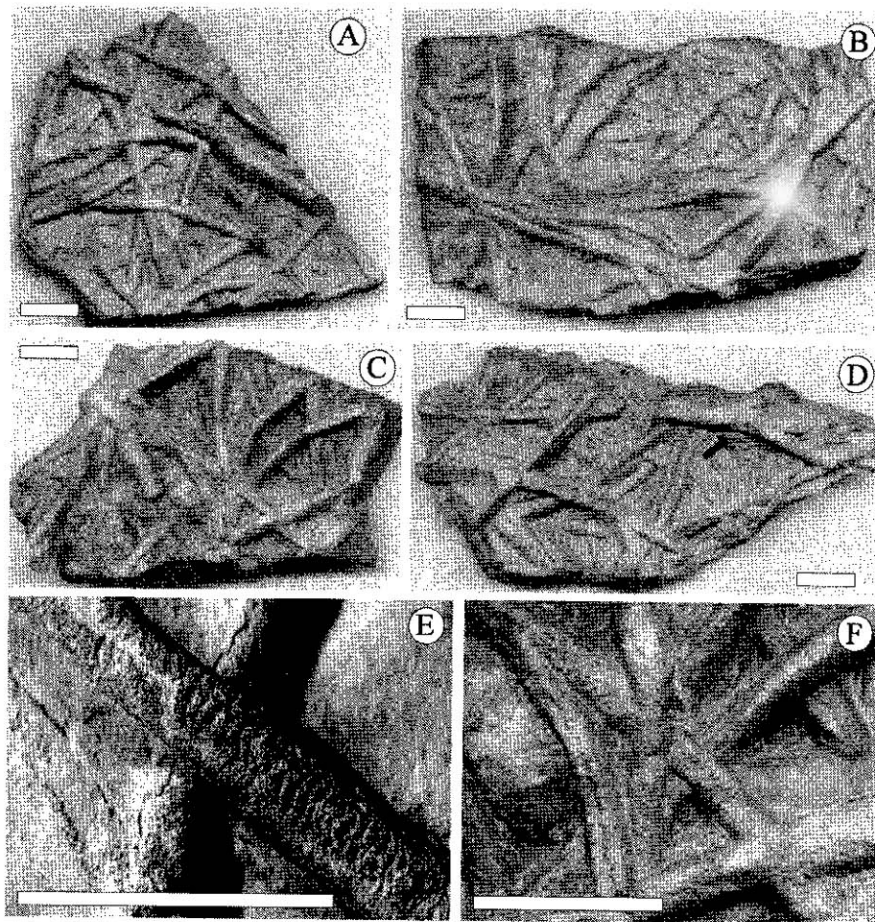


FIG. 3. *Arthropycus minimus* from the Santa Rosita Formation. All views from base of sandstone layers. Scale bar = 1 cm. (A) Holotype. 13213a. General view showing multiple overcrossing among specimens. (B) 13213b. (C) 14950. (D) 14946. Note true branching (arrow). (E) 14947. Close-up showing distinct annulations. (F) 14950. Close-up showing annulation and ventral median groove.

display a distinctive ventral median groove, subcircular to squarish cross-section and delicate, regular annulations (0.10–0.35 mm wide) that are most visible under magnification. Trace fill typically coarser than the host rock. Structures occur as dense monoichnospecific assemblages, where overcrossing (false branching *sensu* Bromley and D'Alessandro, 1987) is common. True branching is locally present (Fig. 3D), but palmate structures are lacking. Typical bifurcations are at acute angle, commonly between 20°–60°. Spreite is typically retrusive.

**Remarks:** *Arthropycus minimus* displays all the diagnostic features of the ichnogenus including regularly transverse, distinct annulations, a shallow median depression (sometimes having been described as “bilobate structures” by local geologists), squarish cross-section and predominantly horizontal components with a secondary teichichnoid spreite (Seilacher, 2000). Although originally described as protrusive by Mángano and Buatois (2003c), analysis of additional specimens and polished slabs reveals a retrusive spreite. Compared with other *Arthropycus*, however, the size of the analyzed specimens is strikingly small. *Arthropycus* typically ranges from 5 to 20 mm

wide (Häntzschel, 1975; Seilacher, 2000). In terms of general morphology and search strategy, the analyzed structures resemble *A. linearis* Seilacher 2000 (fig. 2), which includes the ichnosubspecies *A. linearis protrusiva* from the Upper Ordovician of Benin and Jordan and *A. linearis retrusiva* from the Lower Ordovician of Lybia and Algeria and the Lower Silurian of Argentina and the United States. According to the synonymy recently proposed by Rindsberg and Martin (2003), this form should be referred to as *A. brongniartii*. With rare exceptions, size *per se* is not considered a significant ichnotaxobase (Pickerill, 1994). However, annulations are less pronounced in *A. minimus* than in *A. brongniartii* (Harlan, 1832) and the structures are very delicate, commonly an order of magnitude smaller than *A. brongniartii* (i.e., typically not reaching 1 cm wide). Also, while *A. brongniartii* and *A. alleghaniensis* are commonly intergradational (e.g., Seilacher, 2000, fig. 1A), this is never the case with *A. minimus*. On the other hand, *A. minimus* can not be considered an ontogenetic variation of *A. brongniartii* or *A. alleghaniensis* because they are never found in the same strata or in rocks of the same age (cf. Pickerill, 1994,



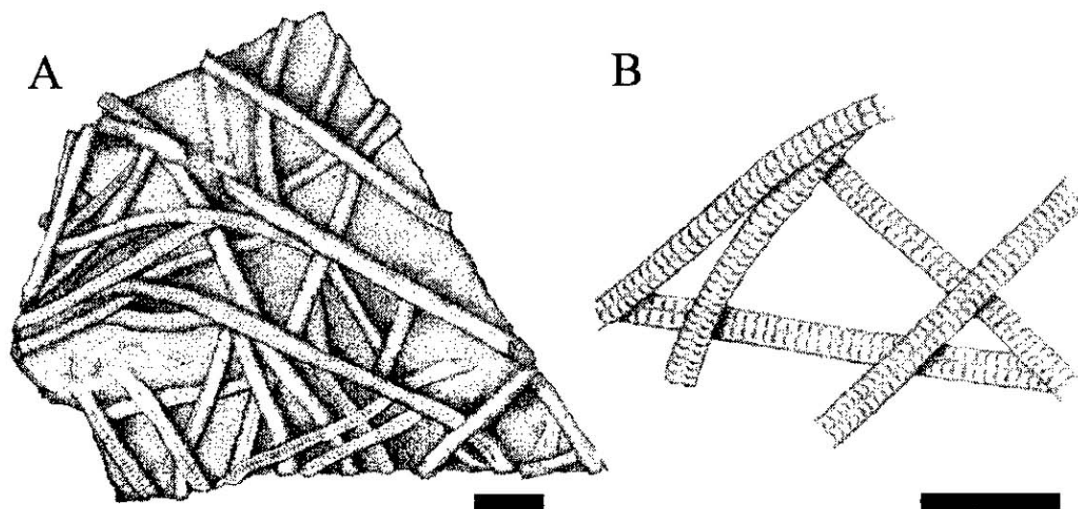


FIG. 4. *Arthropycus minimus* from the Santa Rosita Formation. Base of a sandstone layer. Holotype. Idealized drawing. PIL 13213a. Scale bar = 1 cm. (A) General view showing multiple overcrossing among specimens. (B) Close-up illustrating annulation and ventral median groove.

p. 11). Spiral and scribbling patterns, such as those observed in some specimens of *A. brongniartii* (e.g., Neto de Carvalho et al., 2003, fig. 3d), are absent in *A. minimus*. All these features are considered herein significant at the ichnospecies level.

In a recent study, Seilacher (2000) included in *Arthropycidae*, three ichnogenera: *Arthropycus*, *Daedalus* Rouault 1850, and *Phycodes*. Although quite different in their general form (*Arthropycus* and *Phycodes* are predominantly horizontal linear structures, while *Daedalus* is a vertical spiral structure), the fine morphology, in particular the unique transversal annulations, seem to be present in the three ichnogenera. *Arthropycus* and *Daedalus* Rouault 1850 are typically associated with clean sandstones and *Phycodes* is commonly present at the base of centimeter-thick siltstone or silty sandstone beds within shales (cf. Seilacher, 2000, p. 239). However, *Phycodes circinatum* from the type locality in Thuringia is preserved in quartzites (cf. Osgood, 1970, p. 341) and our specimens of *Arthropycus minimus* are preserved at the base of thin fine-grained sandstone beds interbedded with shales.

Although the size and fine annulations of *A. minimus* are reminiscent of *Phycodes* Richter 1850, *Phycodes* is typically a bundled structure (Seilacher, 1955, 2000; Osgood, 1970; Häntzschel, 1975). The *Bauplan* of *Phycodes* consists of two main strategies to exploit the rich fine-grained sediment: (1) one or a few proximal tunnels that tend to fan out distally [e.g., *P. circinatum* Richter 1850, *P. flabellum* (Miller and Dyer, 1878)] or (2) proximal splitting forming bundles of subparallel tunnels (e.g., *P. parallelum* Seilacher, 2000). *Arthropycus*, on the contrary, presents a master tunnel that may tend to form distal palmate bundles (*A. alleghaniensis* Harlan, 1831) or may explore the sediment in a dominantly horizontal, individual, straight fashion (*A. brongniartii*, *A. minimus*), covering completely some bedding planes.

Uchman (1998) noted that relationships between *Arthropycus* and *Torrowangea* Webby 1970 should be explored. Re-examination of the type specimens of *T. rosei* shows that there

are significant differences between the ichnotaxa. *Torrowangea* is characterized by diagnostic transverse constrictions, but lacks the typical branching pattern, teichinoid spreite, square cross-section and ventral median groove that typify *Arthropycus*. Additionally, constrictions are more irregular and spaced than annulations in *Arthropycus*. *Palaeosaportia loedeli* Borrello 1966 most likely represents poorly preserved specimens of *A. alleghaniensis* (Mángano and Buatois, 2003c).

Specimens illustrated by Mángano and Buatois (2003c, pl. 1, figs. 4, 5) as *Arthropycus* isp. are now included in *Arthropycus minimus*. Also, these authors noted similarities with material illustrated as *Arthropycus* isp. by Aceñolaza and Aceñolaza (2003, fig. 3O) in the electronic version of the paper posted in the Insugeo website by May 2003. These specimens were subsequently figured as *Arthropycus* cf. *alleghaniensis* (*lapsus calami*) by Aceñolaza and Aceñolaza (2003, fig. 2O) in the modified hardcopy version. Unpublished specimens labeled as *Didymaulichnus* sp. in the Instituto Miguel Lillo collection (PILs. 13212, 13213 and 13214) are herein also identified as *A. minimus*.

#### THE PROBLEM OF THE TRACEMAKER

The tracemaker of *Arthropycus* has been historically assigned to worms or arthropods (Häntzschel, 1975). The lengthy continuous structures, open curves, and regularity of the annulation suggest a relatively long vermiform animal as producer of *Arthropycus minimus*. Despite its small size, the annulations of *A. minimus* are locally exquisitely preserved. The fact that the traces were constructed in rather stiff, compact, fine-grained sediment indicates penetration of several centimeters from the water-sediment interface. The regularity of this "ring-like" ornamentation suggests the hydrostatic locomotion of coelomate worms, most likely peristalsis. In annelids, for example, coelom segmentation enables such organisms to burrow efficiently and produce regular structures. They also have a ventral nerve cord with ganglionic swellings and lateral nerves

in each segment, allowing efficient muscular coordination, thus resulting in an extremely coordinated movement. Annelids also have paired parapodia with chitinous setae (chaetae) on each segment. The main function of these structures is to improve traction as *points d'appui* during locomotion. In principle, in a relatively stiff sediment cuticle impressions and setae marks could have been preserved in *A. alleghaniensis* (cf. Seilacher, 2000, fig. 1b). However, the square cross-section of *Arthropycus* does not match the cylindrical shape of annelid structures, instead resembling the flattened morphology of *Curvolithus* and other structures currently assigned to solitary flatworms (Heinberg, 1973; Seilacher, 1990; Buatois et al., 1998). Some of the uncertainty about the *Arthropycus* producer could be clarified through a detailed constructional analysis. Unfortunately, the small size and preservation of *A. minimus* precludes a confident reconstruction of the details of its production.

Recently, Rindsberg and Martin (2003) assigned structures with rough transverse corrugations from the Lower Silurian Red Mountain Formation of Alabama to *Arthropycus brongniartii*. Close examination and detailed functional analysis performed by these authors suggested an arthropod producer, most likely a trilobite. In fact, the path of these annulated structures commonly exhibits breaks, angular segments indicative of a short animal producer (Rindsberg and Martin, 2003, figs. 2B, 4A). Evidence presented by these authors strongly supports an arthropod origin for the Red Mountain specimens. However, in our opinion the material from Alabama displays significant morphologic and ethologic differences from classic specimens of *Arthropycus* (e.g., Harlan, 1831; Borrello, 1966; Pickerill et al., 1984; Fernandes et al., 2000; Seilacher, 2000; Neto de Carvalho, 2003). In contrast to the Red Mountain specimens, the path of *Arthropycus* is remarkably continuous (cf. Seilacher, 2000, figs. 1, 3; Rindsberg and Martin, 2003, figs. 4C, D). The abundant and well-preserved material from the Upper Ordovician to Lower Silurian Balcarce Formation documented by Borrello (1966) also exemplifies the typically tidy and continuous, vermiform path of *Arthropycus*, that led him to describe the structures as genuine annelids rather than trace fossils (Borrello, 1966, p. 10, pl. XI). The complex interconnections and intergradations (with *Rusophycus*, *Nereites*, *Asterosoma*) described by Rindsberg and Martin (2003) for the Alabama specimens are also remarkably absent in typical material from Ordovician and Silurian rocks worldwide.

In recent contributions, Neto de Carvalho et al. (2002, 2003) proposed that while *A. alleghaniensis* was most likely the product of a coelomate worm, *A. brongniartii* represents the construction of an arthropod. The distinction was essentially based on the presence of "chevrons" interpreted as appendage marks in *A. brongniartii*. Contrastingly, the regular transverse annulations with fine parallel wrinkles present in *A. alleghaniensis* were more easily related to the peristaltic movement of a vermiform animal. However, zipper-like annulations ("chevrons" *sensu* Neto de Carvalho et al., 2002, 2003) are locally present in both *A. brongniartii* and *A. alleghaniensis*. Additionally, it is

hard to reconcile the chevron-marks as appendage marks recording the "circling behavior" of an arthropod (cf. Neto de Carvalho et al., 2002, 2003). So far, no clear scratch marks have been documented in *Arthropycus*. Delicate wrinkles in *A. alleghaniensis* from the Lower Silurian of Rochester, New York, were interpreted by Seilacher (2000) as possible impressions of a wrinkled body cuticle. Based on the observation that the wrinkles are not organized in a perfectly parallel fashion, but instead interfere, Rindsberg and Martin (2003) interpreted the fine corrugations as scratch marks. The functional interpretation of these subtle corrugations as scratch marks of arthropods is, however, hard to elucidate. Wrinkles do not "crosscut one another" (cf. Rindsberg and Martin, 2003, p. 205); instead, a set of wrinkles is intercepted by another set in a way suggestive of cuticle contact resulting from high friction penetration of a soft-bodied, hydrostatic-skeleton, animal through the sediment and progressive forward movement. In short, available evidence suggests that *Arthropycus* is a feeding trace (fodinichnion) produced by a worm-like organism, although not necessarily a true worm (cf. Seilacher, 2000). Evidence for a trilobite producer is controversial as *Arthropycus* do not show segments arranged angularly suggesting a short body as is observed in the Alabama material (cf. Rindsberg and Martin, 2003); rather the turns exhibit the "swinging-out of the tail" effect of a long body animal (cf. Seilacher, 2000, fig. 1a). Recently, Baldwin and Strother (2004) fortuitously found a centipede-like fossil in rocks containing *A. alleghaniensis*. A detailed description of this occurrence is awaiting, but this finding may prove that the producer of *Arthropycus* is a non-trilobite, long bodied arthropod. Further functional analysis is needed in order to decipher the constructional model and be able to determine on a more solid basis whether *Arthropycus* is the product of a worm or an elongate arthropod.

## ICHNOTAXONOMIC DISCUSSION

A comprehensive review of the named species of *Arthropycus* is beyond the scope of this paper. However, some problems resulting from the adoption of a wide diagnosis for the ichnogenus will be addressed. Although a considerable number of ichnospecies of *Arthropycus* have been formally defined (Uchman, 1998; Rindsberg and Martin, 2003), some of them have been reassigned to other ichnogenera (e.g., *A. annulatus* Książkiewicz, 1977 in *Ophiomorpha* Lundgren, 1891 and *A. dzulynskii* Książkiewicz, 1977 in *Protovirgularia* McCoy, 1850; see Uchman, 1998), some are most likely *nomina nuda* [*A. minoricensis* Bourrouilh, 1973 in Orr, 1994; "*Arthropycus*" *corrugatus* (Fritsch, 1908) redescribed by Mikuláš, 1992] and some (e.g., *A. hunanensis* Zhang and Wang, 1996) are possible junior synonyms of *A. alleghaniensis*. *Arthropycus siluricus* Schimper, 1890 from the Cambrian of Sardinia was never figured or described and is, therefore, regarded as a *nomen nudum*.

Luo et al. (1994) introduced the ichnospecies *Arthropycus qiongzhusiensis* based on specimens from the Lower Cambrian of Yunnan, China. Transverse annulations are poorly defined and

the specimens were described as tubular and circular in cross-section, lacking the typical squarish cross-section and bilobate appearance of *Arthropycus*. In addition, the illustrated specimens (Luo et al., 1994, pl. I, fig. 4 and pl. II, fig. 3) are isolated structures and do not display any of the typical search strategies of *Arthropycus*: either predominantly horizontal linear components with occasional acute-angle bifurcations or linear components associated with distinct bundles. Accordingly, their affiliation with *Arthropycus* is doubtful at best.

*Arthropycus strictus* Książkiewicz 1977 and *A. tenuis* (Książkiewicz, 1977), described from Cretaceous-Tertiary deep-marine deposits of Poland, display significant differences in general form and fine morphology that do not warrant their inclusion in *Arthropycus*. *Arthropycus strictus* is a cylindrical, simple arcuate structure with delicate annulations (Uchman, 1998). More complete specimens of *Arthropycus strictus* tend to form open bunches with non-imbrication of tunnels (cf. Uchman, 1998, fig. 6). Diagnostic features of *Arthropycus* absent in *A. strictus* are the square cross-section, ventral median groove and zipper-like annulations. Bunches of *A. strictus* differ significantly from the closely spaced or connected elements that form the palmate structures of *A. alleghaniensis* or *A. lateralis* Seilacher 2000. *Arthropycus tenuis* is composed of small, straight, rarely branched structures with fine perpendicular striae. Fine striations are dependent on grain size and cohesion of the substrate, and in most cases are absent due to preservational bias (Uchman, 1998). As in the previous case, these structures are cylindrical, lack the axial ventral depression, annulations are apparently simple (i.e., do not display the zipper-like morphology), and the branching pattern (typically Y or T angle, cf. Uchman, 1998, fig. 7) differs from that present in *Arthropycus*. In fact, Uchman (1998) included *A. strictus* and *A. tenuis* in his group of "simple structures." However, classical examples of *Arthropycus* indicate a complex mining strategy at sandstone-mudstone interfaces reflected in intricate networks, including distal palmate elements with vertical or lateral spreite.

Other specimens included in *Arthropycus* exhibit the articulated morphology but fail to record other diagnostic features, such as the ventral median groove, the squarish cross-section, and the zipper-like annulated structure that record a particular constructional technique. Unfortunately, in many cases the published material is fragmentary and does not document the mode of occurrence of the ichnogenus (e.g., Liñán, 1984; Pickerill et al., 1991; Paczeńska, 1996; Stanley and Feldmann, 1998). Irregularly annulated structures should not be included in *Arthropycus*, unless other diagnostic features (i.e., intergrading sub-circular to square cross-section, ventral median groove) are also present.

## POTENTIAL IN ICHNOSTRATIGRAPHY

Trace fossils are characterized by long stratigraphic ranges and narrow facies distribution. This well-known statement is true for most trace fossils. However, we also know that some biogenic structures can preserve specific chemical or mechan-

ical fingerprints of their producers. If the producers record significant evolution, then the trace fossils may also yield biostratigraphic implications. A classic example of a trace fossil with biostratigraphic implications in lower Paleozoic shallow-marine strata is *Cruziana* d'Orbigny 1842. Although ethological convergence is a common feature recorded in trilobite structures, the combination of fine morphological and behavioral constructional constraints has proved to be of biostratigraphic significance at least for the Cambrian-Silurian time span (Crimes, 1969, 1970, 1975; Seilacher, 1970, 1992, 1994, 1996; Mángano et al., 2001; Mángano and Buatois, 2003c; Mángano and Droser, 2004). Based on functional morphology and construction strategy, many ichnospecies of *Rusophycus* Hall 1852 and *Dimorphichnus* Seilacher 1955 can also be related to a trilobite producer (Seilacher, 1985, 1990). Albeit with more restricted distribution, several other ichnogenera, such as *Dictyodora* Weiss 1884, also display a distinct evolution in morphology and behavioral strategy representing ichnotaxa with biostratigraphic potential (Seilacher, 1967; Benton and Trewin, 1980).

There is yet another group of trace fossils (*Arthropycus*, *Daedalus*, *Phycodes*), included in the ichnofamily Arthropycidae, which has been proposed as yielding biostratigraphic significance (although they cannot be confidently assigned to a particular group of organisms). In particular, the ichnogenus *Arthropycus* is abundant and widespread in Ordovician and Silurian strata, specifically in shallow-marine epeiric quartzites and quartzose sandstones. According to Seilacher (2000), *Arthropycus* has a distinct stratigraphic range and can be used as a biostratigraphic index in Ordovician-Silurian rocks. In his scheme, *A. brongniartii* ranges from the Lower Ordovician to the Lower Silurian, and *A. alleghaniensis* and *A. lateralis* are Lower Silurian. In this section we critically revise occurrences of *Arthropycus* in the stratigraphic record in an attempt to test its utility as a biostratigraphic indicator. The biostratigraphic significance of *A. minimus* is also analyzed.

## Cambrian

*Arthropycus* has been occasionally recorded from Cambrian strata (Alpert, 1977; Liñán, 1984; Legg, 1985; Luo et al., 1994; Paczeńska, 1996). However, most of these taxonomic determinations are uncertain or the age is not confirmed by biostratigraphic or geochronologic data. *Arthropycus* has been considered a useful indicator of the basal Cambrian in studies dealing with the Precambrian-Cambrian boundary. In particular, Alpert (1977) included *Arthropycus* in his Group I (trace fossils indicative of Early Cambrian age) based on his studies on Precambrian-Cambrian successions of the White-Inyo Mountain in California. However, in subsequent contributions (e.g., Crimes, 1987, 1992), *Arthropycus* was included in the group of trace fossils that have their first appearance in Cambrian strata and continue well into the Phanerozoic. Alpert (1975, 1977) mentioned the presence of *Arthropycus* isp. in the Andrews Mountain Member of the Campito Formation, Lower Cambrian of the White-Inyo Mountains, California. However,



no description or illustration of these forms were provided. As previously analyzed, *Arthropycus qiongzhusiensis*, described from the Lower Cambrian of China by Luo et al. (1994), does not display the diagnostic morphology of *Arthropycus*.

Specimens from the Lower Cambrian of Spain described by Liñán (1984) as *Arthropycus alleghaniensis* display some of the diagnostic features of *Arthropycus* (e.g., annulation, ventral median groove). However, the material is fragmentary and, based on the illustration (cf. Liñán, 1984, pl. II, fig. 8a), no definite assignment can be provided. In any case, the size and general morphology of these annulated structures suggest *A. minimus* rather than *A. alleghaniensis*. The described specimens do not display the typical bundled structures recording the feeding strategy of *Arthropycus alleghaniensis*.

Paczeńska (1996) described *Arthropycus strictus* from Lower to Middle Cambrian rocks of Poland. Subsequently, Uchman (1998) removed these specimens from *A. strictus*. According to the description by Paczeńska (1996), these specimens can be tentatively assigned to *A. minimus*. Unfortunately, the illustration does not allow a confident assignment.

Specimens from the Middle Cambrian of Spain referred to as *Arthropycus* sp. by Legg (1985) show strong annulations and a faint median groove, but are vertical, simple, unbranched burrows. According to his Pl. 4, fig. E, the structure seems to be U-shaped in general morphology displaying a vertical spreite. Further analysis is needed in order to determine whether it represents a different feeding program within *Arthropycus* (a new ichnospecies?) or a completely different form.

## Ordovician

In Seilacher's (2000) ichnostratigraphic scheme, *A. bronniartii* is the only *Arthropycus* ichnospecies that occurs in Ordovician rocks. However, *A. alleghaniensis* has been recorded in Ordovician strata in various studies (Baldwin, 1977; Pickerill et al., 1984; Neto de Carvalho et al., 2003). Baldwin (1977) recorded *A. alleghaniensis* from Lower Ordovician rocks of the Cantabrian Mountains, Spain. Although specimens are described as "branched and bunched," the illustrated figure (Baldwin, 1977, pl. 2a) shows straight to slightly curved tunnels, with few side branches that resemble the overall morphology of *A. bronniartii* rather than *A. alleghaniensis*.

Pickerill et al. (1984, fig. 2a) documented a specimen assigned to *A. alleghaniensis* from the Arenigian Armorican Quartzite of the Salamanca area, Spain. The specimen displays the diagnostic characteristics of *Arthropycus* and the burrows are bundled, resembling *A. alleghaniensis*. However, because no clear open palm-like configuration is preserved, further specimens are required to confirm this assignment.

*Arthropycus* has been also documented from the Lower Ordovician Armorican Quartzite of Portugal (Delgado, 1885, 1888; Neto de Carvalho et al., 2003). In a recent contribution, Neto de Carvalho et al. (2003) identified *A. alleghaniensis* and *A. bronniartii* (their *A. linearis*) considering *A. lateralis* as a be-

havioral variant of the former. However, specimens assigned to *A. alleghaniensis* (fig. 2a–d) better resemble the search pattern of *A. bronniartii* with the exception of those illustrated in fig. 2b, whose bunched structures show similarities with *A. lateralis*. Interestingly, the scribbling behavior of one of the specimens of *A. bronniartii* illustrated by Neto de Carvalho et al. (2003, fig. 3d) has also been noted by Rindsberg and Martin (2003) as a common behavior in *Arthropycus*.

In short, the potential presence of *A. alleghaniensis* in the Armorican Quartzite represents an anomaly to the proposed stratigraphic range of this ichnospecies. Re-analysis of *Arthropycus* specimens from this unit of the Iberian Peninsula is essential to test the utility of the Arthropycid ichnostratigraphy. Regardless of their biostratigraphic utility, as noted by Seilacher (2002), *A. lateralis* and *A. alleghaniensis* record two different burrowing programs and stand as distinct ichnospecies. Polished sections of the bundles are essential to reveal the constructional design of these two burrow systems (cf. Seilacher, 2000, figs. 4 and 6).

## Silurian

Lower Silurian examples of *Arthropycus*, in particular *A. alleghaniensis* and *A. bronniartii*, are widespread, including the Tuscarora Sandstone of Pennsylvania (Harlan, 1831; Brett et al., 1998a), the Medina Sandstone of New York and Ontario (Hall, 1852; Brett et al., 1998a, b; Seilacher, 2000), the Vila Maria and Furnas formations of the Paraná Basin, Brazil (Carvalho Moreira and Borghi, 1999; Fernandez et al., 2000), the Trombetas and Nhamundá formations of the Amazonas Basin, Brazil (Fernandez and Borghi, 1996; Rodrigues Nogueira et al., 1999; Fernandez et al., 2001), the Balcarce and Napostá formations of Argentina (Borrello, 1966; Rodriguez, 1988; Seilacher et al., 2004), the Puerto Stephen Formation of the Falkland/Malvinas Islands (Scasso and Mendia, 1985), and the Akakus Sandstone of Lybia and coeval units in Chad (Pflüger, 1999; Seilacher, 2000).

The occurrence of *A. alleghaniensis* in the Balcarce Formation of Tandilia (Argentina) is in need of clarification. Borrello (1966) originally reported this ichnospecies from the La Tinta Formation and suggested an Ordovician age based on the trace fossil content. This information has been repeated in a number of studies (e.g., Fernandes and Borghi, 1996). However, subsequent stratigraphic schemes revealed a more complex stratigraphy, and the La Tinta Formation (or Group) is no longer used (Iñiguez Rodríguez, 1999). Three main units are now recognized: the Upper Precambrian Sierras Bayas Group and Cerro Negro Formation and the lower Paleozoic Balcarce Formation (Iñiguez Rodríguez, 1999), which contains *A. alleghaniensis*. The age of the latter has been controversial due to the absence of body fossils. In fact, a Late Ordovician to Early Silurian age has been suggested for the Balcarce Formation based on its trace fossil content and correlations with coeval strata in North Africa (Seilacher et al., 2004). According to these authors,



*A. brongniartii* occurs in the Upper Ordovician strata while *A. alleghaniensis* is present in the Lower Silurian strata. The Early Silurian age of these strata is further supported by the presence of *Cruziana ancora* (Seilacher et al., 2004). Similar age uncertainties are shared by other units in the area, such as the Napostá Formation of Ventania, whose Early Silurian age is based on the presence of *Daedalus verticalis* (Seilacher et al., 2004).

In short, Silurian *Arthropycus* are typically bundled structures that better fit in *A. alleghaniensis* or *A. lateralis*. However, simpler linear structures with few side branches (*A. brongniartii*) seem to have survived into the Silurian.

### Devonian

*Arthropycus* has been recorded in the Lower Devonian Tadrart Formation of Benin (Turner and Benton, 1983). The age of this unit is based on its stratigraphic position overlying the Acacus Sandstone of Lower Silurian age, but has not been confirmed by biostratigraphic data. In the same paper, the occurrence of *Arthropycus* is also shown in the middle part of an undifferentiated Cambrian-Ordovician succession at Jebel Archenu (Turner and Benton, 1983, p. 450). Again, there is no confirmatory biostratigraphic evidence of this occurrence, and the age of this succession is solely based on its unconformably position on Precambrian strata.

### Carboniferous

Eagar et al. (1985, p. 137) recorded as *Arthropycus* "small branching burrows with poor segmentation" in Carboniferous deltaic deposits of England. Although the burrows are bilobate at the base and sub-quadrate in cross-section, annulations are faint or absent and the bifurcation pattern (with angles up to 80°) is not typical of *Arthropycus*, so confirmation of this assignment is pending further analysis.

Greb and Chesnut (1994, fig. 6e) illustrated *Arthropycos?* (*lapsus calami*) from estuarine deposits in the Pennsylvanian Breathitt Formation of Kentucky. This unbranched, cylindrical structure, having thick annulations, lacks the diagnostic features of *Arthropycus* and should be removed from this ichnogenus.

### Post-Paleozoic

As noted by Häntzschel (1975), post-Paleozoic occurrences are controversial and most likely should be assigned to other ichnogenera (Rindsberg and Martin, 2003). Specimens from Mesozoic-Cenozoic deposits fail to display the diagnostic features of *Arthropycus* (e.g., Mabery, 1971; Frey, 1970, 1972; Frey and Howard, 1970; Chiplonkar and Ghare, 1975; Ghare and Kulkarni, 1986; Yang et al., 1996). The sole presence of annulations has been considered by some researchers enough to include some material in *Arthropycus*. Fine morphologic features and the distinct search pattern of *Arthropycus* are typically absent in proposed post-Paleozoic examples. For example, Yang et al. (1996) recorded *Arthropycus* isp. in Triassic deep-marine deposits of Sichuan, China. However, no description is provided and the poor quality of figures precludes con-

fident re-evaluation. Frey and Howard (1970) tentatively included structures with irregular annulations and Y-shaped bifurcating patterns in *Arthropycus* (cf. Frey, 1970, fig. 4E; Frey and Howard, 1970, fig. 3e). The geometry and general morphology of these trace fossils certainly suggest that they may be placed in *Thalassinoides* Ehrenberg 1944. As previously discussed, specimens from Cretaceous-Tertiary units of Poland, referred to as *A. strictus* and *A. tenuis* (Książkiewicz, 1977; Uchman, 1998), should be removed from *Arthropycus*.

### Significance of *Arthropycus minimus*

Interestingly, small *Arthropycus* forms, such as those illustrated by *A. minimus*, seem to characterize the oldest records of *Arthropycus*. The presence of *A. minimus* in the Santa Rosita Formation of northwest Argentina indicates that *Arthropycus* ranges at least from the Upper Cambrian-Lower Tremadocian, which extends the biostratigraphic utility of this ichnogenus. The morphologic pattern displayed by *A. minimus* is simpler than that of the younger ichnospecies, particularly *A. alleghaniensis*, *A. lateralis* and *A. brongniartii*. This is consistent with the basal position of *A. minimus* within the arthropycid lineage. The possible occurrence of *A. minimus* in Lower Cambrian rocks of Spain and Poland suggests that relatively simple, small *Arthropycus* may have appeared during the Cambrian radiation. The major diversification of the lineage, however, was related to the Ordovician radiation that resulted in the acquisition of maximum size and increasing behavioral complexity.

### PALEOENVIRONMENTAL DISTRIBUTION

*Arthropycus* is a common ichnotaxon in Lower Paleozoic shallow, open-marine environments (e.g., Borrello, 1966; Frey and Chowns, 1972; Baldwin, 1977; Turner and Benton, 1983; Pickerill et al., 1984, 1991; Rodriguez, 1988; Fernandes and Borghi, 1996; Carvalho Moreira and Borghi, 1999; Rodrigues Nogueira et al., 1999; Fernandes et al., 2000; Seilacher, 2000; Neto de Carvalho et al., 2002, 2003; Mángano and Buatois, 2003c). Also, *Arthropycus* has been occasionally mentioned in Late Paleozoic brackish-water, marginal-marine deposits. However, as previously discussed, specimens should be removed from *Arthropycus* (Greb and Chesnut, 1994) or require additional analysis to confirm their identification (Eagar et al., 1985). If further study confirms the presence of *Arthropycus* in Carboniferous strata of England, this will suggest a retreat of this ichnotaxon to brackish-water, marginal-marine environments during the Late Paleozoic.

*Arthropycus* has been rarely recorded in Paleozoic deep marine deposits. Li (1993) described *Arthropycus* isp. A and B from deep-marine facies of Middle Ordovician age in Inner Mongolia (China). However, the indistinctive morphology of these specimens (Li, 1993, pl. I, fig. 5; pl. II, fig. 7) does not warrant their inclusion in *Arthropycus*. In addition, as previously noted, *Arthropycus* also has been frequently

recorded from Mesozoic and Cenozoic deep-marine rocks (Książkiewicz, 1977; Kern, 1978; Yang et al., 1996; Uchman, 1998), but these specimens should be removed from this ichnogenus. In short, to date no reliable examples of *Arthropycus* are known from deep-marine environments.

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