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A RECONSIDERATION OF THE *ARTHROPHYCUS* ICHNOGENUS: DEFINITION, BIOSTRATIGRAPHIC UTILITY, AND A PROPOSAL TO DEVELOP A NUMERICAL ICHNOTAXONOMY

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By

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ABSTRACT

A RECONSIDERATION OF THE *ARTHROPHYCUS* ICHNOGENUS: DEFINITION, BIOSTRATIGRAPHIC UTILITY AND A PROPOSAL TO DEVELOP A NUMERICAL ICHNOTAXONOMY

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Arthrophycus Hall 1852 is a long-studied ichnogenus reported from localities worldwide, including all seven continents and twenty-eight countries. It is most abundant in Ordovician and Silurian strata and is regarded by some ichnologists as having biostratigraphic utility, although other occurrences of the ichnogenus have been reported from the Proterozoic to the Miocene. Imprecise or overly-brief descriptions and ambiguous or unclear illustrations, drawings, and photographs of specimens regarded as *Arthrophycus* have resulted in a taxonomic "wastebasket" and have led to confusion over the biostratigraphic utility of the ichnogenus.

A review of the primary *Arthrophycus* literature converged on the following diagnostic characters for the ichnogenus: annulations, simple form, branches, bundles, shape of cross-section, median groove, and internal structures. Characters such as annulations, branching, and median groove encompass variability not previously discussed in reviews of the ichnogenus. Refining the definition of these characters produced sixteen characters that could be coded for a numerical phenetic analysis of *Arthrophycus* ichnospecies. Cluster analyses revealed two main clusters: a cluster of six (*A. alleghaniensis*, *A. brongniartii*, *A. linearis*, *A. lateralis*, *A. minimus, A. parallelus*) considered to be valid *Arthrophycus* and a second cluster of discredited

ichnospecies, members of which probably belong in other ichnogenera. The cluster analyses were supported by PCO and cladistic analyses.

Only Paleozoic occurrences of *Arthrophycus* are considered valid, including specimens from the Cambrian, Devonian, and Carboniferous, challenging previous conclusions that *Arthrophycus* is confined to the Ordovician and Silurian. This analysis also confirms an hypothesis that *Arthrophycus* originated in the southern continents in the Cambrian, persisted there in the Ordovician, and then expanded to the northern continents during the late Ordovician and Silurian.

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"L'etude de ces fossiles plus que problematiques est un travail tres ingrat…"

(The study of these more than problematic fossils is a very thankless job…)

~ Fritsch, 1908

"A single slab in your cabinet, ornamented in relief with groups of this remarkable fossil, whose figured surface reminds us of the Gothic tracery of ancient sculpture, is of itself an object of admiration."

~ Taylor, 1835

"We will be known forever by the tracks we leave."

~ Native American Proverb

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Chapter I. Introduction and Background

Rationale for Study

Arthrophycus is a well-known ichnogenus (Figure 1.1) with specimens reported from localities around the world (Seilacher 2007a), and is often cited as having biostratigraphic utility. Imprecise descriptions and ambiguous or unclear illustrations, drawings, and photographs of specimens regarded as *Arthrophycus* have resulted in a "wastebasket" taxon (as used by Plotnick and Wagner 2006) and have led to confusion over the biostratigraphic utility of the ichnogenus. Häntzschel's (1975) description of the ichnogenus in the *Treatise of Invertebrate Paleontology* has been the standard until a recent, sweeping reconsideration of "arthrophycid" burrows (Seilacher 2007a). Seilacher's (2007a) interpretation goes far beyond a strict morphological taxobasis advocated by other ichnologists (e.g. Keighley and Pickerill 1996), and his "fingerprint" for the arthrophycids is not observable in many published descriptions of trace fossils assigned to *Arthrophycus*, further suggesting that a thorough review of the ichnogenus is in order.

Seilacher (2007b) and other authors have suggested that *Arthrophycus* can be used in biostratigraphy. Relatively short-lived fossil species, known as index fossils, are often used to date formations in which they are found. *Arthrophycus* has been used in this manner (e.g. Silva 1951, Kumpulainen *et al.* 2006), but this technique is useful only if the ichnospecies is truly stratigraphically limited, or the dates assigned will be of little worth. Beginning at least as early as Conrad (1839), several authors have reported *Arthrophycus* as an index fossil for the Ordovician and Silurian (e.g. Moore 1933, Shimer and Shrock 1944), but others have questioned this use of the ichnogenus

(Young 1955, Fernandes and Borghi 1996). Stratigraphically, *Arthrophycus* may be best known from Ordovician and Silurian strata (e.g. Häntzschel 1975, Seilacher 2000), but other specimens have been reported from the Proterozoic (Mukherjee *et al.*1987) to the Cretaceous (e.g. Frey and Howard 1970, Banerjee 1982) and even to the Miocene (Uchman and Demircan 1999). However, reports of *Arthrophycus* from Devonian and Carboniferous strata have been questioned (Mángano *et al.* 2005a), and post-Paleozoic occurrences of *Arthrophycus* are highly suspect (Häntzschel 1975, Mángano *et al.* 2005a).

Objectives

The goals of this project are to (1) bring diagnostic coherence to the ichnogenus *Arthrophycus*, (2) clarify whether the ichnotaxon is a valid index fossil for the Ordovician/Silurian, and (3) evaluate the use of a numerical approach to ichnotaxonomy.

History of Trace Fossils

Essentially, the history of trace fossils begins with fucoids. Of 258 genera named before 1900 that are now known as trace fossils, 120 were called fucoids, interpreted as fossil seaweed or algae (Osgood 1975a). From 1822 to 1881, at least 130 species of the genus *Fucoides* were named (James 1893b). Some ichnogenera, such as *Chondrites* and *Cruziana*, did appear plant-like, and the drive to publish likely supported the large numbers of overly facile descriptions (Osgood 1975a). Dawson (1864) was among the first to recognize that not all of the supposed "fucoids" were plants, but that some were the work of trilobites. The papers of the following years focused mainly on the genera *Rusophycus* (as had Dawson) and *Cruziana* (Osgood

1975a). Nathorst (1881) was the first to find widespread, though not universal, acceptance for his view that these structures were fossil traces. Nathorst worked on modern depositional environments along the Swedish coastline and argued that a fragile little alga was unlikely to make convex impressions in sandstone, but would most likely have been crushed flat. However, not everyone was convinced. In an encyclopedic work, Schimper and Schenk (1879-1890) classified trace fossils such as *Arthrophycus* with the "*Algae incertae sedis*," a large group within the seaweeds and algae that spanned twenty-five pages.

Progress toward understanding the true nature of trace fossils came in the 1920s with works by Richter (Osgood 1975a). Further understanding resulted from Abel's (1935) large and standard reference book *Vorzeitliche Lebensspuren*, in which he discussed a large number of trace fossils, both vertebrate and invertebrate, and even included coprolites. German authors then held sway for a number of years, writing many influential trace fossil papers (Osgood 1975a). Perhaps chief among these was Seilacher, who developed an ethological (behavioral) scheme of classifying traces (1953) and recognized a number of ichnofacies grouping ichnofossils by depth (1964). Finally, in 1962, Häntzschel wrote the first version of the portion of the *Treatise of Invertebrate Paleontology* that dealt with trace fossils. The great advantage of this work was that it effectively organized many genera of trace fossils, reducing their synonyms and providing a useful encyclopedia with illustrations (Osgood 1975a).

Currently, trace fossils are defined most basically as ancient structures produced in or on the substrate by animals (Frey 1973, Bromley 1990). The International Code of Zoological Nomenclature defines an ichnotaxon as "the fossilized work of an organism" and, as do most authorities, restricts trace fossils to "the result of the activity of the animal" and not animal parts or molds of the inactive body (ICZN 1999). Though a few details need to be hammered out, most workers agree with these basic definitions (e.g. Häntzschel 1975, Bromley 1990).

Trace fossils remain important fossils to study. They add to our knowledge of both soft and hard-bodied animal diversity (Osgood 1975b) and can be used in paleoecological studies (e.g. Pacześna 1996). Other examples of problems that trace fossils can solve include oxygen levels, salt levels, current direction, and deposition rate (Seilacher 1964a, Bromley 1990). Trace fossils generally cannot be transported without destroying the trace (Seilacher 1964a), so the state of the traces is evidence of how much the substrate has changed (Bromley 1990). Ichnofossils are more reliable records of behavior than body fossils are (Osgood 1975b) and are common in strata that do not preserve body fossils (Bromley 1990). A notable recent example, and one that highlights the importance of trace fossils, is the report of new trackways of Devonian tetrapods, eighteen million years before the first known body fossils of tetrapods and ten million years before the first known elpistostegids such as *Tiktaalik* (Niedźwiedzki *et al.* 2010).

Ichnotaxonomy

The goal of any classification scheme is to group similar things together while separating them from unlike things (Simpson 1975). Trace fossils are classified the same way as biologic taxa, using a basic Linnaean binomial system of ichnogenus and ichnospecies (Bertling *et al.* 2006, Bertling 2007). Significant differences in morphology are taken to exhibit differences at the ichnogenus level and lesser differences differentiate ichnospecies (Bertling *et al.* 2006). However, in practice, differences between ichnogenera and ichnospecies depend largely on the individual researcher (Magwood 1992). There is no widely accepted suprageneric classification for trace fossils; some suggest that ichnofamilies be based solely on morphology and used only for convenience, with no requirement that every ichnogenus be placed in an ichnofamily (Rindsberg 1998, Bertling *et al.* 2006).

Recognizing and diagnosing trace fossil taxa has always been problematic, as different researchers may disagree on what constitutes a valid group. Many bases for classification have been proposed and/or used, including morphology, supposed behavior, substrate, size, preservation, supposed producer, type of fill, geologic age, and location (Magwood 1992, Pickerill 1994, Demathieu and Demathieu 2002, Bertling *et al.* 2006, and Bertling 2007). Most of these proposed ichnotaxobases are not useful for all types of trace fossils and are subject to the interpretation of the worker (Magwood 1992). Diagnoses of trace fossils should therefore "be restricted to observations" rather than subjective interpretations (Minter *et al.* 2007).

Although complete consensus among ichnologists is still lacking, trace morphology has emerged as the exclusive acceptable ichnotaxobase (Fürsich 1974, Keighley and Pickerill 1996), as the interaction of an animal with its environment is preserves (Fürsich 1974). Substrate criteria are still used in special cases, mostly for borings in hard substrates or wood (Bertling *et al.* 2006). In the case of *Arthrophycus*, the trace is not a boring into hard substrate, so the substrate criterion is not applicable; morphology of the trace is the lone remaining criterion on which to base its taxonomy.

Morphological criteria can be further broken down into subcategories, including overall shape (especially type of branching, if present), cross-section, orientation with respect to substrate, surface features, internal structure, and wall lining (Bertling *et al.* 2006, Bromley 1990, Magwood 1992, Rindsberg 1998, Pickerill 1994, and Bertling 2007). These features must be easy to preserve and identify, or they lose their effectiveness in ichnotaxonomy (Magwood 1992, Bertling *et al.* 2006, Minter *et al.* 2007); the ichnotaxobases should be features that show little variability (Demathieu and Demathieu 2002).

Some workers (e.g. Magwood 1992) persisted in reading specific producer behavior into the trace morphology, but behavioral inferences are not always clear, objective, or supported by other workers (e.g. Bertling *et al.* 2006). However, behavior is still an important consideration in trace fossil studies, as behavior is considered to be a major component of what might be regarded as the "extended phenotype" (Dawkins 1982) of a trace-making organism, along with morphology (Bertling *et al.* 2006). Some characters may provide clues to the trace ethology, and would then be acceptable as ichnotaxobases (Keighley and Pickerill 1996). Although the specific trace-maker is seldom known, this is no different conceptually than studying a vertebrate animal using only teeth.

Because so many proposed observations and criteria for ichnotaxobases are subject to researcher interpretation, it is desirable to develop an objective, numerical means of trace fossil classification. The advantages of a numerical method over a subjective method are that it should be reproducible and systematic, and can introduce some controlled subjectivity that is preferable to uncontrolled subjectivity. The morphological variation among trace fossils will necessitate a slightly different list of positively scored characters to be encoded for each group of trace fossils studied, but the same basic techniques can apply to all such numerical analyses in ichnotaxonomy.

Background of Phenetics

Numerical phenetics, previously known as numerical taxonomy, is the quantitative method proposed herein as a new technique for the study of ichnotaxonomy. The technique of phenetics uses large numbers of characters to classify items (Sokal 1966), and thus is suitable for quantitatively analyzing the trace fossil morphological characters. Cluster analysis or other measures of similarity, using phenetic characters, might be used to reveal similarities among the ichnospecies of *Arthrophycus* without assuming patterns of descent (Blackith and Reyment 1971).

Cladistics, the type of phylogenetic analysis now popular for biological taxa, might be considered problematic in the study of trace fossils. This is because an evolutionary "history" or relationships cannot be assumed for trace fossils that bear a resemblance to each other because of the multiple ways that many organisms can make very similar traces and because trace fossils do not breed or produce "offspring" that can have a meaningful history. Cladistics uses only shared derived charactes, which introduces polarity to the character states and emphasizes the effect of the outgroup, but phenetics bases affinities on both primitive and derived states, without weighting either.

Methods

The main portion of my research involved gathering all reports of *Arthrophycus* in the literature to create a database of all known occurrences. To do this, I created an annotated bibliography and worked outward, searching for papers mentioned in each source. I also used numerous internet searches and databases, including Georef, Google Scholar, ION (Index to Organism Names), the Zoological Record, and the Paleobiology Database. These references then formed the data for my synthesis of previous work done on *Arthrophycus* and for histograms of reports of the ichnogenus throughout geographic time and space. I also entered these records into Microsoft Excel databases to condense the bibliography into essential points and organize references efficiently by time, space, and ichnospecies.

A subset of these references was in languages other than English, requiring translation for proper evaluation of the specimens described therein. Two of Harlan's original descriptions and part of Göppert's involved some Latin, which Dr. Robert Anstey of Michigan State University kindly translated. I was able to use "Google Translate" for languages that are based on the Roman alphabet, including seven papers in French, eight in German, fifteen in Portuguese (mostly Brazilian), six in Spanish, and one in Romanian. For all of these, I transcribed the papers into Microsoft Word by hand and then fed them into the translation program online. Four references in Chinese, including two descriptions of new species, were beyond the powers of Google Translate. Dr. Yue Li of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, kindly translated the relevant portions of these sources.

All of these papers were potentially subject to error throughout the transcription and/or translation process. Although I made every effort to transcribe papers accurately, I had little familiarity with most of these languages and was unlikely to catch any typing mistakes. "Google Translate" and Drs. Anstey and Li may also have been fallible. However, I did find several mistakes when the translation program returned a nonsense answer, and the resulting translations made enough sense that I am confident that they retained the salient points. In addition, only four of the papers for which I used "Google Translate" described new species, for which detail and precise wording is most important; other papers that were translated were only reports of *Arthrophycus* occurrences. Of the four papers describing new species, three were in German, the language with which I am most familiar and would be most likely to catch any errors in transcription or translation.

Besides the literature search, I traveled to seven museum collections to examine as many specimens of *Arthrophycus* in person as possible. These visits were to the Cleveland Museum of Natural History (CMNH), the Ohio State University (OSU), the Geier Collections of the Cincinnati Museum (UCGM), the Yale Peabody Museum (YPM), the American Museum of Natural History (AMNH), the New York State Museum (NYSM), the Buffalo (NY) Museum of Science (BMS), and the Paleontological Research Institution (PRI). During each visit, I took digital photographs of *Arthrophycus* and noted qualitative characters on a data sheet designed for this purpose (Figure 1.2). I measured quantitative characters with a simple ruler at all the collections except for that of Yale Peabody, where I used digital calipers. I chose the individual candidates for the measurements of smallest and largest diameter mostly by eye, but made several measurements if I had any doubt as to which was the smallest or largest individual.

While at these museums, I also examined specimens of genera supposedly related to *Arthrophycus*, including *Fucoides*, *Daedalus*, and the occasional unmarked mystery cabinet. I examined specimens of *Fucoides* because *Arthrophycus* was originally classified under that name; the search produced a number of specimens that were actually *Arthrophycus*, as well as a few specimens of true seaweed fucoids that served as useful comparisons and revealed insights into the ichnogenus history. Ichnospecies of *Daedalus* may be related to *Arthrophycus* by morphology or trace-maker and thus merited inspection for purposes of comparison. The mystery cabinets occasionally produced unlabelled specimens of *Arthrophycus*, including an unnamed and unnumbered specimen found at the New York State Museum and described herein.

For most specimens, I had to rely on published photographs and drawings; many of these are grainy or otherwise indistinct. In an attempt to surmount the limitations of poor reproductions, I requested loans or better pictures from authors and museum staff, but rarely received a response. Efforts to request loans of specimens were not successful either; partly because trace fossils commonly are not given catalog numbers. As a result, I have had to rely on the published figures for many *Arthrophycus* specimens.

Once I had collected my data and published reports of *Arthrophycus*, I began to condense the data and establish a list of diagnostic characteristics for the ichnogenus, which I used to evaluate each proposed occurrence and ichnospecies. I assessed each occurrence as belonging to one of three categories: conformable to *Arthrophycus*, unverifiable (usually noted only in a list without a detailed description or figures), and not conformable to *Arthrophycus*. If the published photographs were of poor quality or questionable as to their characters, but the written description included references to key morphological characteristics of *Arthrophycus*, I made decisions based primarily on the written description. A new ichnospecies, however, must have a good quality photograph that clearly shows salient features of *Arthrophycus* to be considered as a valid member and new species of the ichnogenus.

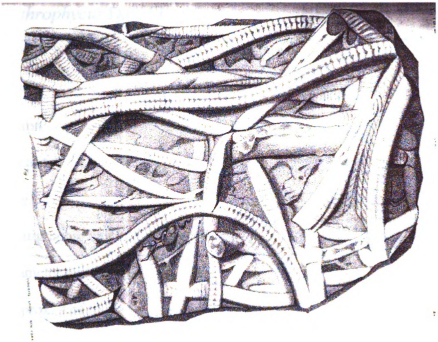


Figure 1.1a: Sketch of *Arthrophycus alleghaniensis*, from Hall (1852). Silurian, Medina Sandstone, New York.

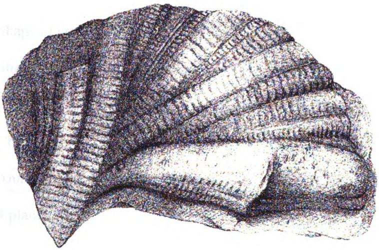


Figure 1.1b: Sketch of *A. alleghaniensis*, from Hall (1852). Silurian, Medina Sandstone, New York.

Arthrophycus Data Sheet

Date:

ID#

Taxon

Locality

Age

Stratigraphic unit and lithology

Diameter max/min

Approx. # of traces

Length of "full" traces

Branching (true, pseudo, not)

Spreite or backfill

Shape of cross-section

Shape of overall structure

Bilobate

Chevrons

Annulations (width if present)

---

planes

Orientation with respect to others

Other structures, trace or body fossils, features

Sketch:

Figure 1.2: Data sheet used to characterize museum specimens of *Arthrophycus*.

Chapter II. History of *Arthrophycus* and definition of characters

History of Arthrophycus

The history of *Arthrophycus* begins with initial descriptions of specimens as fucoids by Eaton (1820), but he did not name the specimens formally. A formal name had to wait until 1831, when Harlan described the first ichnospecies of what is now *Arthrophycus* under the name *Fucoides*. He described *Fucoides alleghaniensis* n. sp. in that year and then followed it with a description of *F. brongniartii* n. sp. in December 1831 (published in 1832). As was common at the time, Harlan placed both new species into the group of fucoids, or "seaweeds." However, the fucoid group was a common wastebasket designation at the time (Dawson 1964) and often included fossils that were not "seaweeds" at all (Shimer and Shrock 1944).

Eaton (1832) referred to fossil specimens that have since been placed in *Arthrophycus* on the basis of the descriptions (the actual types are lost) (Rindsberg and Martin 2003). Eaton's fossils, from the Medina Sandstone, were described as branched, long, curved, and occurring in layers. Eaton placed the specimens into *Encrinus giganteus* Eaton, 1832, later placed in synonymy with *Arthrophycus* (his specimens may have been either *A. alleghaniensis* or *A. brongniartii*) (Bassler 1915, Rindsberg and Martin 2003).

The next account of *Arthrophycus* (as *Fucoides*) came from Taylor in 1834, who described abundant specimens of *F. alleghaniensis* in Pennsylvania, near the locality where Harlan had found his original specimens. Taylor followed this paper with another in 1835, in which he described finding numerous *F. alleghaniensis* specimens *in situ*, as well as specimens of the rarer *F. brongniartii*.

In a paper read in 1834 but published in 1836, Harlan briefly mentioned the two species of *Fucoides* that he had previously published and noted some particular points in which his species differed from specimens that other authors had referred to them. In this critique, he distinguished three important characters of *F. brongniartii* that those other specimens lacked: grooves, branching, and a rougher texture of the surrounding sandstone matrix. Harlan also observed that the specimens he excluded from *F. alleghaniensis* contained a filling of "convex layers of sandstone," which puzzled him, because he thought that his *Fucoides* specimens were similar to aquatic cryptogamae (algae). In a last note to this paper, Harlan recorded that Mantell (1834) had given an unrelated fossil the name *Fucoides brongniartii*, but that the specimens were not of the same form as those he (Harlan) described.

Conrad also mentioned Harlan's *Fucoides* in several reports (1837, 1838, 1839). In the first (1837), he referred to both *F. alleghaniensis* and *F. brongniartii* as present in the Medina Sandstone. In 1838, he used the name *F. harlani* for the first time in the literature ("*Fucoides harlani* nobis (*F. brongniartii* Harlan)") without giving a reason for the change in specific name. In 1839, Conrad again used the name *F. harlani* to describe Harlan's fossils, which he found in abundance throughout New York, Pennsylvania, and Virginia. However, he noted that *F. harlani* was restricted to the Medina Sandstone, thus recording the first opinion that *Arthrophycus* is limited biostratigraphically.

One author described *Arthrophycus* as a crinoid. De Castelnau (1843) placed specimens into the crinoid genus *Crinosoma*, noting that the specimens were poorly preserved and different from any known crinoid form, and thus deserving of a new generic name. No other authors have used the name since 1843, but *Arthrophycus* was used many times after Hall coined it in 1852, so *Crinosoma* is a *nomen oblitum* and *Arthrophycus* is a *nomen protectum* (Rindsberg and Martin 2003).

Hall (1852) redescribed Harlan's fossils as *Arthrophycus* in his great work on the paleontology of New York and referred to *A. harlani*, making no distinction between Harlan's *F. alleghaniensis* and *F. brongniartii* (James 1893a also considered the two ichnospecies to be the same form). In the same year, Göppert (1852) described Harlan's *F. alleghaniensis* as *Harlania halli* (and also placed *F. brongniartii* under *Harlania halli*). In a case in which two taxonomic names are published in the same year, the first reviewer (Miller 1877) decides upon the name to be preferred in the future; Hall's *Arthrophycus* prevailed (Rindsberg and Martin 2003). It is also possible that the relevant section of Hall's (1852) paper was actually composed in 1850, thus taking precedence over the later work of Göppert (1852) (James 1893a).

However, in Europe, Hall's work was mistakenly dated as 1853, leading researchers there to use the name *Harlania* as late as 1966 (Gubler *et al.* 1966), but the practice is no longer common. The name *Harlania* is widespread only in Jordan, where an Ordovician layer there has been informally named the "*Harlania* Shale" (Selley 1972) and thus the name *Harlania* remains in use for the fossils as well (e.g. Eschard *et al.* 2005; Turner, Makhlouf, and Armstrong 2005).

James and other researchers ultimately supported *A. alleghaniensis* as the best name for the species, noting that *F. alleghaniensis* was a valid name, adequately illustrated and with correct format by Harlan (1831), so there was no need for Conrad (1838) and Hall (1852) to change from this earliest species designation (James 1893a, Rindsberg and Martin 2003). Some confusion remains: museum specimens are cataloged variously as *F. alleghaniensis*, *F. harlani*, *A. harlani*, *A. alleghaniensis*, *H. alleghaniensis*, and so on. Though most authors adhere to one name, at least one used two apparently synonymous names (*A. harlani* and *A. alleghaniensis*) in the same paper (Moneda 1963).

Identity of *Arthrophycus*

Some authors, beginning with Seilacher (1955), have proposed a merger of *Arthrophycus* with the ichnogenus *Phycodes*. However, the two ichnogenera possess distinctive features and differences (e.g. size, prominence of annulations, relation to sediment as seen through internal structure) that merit separate ichnogeneric designations (Osgood 1970). Individual *Arthrophycus* specimens are not always observed in bundles, which is additional evidence against a synonymy with *Phycodes*, which is always bundled (Uchman 1998). The idea of merging the two ichnogenera has now largely disappeared (Häntzschel 1975, Pickerill *et al.* 1984).

Even once the fossils now known as *Arthrophycus* had a name that most ichnologists could agree upon, their biological affinity still remained in question. Along with being considered blooms or stalks of fucoids or other plants, *Arthrophycus* has also been identified as traces of many different types of other organisms or even as inorganic forms (Häntzschel 1975). The plant idea had its heyday from 1831 to 1901 (e.g. Harlan 1831, Schimper and Schenk 1890, Herzer 1901) and was resurrected briefly in the mid-twentieth century (Becker and Donn 1952, Duimovich 1963), but the hypothesis has since received no support.

The suggestion that *Arthrophycus* could be inorganic is actually far simpler than it first appears. No one has ever proposed that the entire ichnogenus is inorganic; rather, a few isolated specimens have been dismissed as actually inorganic. This is limited to two reports: that of Schiller (1930) and Kulkarni and Borkar (2002). Schiller's paper described some putative *Arthrophycus* specimens from Argentina that he determined were tectonic products rather than organic remains, but he allowed other specimens of *Arthrophycus* in other rocks to be true fossils. In the second case, Kulkarni and Borkar (2002) determined that reputed *Arthrophycus* from the Proterozoic of India (described by Mukherjee *et al.* 1987) were inorganic in nature.

Debate still rages as to the producer of *Arthrophycus*; suggestions include worms of many types, trilobites and other arthropods, gastropods, echinoderms, and various unknown animals (see Tables 2.1 and 2.2). Imprints of non-moving animals have also been suggested, including worms (Borrello 1966), crinoids (de Castelnau 1843), and octocorals (Fauchald, pers. comm.). Though the most popular suggestion is that some kind of worm-like animal made the traces known as *Arthrophycus* (including works up to 2009, e.g. Miller *et al.* 2009), many of the more recent publications favor an arthropod producer, whose appendages would have been best-suited to make the ridge-like annulations seen in most specimens of the ichnogenus. In a personal communication, Kristian Fauchald of the Smithsonian Institute, an expert on modern polychaete annelids, indicated that an annelid would be unlikely to make these annulations while moving (Brandt *et al.* 2008). An interesting new candidate for the trace-maker is *Tanazios dokeron*, the Silurian crustacean-like creature from England figured in Siveter *et al.* (2008). However, a full discussion of the trace-maker is outside of the scope of this research.

"Official" Diagnosis of *Arthrophycus*

Given its varied and confusing history, the diagnostic characteristics required for *Arthrophycus* have become rather blurred over time. Therefore, a review of the original descriptions is in order.

Harlan's original Latin (1831) description of *F. alleghaniensis* reads as follows: "*Fucoides alleghaniensis*: *Fronde compressa, rugata; apice recurva, obtuse; ramis inequalibus, digitatis et fastigiatis, enervibus, nudatis*." This translates to "frond compressed, wrinkled, recurved bluntly at its apex; branches unequal, fingerlike structure in a separated bundle, weakly differentiated and stripped of any coverings." He then went on to say:

> "They lie upon each other three or four layers deep…project in bold relief from the surface, with their distal extremities disposed in every direction; they appear to have been of different ages, and vary in size accordingly from two to five inches in length, the largest being eight tenths of an inch in thickness. In breadth they vary from one to five tenths of an inch…gently arched from the base towards the apex, and more or less recurved at top; in every instance the apex is curved downwards and sinks into the stone. The superior surface of both the stalk and branches is cylindrical, transversely wrinkled by irregular channels, and marked by a longitudinal depressed line…They have grown in such profusion and are so crowded together that the commencements or bases of the stalks are for the most part concealed…The branches are compressed laterally as well as the stalk."

Hall's (1852) original description of *Arthrophycus* is as follows:

> "Stems simple or branching, rounded or subangular, flexuous, ascending, transversely marked by ridges or articulations. The species of this genus yet known consists either of simple elongated stems of nearly equal dimensions throughout, or those which divide near the root into several branches and afterwards remain simple."

Göppert's (1852) description of *Harlania*, translated from the Latin, is: "straplike simple turflike aggregate or dichotomous branch, in younger states longitudinally sulcate, branches of adults subcylindrical interrupted transversely by elevated ridges."

In the Treatise of Invertebrate Paleontology, Häntzschel (1975) described *Arthrophycus* as:

> "Bundles of annulated curved burrows, simple or branched, subquadrate in cross section, mostly 1 to 2 cm. in diameter, up to 60 cm. long, commonly bilobate with median longitudinal depression; surface showing strong, very regularly spaced transverse ridges; internal chevron-shaped filling."

When analyzing the four above descriptions, several important points emerge. All four authors mentioned five characteristics: transverse ridges or annulations, simple overall form, branches, bundles, and a somewhat compressed cross section. Therefore, to be considered a valid ichnospecies or specimen of *Arthrophycus*, the specimen should possess most or all of these five characters. Harlan (1831), Göppert (1852), and Häntzschel (1975) mentioned a longitudinal depression, as did Hall (1852) in his separate description for *A. harlani*. In addition, Häntzschel (1975) mentioned an internal filling and Hall (1852) mentioned nearly equal dimensions throughout, both of which have been noticed by subsequent authors. Finally, three of the authors agreed on an approximate diameter of 1-2 cm for their specimens. These characters shall all be discussed more fully below.

Taxonomically Important Characters from Original Diagnoses

The following characters are shared among the original descriptions of *Arthrophycus* by Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975).

Annulations

Annulations are present in all the proposed ichnospecies of *Arthrophycus* examined herein, with only a few exceptions in which the character is faint or not mentioned (e.g. some specimens of *A. tenuis*); no proposed ichnospecies is without them completely. Harlan (1831) referred to transversely wrinkled channels, Hall (1852) to transverse ridges or annulations, and Göppert (1852) and Häntzschel (1975) mentioned transverse ridges. Possession of this character state is thus an important requirement to be *Arthrophycus* (Figure 2.1); specimens lacking annulations are very questionable (e.g. Pettijohn and Potter 1964) and may instead be *Paleophycus*, *Phycodes*, or other traces that are otherwise similar in form to *Arthrophycus*.

Simple form

Simple form or structure is another common theme in *Arthrophycus* descriptions (Figure 2.2). Hall (1852), Göppert (1852), and Häntzschel (1975) used the term "simple," while Harlan (1831) described his fossils as "fingerlike" and "stripped of any coverings." These structures may be branched or form bundles, but ultimately the individual trace is simple in form. This shape is rarely perfectly straight but curves or arches, as both Harlan (1831) and Häntzschel (1975) wrote in their descriptions and Hall (1852) added in his description of *A. harlani*.

Branches

Branches are also a common feature: Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975) all included branching for *Arthrophycus* and most other authors do as well. However, some proposed ichnospecies of *Arthrophycus* (e.g. *A. brongniartii*) do not exhibit branching, and the lack of branching is often cited as one of the reasons for a distinct new ichnospecies designation. The presence or absence of branching need not be a problem, for both Hall (1852) and Häntzschel (1975) observed that specimens may be simple *or* branched, likely alluding to this variation. If branching is present, it may manifest itself as "simple branching" with few (typically two to three) structures involved (Figure 2.3), "pseudo-branching" (unrelated branches cross over one another) (Figure 2.4), or "palmate branching" (many branches form a bundle or fan, as discussed below) (Figure 2.5).

Bundles

Bundles or aggregates of traces feature in all four of the above original descriptions. Traces may appear to converge into one thick and relatively narrow bundle (Harlan's (1831) "stalk") (Figure 2.6), or into a fan-like structure that is largely two-dimensional (Figure 2.5). As with branching, bundling is a common and well-known character, but is not essential to all *Arthrophycus* (e.g. *A. brongniartii*).

The particular type of bundling in *A. lateralis* Seilacher 2000 is part of the justification for its designation as a separate ichnospecies (Seilacher 2000). The bundling prominent in *A. alleghaniensis*, the most familiar ichnospecies of the ichnogenus, likely led to the ichnospecies's initial description as plant-like. The different types of bundling (and also branching) may intergrade, as an individual trace may emerge from its bundle to be predominantly straight and independent or may cross other traces (Figure 2.7). It is often impossible to trace a particular trace for very long before it descends into the matrix (Figure 2.8), further complicating the issue.

Cross-section

Cross-section is the final common character from the four original descriptions of *Arthrophycus*. Although Harlan (1831) referred to his specimens as "cylindrical," he also mentioned compression of the branches and stalk. Hall (1852) described his specimens as "rounded or subangular," Göppert's (1852) were subcylindrical, and Häntzschel (1975) used the term "subquadrate." Of the twenty-three *Arthrophycus* ichnospecies, seven are characterized as subquadrate, eight are cylindrical or elliptical, and eight do not include a description of the cross-section.

Median groove

A median groove or longitudinal depression (Figure 2.9) was mentioned in the works of Harlan (1831), Göppert (1852), and Häntzschel (1975), while Hall (1852) included the feature in his description of *A. harlani*. The groove is a common feature in *Arthrophycus* specimens and is found in nearly half of the purported ichnospecies (nine of them show it, nine do not, and the remaining four are unclear in the published photograph or not mentioned in the written description). Some authors have mentioned the difficulty of preservation of such a delicate feature (MacNaughton and Pickerill 2003, Miller *et al.* 2009) and even specimens that are otherwise clearly *Arthrophycus* do not have a groove or have only an indistinct median groove (Figure 2.10). Regardless, the feature is both common in specimens and well-known.

Internal structures

Internal structures are not mentioned often in published descriptions of *Arthrophycus*, as recognition of them requires cut and polished or broken specimens in which a cross-section is observable (Figure 2.11). Nevertheless, internal structure may prove to be a diagnostic feature for *Arthrophycus*. Among the primary descriptions of *Arthrophycus* given above, only Häntzschel (1975) described the filling, as "chevron-shaped," though Harlan noted internal structures in a later paper (1836). Sarle (1906) presented the internal structures of *Arthrophycus* to determine how the animal burrowed and then used those structures as evidence that *Arthrophycus* was a trace fossil rather than a plant or organism. Seilacher (2000) has used variation in internal structures as a basis for subspecies of *Arthrophycus* (*A. linearis* subsp. *protrusiva* and subsp. *retrusiva*).

Constant diameter

Constant diameter of individual traces featured in only Hall's (1852) work among the four primary descriptions, but it is used often as an important characteristic of *Arthrophycus*. Except where branching and bundling make the diameters of individual burrows indistinct, *Arthrophycus* has a very consistent diameter along its length, as subsequent authors have observed (e.g. Dalloni 1934, Neto de Carvalho *et al.* 2003, Kumpulainen *et al.* 2006).

Size

Size (width or diameter) of individual *Arthrophycus* traces is the final common character among three of the four authors above: the descriptions of Harlan (1831), Hall (1852), and Häntzschel (1975) agreed on an approximate diameter of 1-2 cm. This approximate diameter remains typical of the *Arthrophycus* ichnogenus (Tables 2.3 and 2.4), but reports for *A. alleghaniensis* alone range from a minimum of 0.25 cm (Liñán 1984) to a maximum of 6 cm (Burjack and Popp 1981). However, the smallest and largest measurements are not typical of the ichnospecies and some of them may not even be validly assigned to *Arthrophycus*. A more typical range for *A. alleghaniensis* is 0.5 to 1.5 cm (Table 2.3); other ichnospecies tend to have rather small ranges of reported sizes, often with a difference of only a few millimeters between the minimum and maximum, because fewer authors have remarked upon them or reported new occurrences (Table 2.4).

Preserved burrow length is not always reported, and this measurement is far less reliable than that of diameter because burrows of *Arthrophycus* do not have distinct starting or ending points, but weave under one another or disappear off the edge of the preserved rock slab (Sarle 1906). Because the full length of *Arthrophycus* traces is seldom preserved, authors who do report length measurements often include very large ranges or simply note the longest preserved burrow that they could follow without doubt as to its identity (e.g. Häntzschel 1975).

Although size is not usually considered a valid ichnotaxobase because it may be more closely correlated with the size of the trace-maker than the actual trace morphology (Fürsich 1974, Bertling *et al.* 2006, Bertling 2007), authors have used it nonetheless (e.g. Osgood 1970, to differentiate *Arthrophycus* from *Phycodes*; also Magwood 1992); size is also an easy character to measure and may help to reveal the trace-maker's identity. At least one ichnotaxonomist allows that size may be acceptable for ichnospecific designations, but probably not for ichnogenera (Pickerill 1994).

Additional Characters

Other characters appear in subsequently published descriptions of *Arthrophycus* but were not mentioned in the cited primary descriptions. These other characters include wrinkles or fine ornamentation, orientation with respect to the substrate and to other individuals of *Arthrophycus*, and association with non-*Arthrophycus* traces. Some authors have questioned whether a single trace can be classified as *Arthrophycus* or if *Arthrophycus* must refer to an aggregate of many traces, preferably in bundles (Pickerill *et al.* 1991, Fernandes *et al.* 2002). Furthermore, some workers have wondered whether *Arthrophycus* is always found in monoichnospecific assemblages or if it can be associated with other body or trace fossils (Mángano *et al.* (2005a)). Because none of these characters was mentioned in any of the four original descriptions, it remains in question whether these additional characters should be accepted as diagnostic or not. These additional characters are discussed more fully below.

Wrinkles

Wrinkles or fine ornamentation on the surface of the trace require exceptional preservation and photography. In most cases, one or both of those is lacking in published descriptions. However, fine wrinkles along the annulations have been seen in *A. alleghaniensis* (Figure 2.12) and *A. brongniartii* (Rindsberg and Martin 2003) (and as *A. linearis*, by Seilacher 2000).

Orientation with respect to substrate

The orientation with respect to the substrate is a feature that may elucidate what the trace-maker was doing in or on the sediment. *Arthrophycus* traces commonly lie more or less parallel to bedding; some specimens show gentle arching in the vertical dimension (Figure 2.13). The traces may have several layers of primarily flat-lying traces atop one another (Figure 2.14). Others, however, twist in many directions and in all three dimensions (Figure 2.15) and some traces may run perpendicular to the bedding and to surrounding *Arthrophycus* (Figure 2.16).

<u>Orientation relative to other traces</u>

The orientation with respect to other traces is also important in *Arthrophycus* and may help to differentiate among ichnospecies. These include *A. lateralis* (Seilacher 2000), which has a particular pattern to its palmate form, and *A. parallelus* (Brandt *et al.* 2010), which is primarily parallel. Apart from branching or bundling, described *Arthrophycus* traces can have different orientations with respect to one another. Some are markedly parallel, others form a radial pattern, and most intersect each other in a way that looks similar to branching (termed pseudobranching above). In large slabs containing many *Arthrophycus*, there are even more patterns of orientation, such as "twisting" (Figure 2.17) and "loops" (Figure 2.18). Of course, in instances of only one trace, this character does not apply.

<u>Number of traces</u>

The number of traces necessary to be considered *Arthrophycus* has been a subject of debate. As Pickerill *et al.* (1991) stated, isolated specimens of *Arthrophycus* are "atypical and not clearly understood." At least thirteen examples of published isolated *Arthrophycus* specimens exist, including both those placed in *Arthrophycus* with no ichnospecies designation and others that have been designated as new ichnospecies. New ichnospecies herein called "singletons" include both *A. corrugatus* Fritsch (1908) and *A. dzulynskii* Książkiewicz (1977), while those placed in "*Arthrophycus* isp." include Akpan and Nyong (1987), Bhargava *et al.* (1984), Lin *et al.* (1986), Stanley and Feldman (1998), and Terrell (1972). Oddly, the specimen that

Pickerill *et al.* (1991) placed under "*Arthrophycus* isp." was also an isolated specimen. It should be noted that the "isp." designation indicates that the authors were not sure of species designation, and thus it may also be questionable whether many of the specimens are correctly assigned to *Arthrophycus*.

Conversely, Pickerill *et al.* (1991) classified as singletons specimens from Bjerstedt (1987) and Durand (1985), which in fact have multiple individuals of *Arthrophycus*. Pickerill *et al.* (1991) also misinterpreted a specimen described by Legg (1985), which may be a single stack of several traces of *Arthrophycus*. Some traces reported as *Arthrophycus* have very few individuals, perhaps as few as two or three forming a single branch structure (e.g. Luo *et al.* 1994). This is particularly characteristic of the Cretaceous examples described in several publications by Howard and Frey in the 1960s and 1970s (e.g. Howard 1966, Frey and Howard 1970, Frey 1972).

Associated fossils

Associated trace or body fossils are not common in slabs with *Arthrophycus* specimens. *Arthrophycus* is usually included in the *Cruziana* ichnofacies, which is known for a predominance of cubichnia (resting traces) and arthropod tracks and burrows, without many grazing tracks, and is characteristic of shallow marine deposits above wave base (Seilacher 1964a). Unsurprisingly, *Cruziana* and the related *Rusophycus* (Figure 2.19) are the most common ichnofossils cited in association with *Arthrophycus* (e.g. Turner and Benton 1983, Seilacher *et al.* 2002, Poiré *et al.* 2003, Mángano *et al.* 2005a), as well as specimens of *Daedalus* (Miller *et al.* 2009). *Arthrophycus* has been noted in the same assemblage as *Teichichnus* (Pacześna 1996) and specimens of *Dictyodora* (Orr 1994) and the lump-like *Lockeia* have also occurred with *Arthrophycus* (Brandt *et al.* 2010) (Figure 2.20). The only reported case of a body fossil occurring "from sedimentary sequences containing analyzed *A. alleghaniensis*" is the centipede-like fossil found by Baldwin and Strother (2004), who suggested centipede-like animals as the trace-maker of *Arthrophycus* in part as a consequence of that association.

Gradation Between *Arthrophycus* and Other Ichnogenera

Part of the joy in interpreting trace fossils is that one animal can make numerous traces and numerous animals can produce or use the same trace (Osgood 1975b, Bromley 1990, Magwood 1992, Minter *et al.* 2007). Many animals make similar burrows for similar reasons or with similar behaviors (Bromley 1990); the simple U-shape found in burrows such as *Diplocraterion* is an example (Osgood 1975b). In addition, traces made by one animal can also be preserved differently in different substrates (Osgood 1975a, Bromley 1990). Any of these problems may produce burrows that appear to be the same, or make unreal differences apparent (Osgood 1975b). Gradational traces are particularly well-known between the probable trilobite traces *Cruziana* and *Rusophycus* (Keighley and Pickerill 1996).

Arthrophycus is hardly immune to these problems of gradation, as the plethora of potential trace-makers indicates. Similarity of body plans among such large groups as the annelids, priapulids, and nemerteans makes a positive identification of individual producer difficult and differentiation among similar makers with similar behaviors almost impossible (Osgood 1975b). Some evidence of intergradations between *Arthrophycus* and other ichnogenera exists in the Silurian of Alabama, where specimens of *Arthrophycus* show a similarity to *Nereites biserialis*, *Rusophycus*-like structures, and possibly others (Rindsberg and Martin 2003). However, such intergradations are rare in *Arthrophycus*.

Suprageneric Classification of *Arthrophycus*

Although trace fossils need not be organized beyond the generic level (ICZN 1999), a few authors have attempted higher hierarchy levels. In one such scheme, *Arthrophycus* was grouped most closely with *Rhabdoglyphus* Vassoevich, 1951, and *Scalarituba* Weller, 1899, in the superichnofamily Unilobatoidea, with *Cruziana* placed in the same ichnoorder (Mikuláš 1992). However, such schemes are uncommon and other authors have not chosen to follow them; descriptions of ichnogenera are instead listed in alphabetical order or grouped by ethology (repichnia, cubichnia, etc.).

In a recent attempt at a suprageneric classification, Seilacher (2000 and 2007a) grouped *Arthrophycus* with *Daedalus* and *Phycodes* to create the family-rank arthrophycids, together with the teichichnids. He grouped these ichnofossils based on what he perceived as their similar "fingerprint" of regular annulations, backfill structures, and blind tube endings. Other authors support Seilacher on this point, including Sarle (1906) and Brett (pers. comm.), noting the similarity between *Daedalus* and *Arthrophycus* in particular. Although some of the spiral-form ichnospecies of *Daedalus* initially appear to be very different from the simple structures of *Arthrophycus*, others are quite similar, possessing annulations, a possible median groove, and occasionally a bundle or fan-like structure (Durand 1985) (Figure 2.21).

Morphological Issues Raised in Previous Work

Singletons vs. multiple traces

Although *Arthrophycus* is commonly described as a gregarious trace, occurring in the hundreds on larger specimens (e.g. Miller *et al.* 2009), other authors have attempted to include in the ichnogenus specimens that consist of a single trace (e.g. Książkiewicz 1977, Bhargava *et al.* 1984, Pickerill *et al.* 1991). In their descriptions, Harlan (1831), Hall (1852), and Häntzschel (1975) referred to groups of traces and their orientations to one another (branching and bundling), although the first two authors interpreted *Arthrophycus* as a plant or mass of plants rather than groups of traces. More recent authors have excluded reports of singletons from *Arthrophycus* (e.g. Mángano *et al.* 2005a).

In some cases, a reported specimen is a singleton based on the sampled rock size – only one or a few traces can fit on the surface, or a trace may have broken from the rest of the matrix (Figure 2.22). However, this is not the case for most published specimens – the rest of the rock surface is devoid of traces (e.g. Akpan and Nyong 1987, Pickerill *et al.* 1991).

Many questionable assignments to *Arthrophycus* are either singletons (e.g. Akpan and Nyong 1987) or single branches of one or two traces (e.g. Howard and Frey 1966). Some museum collections include single traces or structures that have been referred to *Arthrophycus*, likely in error as they lack diagnostic features of the ichnogenus (Figure 2.23). Published descriptions of putative *Arthrophycus* singletons encourage proliferation of the concept despite the departure from the type concept that these specimens represent.

If trace fossils are understood to be records of ancient behavior, then a propensity to be gregarious is a part of that behavior, whether it is true "social behavior" (many individuals making traces at close to the same time) or merely apparent (a few individuals making many traces in the same spatial area). Behavior can be a morphologic character (and thus a legitimate ichnotaxobase) because it is part of the "extended phenotype" (Dawkins 1982) of the maker of *Arthrophycus*. Therefore, gregarious behavior, as evidenced by multiple co-occurring traces, should become part of the ichnogenus diagnosis, and that traces that are too small or broken to properly display that behavior but containing all other characteristic traits be termed "*Arthrophycus*-like."

Median groove

Much of the *Arthrophycus* research summarized above raised the question of the taxonomic importance of the median groove. A median groove was included in the initial descriptions of Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975), as well as in the diagnoses of many other authors, for *A. alleghaniensis* and most of the other ichnospecies and *Arthrophycus* isp. reports. However, a groove can be effaced, either by a lack of substrate cohesiveness or dewatering before lithification, or by post-lithification weathering. Some authors reported a median groove in their specimens, but wrote that it was faint or not present along the full length of the trace or traces (e.g. Metz 1998, Fernandes *et al.* 2000, Kumpulainen *et al.* 2006).

In addition, recognition of a "groove" can disappear upon closer inspection. This is evident in a number of the specimens of *Arthrophycus* from the classic Medina Sandstone examined during museum visits. The annulations in these specimens are not really "ring" structures, but exhibit a "pinched" appearance toward the middle of the trace (Figure 2.12). The ridges still have a faint dip toward the middle as in the groove, but the shape of the annulations is the primary contributor to the appearance of a full groove. One of the figures of *Harlania* in Bender (1963) also shows this, demonstrating that the feature is not limited to the Silurian of New York, and it is likely that "pinching" of annulations creating the illusion of a median groove exists in other *Arthrophycus* specimens but has not yet been recognized; the poor quality of many published figures makes that even more difficult to determine.

Because of problems with preservation, recognition, and reporting, some authors (e.g. Pickerill *et al.* 1991) suggested that a median groove need not be a diagnostic criterion for inclusion in *Arthrophycus*. In the review of *Arthrophycus* literature, presence of a median groove was considered support for inclusion in *Arthrophycus*, but, because of the preservation and recognition factors discussed above, the apparent absence of a median groove was not considered evidence that a specimen should be excluded from *Arthrophycus*. The presence or absence of a median groove should remain in the diagnosis for the ichnogenus because it is so common and should not be excluded just because it may be lost occasionally.

As a final note, the median groove, where present, may influence the choice of the most likely trace-maker. A median groove or furrow is often interpreted as the work of a multi-limbed animal that cast sediment toward the midline of its body as it processed the substrate (in fodinichnia) or moved along the substrate (in repichnia).

Branching and bundles

Although branching and bundling were mentioned explicitly by Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975) in their diagnoses of *Arthrophycus*, a few authors have suggested that neither characteristic is diagnostic for *Arthrophycus*. This claim originated with Pickerill *et al.* (1991), from those who have cited that work (e.g. Fernandes and Borghi 1996, Fernandes *et al.* 2002), or from those who have placed singletons into *Arthrophycus*. However, the branched nature of *Arthrophycus* should remain part of the ichnogeneric diagnosis. Even the name *Arthrophycus* means "jointed plant," referring to the perceived branching of the structures. Some branching may be pseudo-branching that occurred when individual traces crossed over one another, but branching as a character is present in anything that can be considered *Arthrophycus*.

The *type* of branching, however, can differ among ichnospecies of *Arthrophycus*. Ichnospecies may have prominent or minor branching, but branches must be present in some form. Branching can take the form of prominent bundling and palmate shapes in *A. alleghaniensis* and *A. lateralis* or the cross-over pseudo-branches in the more independent *A. brongniartii* and *A. minimus*. Even *A. parallelus*, noted for its rather independent and predominately parallel traces, exhibits pseudo-branching in places.

Some authors have noticed a difference in branching that they did not choose to use as evidence for a new species. Fernandes and Borghi (1996) and Fernandes *et al.* (2000) mentioned both a dichotomous form and one with "several new branches starting from a single point." This may reflect the difference between the palmate bundles of *A. alleghaniensis* and *A. lateralis* and the simpler branching or pseudo-branching of *A. brongniartii* (all of these have been found by these authors in Brazil), or it may indicate something different.

<u>Size of traces over time</u>

As stated above, reports of width in *Arthrophycus* can vary tremendously, from 2.5 to 60 mm in one ichnospecies alone, and 0.5 mm to 60 mm in the entire ichnogenus (Tables 2.3 and 2.4). Small size may be primitive (Mángano *et al.* 2005a), or reflect environmental stress (MacEachern *et al.* 2005) or nutrient availability (Fernandes 2001), or perhaps the age or growth stage of the trace-maker.

A number of the smaller proposed ichnospecies of *Arthrophycus* are known from the Cambrian. These include *A. qiongzhusiensis*, *A. strictus* (specimens from Pacześna 1996 only), and *A. minimus*. Mángano *et al.* (2005a) suggested that small size is therefore a primitive characteristic of *Arthrophycus*. However, size may also reflect environmental stress (MacEachern *et al.* 2005). A number of the authors working in Brazil noticed a smaller size in *Arthrophycus* in the latter portion of the time range there (Early Devonian) (Fernandes *et al.* 2000) and have posited that the small size is a result of nutrient availability (Fernandes 2001).

Mángano *et al.*'s (2005a) assertion that small size is characteristic of geologically older *Arthrophycus* is further countered by small ichnospecies from younger strata. Those ichnospecies in the Cretaceous and Cenozoic (*A. strictus* and *A. tenuis*) may not be valid *Arthrophycus* as discussed above, but *A. parallelus*, from the Carboniferous, has a size range within that of *A. minimus*. *A. elegans*, while not a valid ichnospecies but possibly validly included in *Arthrophycus*, also exhibits small size and is from the Carboniferous. Small size is therefore not necessarily primitive in *Arthrophycus*.

To test for trends, or lack thereof, of the size of *Arthrophycus* over time, I produced a graph of width over time (Figure 2.24). To do this, I recorded a list of all reported widths of *Arthrophycus*, excluding those that were designated only as "*Arthrophycus* isp." and recording all reports for whatever ichnospecies name the authors had originally used (e.g. both *A. brongniartii* and *A. linearis* are in the graph separately) (see Tables 2.3 and 2.4). I also included an unidentified specimen from the New York State Museum in Albany, NY, designated as "Albany." (See Chapter IV for further discussion of this specimen.) Most of the width measurements were reported as ranges (e.g. 3.5 to 4.5 mm); I used the midpoint for each one.

The dates of the occurrences are reported in the literature only as periods (Cambrian, Ordovician, etc.) rather than as absolute dates. To portray the time distances between periods as accurately as possible, especially in the case of the distances between the Paleozoic and the Cenozoic occurrences, the midpoint of the reported time period was used, using the International Stratigraphic Chart (Ogg 2008) for the dates. For example, the Cambrian period is calculated as [(542.0 - 488.3) / 2] + 488.3 to get a midpoint age of 515.15 million years. For reported ages that encompassed two periods, the boundary between those ages was used (e.g. "Ordovician to Silurian" is 443.7 million years). These dates are imperfect, but they are preferable to a scheme without numbers at all, which would require a non-numerical coding along the time axis.

The resulting graph showed some interesting trends (Figure 2.24). *A. alleghaniensis* was notable for its large range over both time and width range, but one must also note that the ichnospecies also had the largest number of measurements, by far (n = 27, compared to the next largest n = 4 for both *A. linearis* and *A. tenuis*). As noted earlier, there were small individuals throughout the range of *Arthrophycus* and no trend in size over time, though the larger individuals were concentrated in the middle of the time range (Silurian) (see Figure 2.25 for a close-up of this crowded region). A few of the ichnospecies, such as *A. linearis* and *A. brongniartii*, had a larger range in size, but most ichnospecies had smaller ranges or few reports.

<u>Annulations</u>

Although most authors noted annulations in their photographs or drawings and mentioned it in their descriptions, defining what is meant by the term "annulations" was not self-evident. In the four primary descriptions of *Arthrophycus*, Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975) all observed annulations in their specimens. However, a definition of the term was rarely, if ever, given. Annulations are raised bands separated by thin grooves, perpendicular to the long axis of the trace, and are usually regularly spaced. With closer inspection, it was evident that not all annulations in ichnospecies placed in *Arthrophycus* have the same shape: some are concavo-convex like cupped shells, some have a zippered chevron appearance that has more of a v-shape than do the concavo-convex annulations, and some are biconvex like dumbbells. This biconvex shape is the form common in *A. alleghaniensis* and *A. brongniartii* and that appears to be pinched in the middle.

Table 2.1: Authors who have suggested some kind of worm-like animal as the trace-maker of *Arthrophycus*.

Reference	**Specific Suggestions**
Abel 1935	*Lanice*-like
Borghi *et al.* 1996	polychaete
Downey 1980	segmented annelid, e.g. Nephtyidea
Fernandes *et al.* 1995	sedentary polychaete
Fernandes *et al.* 2002	worm-like
Häntzschel 1975	
Konate *et al.* 2003	
Książkiewicz 1977	polychaete
Kumpulainen *et al.* 2006	
Lin *et al.* 1986	
Mángano *et al.* 2005	coelomate
Miller *et al.* 2009	endobenthic annelid or annelid-like
Moore 1933	
Neto de Carvalho *et al.* 2003	coelomate
Pickerill *et al.* 1991	sedentary polychaete
Sarle 1905	
Sarle 1906	polychaete
Schuchert 1916	lobworm-like
Seilacher and Alidou 1988	
Seilacher *et al.* 2003	
Seilacher 2007a	

Table 2.2. Additional suggestions for the *Arthrophycus* trace-maker.

Reference	**Organism**	**Specific Notes**
Konate *et al.* 2003	Trilobite	
Kumpulainen *et al.* 2006	Trilobite	
Neto de Carvalho *et al.* 2003	Trilobite	
Rindsberg and Martin 2003	Trilobite	trinucleine trilobite
Baldwin and Strother 2004	Arthropod	centipede-like
Borghi *et al.* 1996	Arthropod	
Brandt *et al.* 2008	Arthropod	non-trilobite, long-bodied arthropod
Fernandes *et al.* 1995	Arthropod	
Häntzschel 1975	Arthropod	
Kumpulainen *et al.* 2006	Arthropod	xiphosuran
Mángano *et al.* 2005	Arthropod	
Neto de Carvalho *et al.* 2003	Arthropod	(for *A. brongniartii*)
Pickerill *et al.* 1991	Arthropod	
Ksiazkiewiecz 1977	Gastropod	(for *A. dzulynskii*)
Książkiewicz 1977	Echinoderm	(for *A. annulatus*)
Sarle 1906	Echinoderm	ophiuroid
Brandt *et al.* 2008	Unknown	poorly-fossilized
Pemberton and Risk 1982	Unknown	soft-bodied "experiment"
Schimper 1869	Unknown	no modern analogue

Table 2.3: Reported sizes of *A. alleghaniensis* specimens.

Date	Author 1	Author 2	Width (mm) (=diameter)	Length (mm)	Ann. width	Notes
1977	Baldwin		5 to 25	~200	3:1 w:a	
1996	Borghi	Moreira	15			
1966	Borrello		3 to 12	50 to 150		
1981	Burjack	Popp	15 to 60			
1934	Dalloni		5 to 20			
1980	Downey		~6 to 10			estimated from figures
1985	Durand		20 to 30			
2000	Fernandes	Borghi	5.21 to 7.68	139.8	0.78 to 2.12	
2002	Fernandes	Borghi	~6 to 8			estimated from figures
1852	Hall		~6.3 to 12.7			given in inches
1975	Hantzschel		~10 to 20	up to 600		
1831	Harlan		~20.3	50.8 to 127		given in inches
2006	Kumpulainen	Uchman	5 to 13		1 to 2	
1984	Linan		2.5 to 4			
1998	Metz		4 to 9	up to 130	1 to 2	
2009	Miller	Webb	~10			grainy figures
2003	Neto de Carvalho	Fernandes	8 to 22		2.5	estimated from graph
1999	Nogueira	Truckenbrodt	20 to 60	up to 1000	3.3	
1984	Pickerill	Romano	6 to 11	up to 50	1.4 to 2	
2003	Poire	Spalletti	~8			estimated from figures
1923	Prouty	Swartz	5 to 15			
2000	Seilacher		5 to 15			
2003	Seilacher	Cingolani	~10			estimated from figures
2007a	Seilacher		~15 to 20			estimated from figures
1944	Shimer	Shrock	5 to 25			
1983	Turner	Benton	10 to 20		2.5 to 3.3	
1955	Young		~8.5			estimated from figures

Table 2.4: Reported sizes of *Arthrophycus* specimens, all ichnospecies except *A. alleghaniensis*.

Isp	Date	Author 1	Author 2	Width (mm)	Length (mm)	Ann. Width	Notes
annulatus	1977	Książkiewicz		~10	100	2.0 to 2.5	
brongniartii	2006	Kumpulainen	Uchman	5 to 10		0.9 to 2.0	
brongniartii	2003	Rindsberg	Martin	9.3 to 14.1			
F. brongniartii	1832	Harlan		XX	XX	XX	
linearis	2003	Neto de Carvalho	Fernandes	10 to 27			estimated from figure
linearis	1997	Seilacher		XX	XX	XX	
linearis	2000	Seilacher		~8	up to ~140		estimated from figure
linearis	2002	Seilacher	*et al.*	~9	~80		(if simplex = linearis)
linearis	2003	Seilacher	Cingolani	~10	~65		estimated from figure
R. corrugatus	1908	Fritsch		XX	XX	XX	
corrugatus	1992	Mikulas		10 to 12	120	2	
dzulynskii	1977	Książkiewicz		10 to 11	80	1	
elegans	1901	Herzer		1.6 to 4.8		0.85	given in inches
flabelliformis	1940	Hundt		XX	XX	XX	
hunanensis	1996	Zhang	Wang	8 to 10	90 to 130		
krebsi	1941	Hundt		XX	XX	XX	
lateralis	2002	Fernandes	Borghi	~8	20 to 50		estimated from figure
lateralis	2000	Seilacher		XX	XX	XX	
unilateralis	1997	Seilacher		XX	XX	XX	
minimus	2005	Mangano	Carmona	1.8 to 4.8	up to 200	0.1 to 0.35	
minimus	2005	Mangano	Buatois	1.8 to 4.5	up to 200	0.1 to 0.35	
minoricensis	1973	Bourrouilh					PhD
minorcensis	1995	Llompart	Wieczorek	XX	XX	XX	
minoricensis	1994	Orr		10			
montalto	1889	Lesley		XX	XX	XX	
parallelus	2010	Brandt	*et al.*	3.5 to 4.5		0.9 to 1.9	
qiongzhusiensis	1994	Luo	Tao	1 to 2	25 to 40	1	
siluricus	1879/1890	Schimper		XX	XX	XX	

Tab. 2.4 continued							
simplex	2003	Konate	Guiraud	~5 to 10	~100		estimated from figure
simplex	2002	Seilacher	*et al.*	~9	~80		estimated from figure
strictus	1977	Książkiewicz		1.5 to 2.0	50 to 60	0.5	
strictus	1996	Paczesna		3 to 6	12 to 25		
tarimensis	1994	Yang		3 to 4		0.5	
S. tenuis	1984	Alexandrescu	Brustur	1 to 2	3 to 35		
S. tenuis	1977	Książkiewicz		0.5 to 1.0	10 to 40		
tenuis	1999	Uchman		0.6 to 0.7	5 to 15		
cf. tenuis	1999	Uchman	Demircan	1.0 to 1.5	up to 35		

Figure 2.1: Specimen of a "typical" *Arthrophycus* from the Silurian of New York, Medina Sandstone. Note regular annulations running perpendicular to the long axis. BMS E20774. Scale bar represents 1 cm.

Figure 2.2: Specimen of *A. alleghaniensis* showcasing the rather simple form and finger-like shape of the traces. Silurian of New York, formation unknown. OSU8391. Scale bar represents 1 cm.

Figure 2.3: Example of branching (arrows) in *A. alleghaniensis*. Silurian of New York, formation unknown. OSU8391. Scale bar represents 1 cm.

Figure 2.4: Example of *A. alleghaniensis* with pseudo-branching, in which two otherwise independent traces cross one another. Silurian of New York, formation unknown. OSU8391. Scale bar represents 1 cm.

Figure 2.5: Wide palmate bundling in a specimen of *A. alleghaniensis*. Silurian of New York, Medina Sandstone. YPM38353. Scale is in mm.

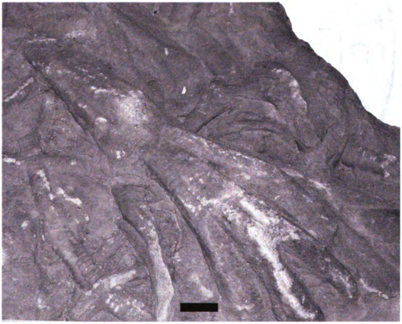


Figure 2.6: Specimen with narrower bundles of *Arthrophycus*. Silurian of Martinsburg, PA, Clinch Sandstone. CMNH3819. Scale bar is 2 cm long.

Figure 2.7: Specimens of *Arthrophycus* exiting various intergrading branching and bundling patterns. Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 2 cm.

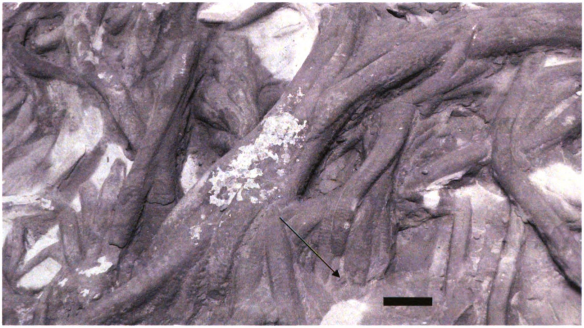


Figure 2.8: Specimens of *Arthrophycus* that disappear almost immediately from their bundles and descend into the matrix (arrow). Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 2 cm.

Figure 2.9: Specimen of *Arthrophycus* with a clear median groove (arrow). Silurian of western New York, Medina Group. YPM7365. Black portion of scale is 5 cm long.

Figure 2.10: *Arthrophycus* with faint or indistinct median groove. This close-up of YPM7365 shows that even clear median grooves can appear indistinct depending on the magnification or lighting. Scale bar represents 1 cm.

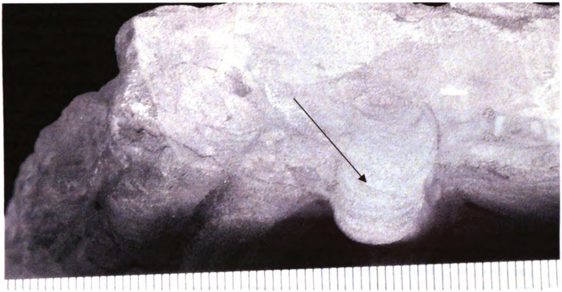


Figure 2.11: *Arthrophycus* with spreiten (arrow) revealed on a polished cross-sectional surface. Silurian of New York, Medina Group. YPM150650. Scale is in mm.

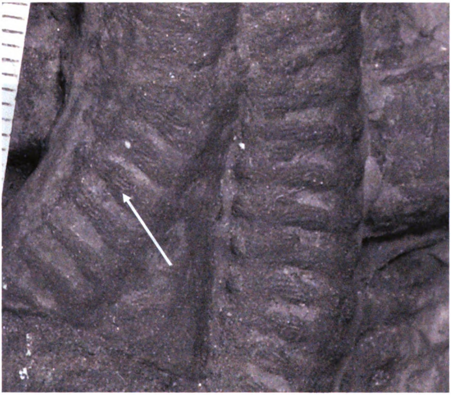


Figure 2.12: Specimens of *Arthrophycus* with fine striations (arrow) on top of the individual annulations. These annulations also display a pinched shape toward the middle, lending to the impression that a groove is present. Silurian of New York, Medina Sandstone. YPM150639. Scale is in mm.

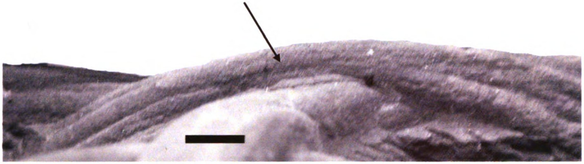


Figure 2.13a: Specimen of *Arthrophycus* displaying vertical arch or bowing (arrow) as it passes over another specimen (or under, if the specimen is inverted as most are). Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 1 cm.

Figure 2.13b: Bundled specimen of *Arthrophycus* displaying vertical arch. Silurian of Para, Brazil, sandy shale. NYSM6176. Scale is in mm.

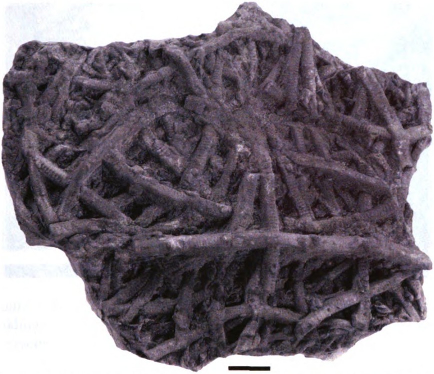


Figure 2.14: Sample of *Arthrophycus* in which many primarily flat-lying traces cross over one another. Silurian of Grimsby, Ont., Grimsby Sandstone. BMS E3799. Scale bar represents 2 cm.

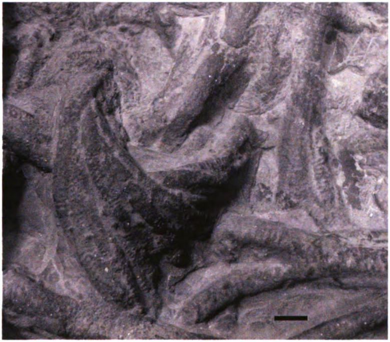


Figure 2.15: Complicated arrangement of *Arthrophycus* in which traces go in many directions. Silurian of Medina, NY, Medina Sandstone. NYSM2. Scale bar represents 1 cm.

Figure 2.16: Flat-lying *Arthrophycus* traces with other traces perpendicular to the bedding. Silurian of Lockport, NY, Medina Group. YPM508647. Scale bar represents 1 cm.

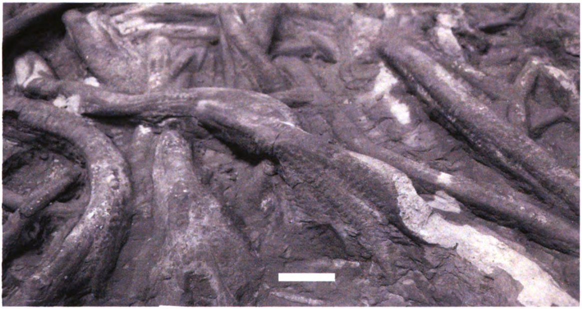


Figure 2.17: Twisting of *Arthrophycus* traces with respect to one another, in three dimensions. Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 2 cm.

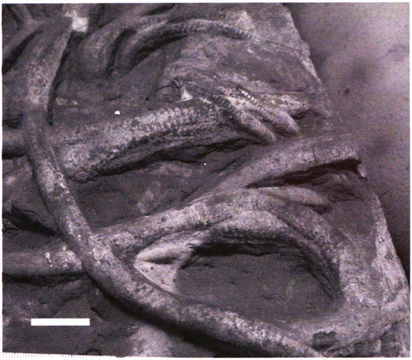


Figure 2.18: Large loop pattern of *Arthrophycus* traces. Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 2 cm.

Figure 2.19: *Arthrophycus* (arrows) co-occurring with *Rusophycus* (circle). Silurian of Lewiston, NY, found loose. BMS E25610. Scale bar represents 2 cm.

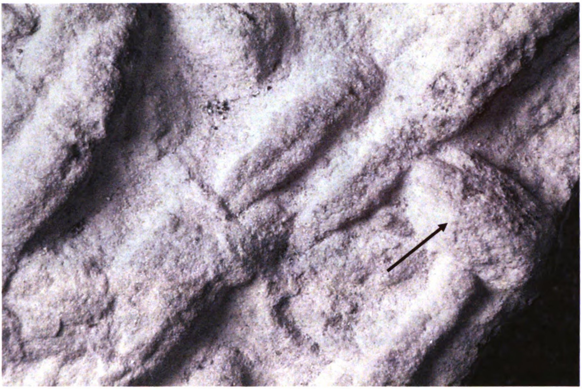


Figure 2.20: *A. parallelus* co-occurring with *Lockeia* (arrow). Pennsylvanian of Michigan, Grand River Formation. University of Michigan Museum of Paleontology (UMMP) 73822. Traces are approximately 4 mm wide.

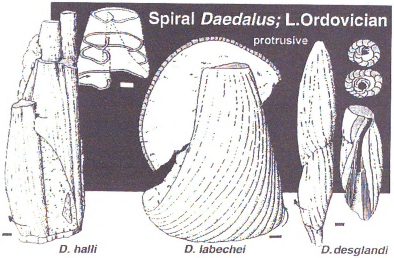


Figure 2.21a: Sketches of three different ichnospecies of Ordovician *Daedalus*, from Seilacher (2000). Scale bars are in centimeters.

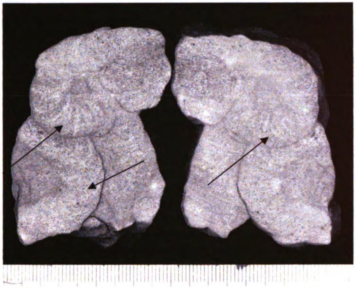


Figure 2.21b: Polished cross-section of *Daedalus archimedes*, showing the spreiten of the trace (arrows). Silurian of Medina, NY, Medina Sandstone. YPM35825. Scale is in mm.

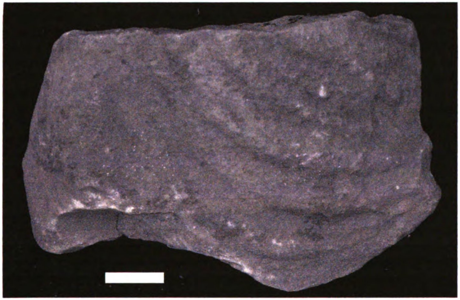


Figure 2.21c: Non-spiral specimen of *D. archimedes*, which appears more similar to *Arthrophycus* than the spiral version does. Silurian of Medina, NY, Medina Sandstone. YPM35822. Scale bar represents 1 cm.

Figure 2.22: Specimen of *Arthrophycus*. Silurian of Lockport, NY, Medina Group. YPM35814. I suggest that morphotypes known only from a few individuals, such as this one, be termed "*Arthrophycus*-like." Scale is in mm.

Figure 2.23: Example of a specimen referred to *Arthrophycus* (arrow), almost certainly in error, along with specimens of *Gordia*. Devonian of Ohio, Chagrin Shale. CMNH3705. Scale is in cm.

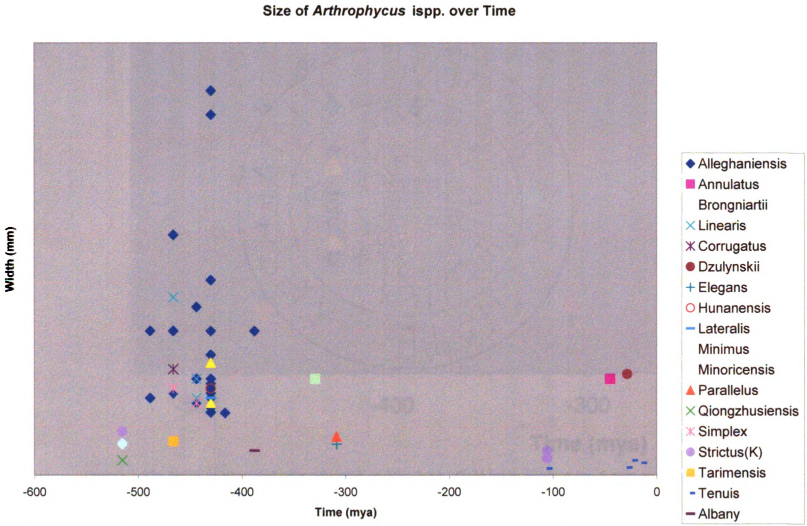


Figure 2.24: Size of ichnospecies of *Arthrophycus* over time. Gridlines mark every 5 mm in width and start from 0 mm.

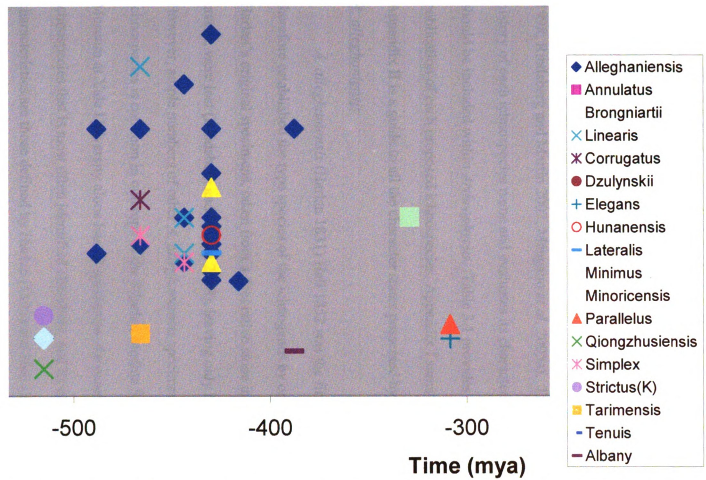


Figure 2.25: Inset of crowded area of graph in Fig. 2.24. Grid lines mark every 5 mm and start from 0 mm.

Chapter III. Definition of *Arthrophycus*, Part I.: qualitative critique of previous reports of *Arthrophycus*

There have been twenty-three ichnospecific names included under *Arthrophycus*, but many of these assignments have been questioned (e.g. Uchman 1998, Rindsberg and Martin 2003, Mángano *et al.* 2005a). This section details the history of each ichnospecies name and evaluates its characters to determine whether it should be included within *Arthrophycus*. Table 3.1 provides a guide to the first publication of each proposed ichnospecies, Appendix I sums up all the reports, and Appendix II is a guide to all the character states possessed by each ichnospecies.

A. alleghaniensis

A. alleghaniensis (Harlan 1831) Hall 1852 was the first species published and therefore established the type species of the ichnogenus by original monotypy. Harlan's original specimens, taken from a decorative stone in front of a Pennsylvanian tavern, were lost (Rindsberg and Martin 2003), leaving only his drawings (Figure 3.1). However, ample numbers of other *A. alleghaniensis* specimens remain, as the ichnospecies is common in outcrops of the Silurian Medina Sandstone. The Peabody Museum at Yale University alone has 58 specimens, for example. This is also the ichnospecies that is most often identified elsewhere, and its morphological characteristics are those defined by Harlan (1831) and Hall (1852), and discussed more fully in Chapter II.

A. alleghaniensis has appeared in many works since its original descriptions by Harlan (1831) and Hall (1852). The following are critiques of reports of *A.*

alleghaniensis and its synonyms in the literature. These are listed alphabetically by author and chronologically in cases of multiple papers by the same author.

Aceñolaza and Aceñolaza (2003) reported *A. alleghaniensis* from the Cambrian-Ordovician Balcarce Formation of Argentina. The authors did not include a detailed description, but the figure of *Arthrophycus* cf. *alleghaniensis* conforms to the original concept, as observable features include a mass aggregate of finger-like shapes with annulations and possible median grooves. Their figured *Arthrophycus* isp. is probably also *A. alleghaniensis*, for the specimen has those same features.

Baldwin (1977) described *A. alleghaniensis* from the Cambrian-Ordovician Barrios Formation of Spain. He noted the regular annulations, general curving shape with some bundles, and retrusive spreiten in cross-section. He also reported a large number of individuals of varying sizes (5 to 25 mm wide). Baldwin's figure shows a mass of these structures, which conform to *A. alleghaniensis* on the basis of the annulations, shape, bundles, and retrusive spreiten, though Mángano *et al.* (2005a) suggested that, for their lack of bundles, they might be more properly assigned to *A. brongniartii*. It is also possible that the specimens represent an intergradational form.

Bender (1963) reported "*Harlania alleghaniensis*" from the Silurian *Sabellarifex* Sandstone of Jordan. He included no written description, but did discuss where and when the ichnogenus had been reported in previous work. His two figures show traces with annulations, median groove, and the general shape found in *Arthrophycus*; one even shows the "pinching in" of the annulations discussed below. The general shape of the specimens figured may indicate *A. brongniartii* rather than *A.*

alleghaniensis, but these specimens can be regarded as *Arthrophycus* on the basis of the presence and shape of annulations, median groove, and general shape of the trace.

Bender (1968) also reported *Harlania alleghaniensis* from the Silurian "worm-burrows sandstone" of Jordan and included two figures. One of these shows *Arthrophycus* from the middle Ordovician of Jordan; the other shows a cross-section from the same location. The first figure shows an *A. brongniartii*-like shape and orientation, with annulations and a median groove. The cross-section shows spreiten, but Bender did not discuss them. These specimens conform to the definition of *Arthrophycus*.

Borghi *et al*. (1996) reported *A. alleghaniensis* from the Silurian Furnas Group of Brazil. The authors thought of *Arthrophycus* as monospecific and so referred their specimens to *A. alleghaniensis*, but the relatively isolated nature of the individuals described is probably better suited to *A. brongniartii*. Without a more detailed description and figure, this report remains doubtful to some degree.

Borrello (1966) described *A. alleghaniensis* from the Ordovician-Silurian (?) La Tinta Formation of Argentina. The dating of the La Tinta Formation has been questioned (e.g. Mángano 2005a), and Borrello himself was not at all precise in his paper, indicating only that the formation was early Paleozoic. I have used an approximate Ordovician-Silurian date for Bollerro's specimens based, on the diagrams presented in Zimmermann and Spalletti (2009) and on support from Burjack and Popp (1981). From his specimens, Borrello (1966) identified transverse annulations, the median groove, a variety of cross-sectional shapes, and a variety of branching patterns that included palmate fans. Most of his measured sizes were on the small side, with a range of 3-12 mm in width. His impressive eleven illustrated plates of *Arthrophycus* specimens show both bundled and independent individuals, sometimes even grading into one another. He speculated about the trace-maker, thinking that a particularly curvy vermiform specimen resembled "true type annelids" more than it did trace fossils. Regardless, the specimens clearly belong in *Arthrophycus* based on their transverse annulations, median groove, variety of cross-sectional shapes including subquadrate, and variety of branching patterns including palmate fans.

Burjack and Popp (1981) described large *A. alleghaniensis* specimens from the Silurian Vila Maria Formation of Brazil. Their specimens were sinuous, with some branching, and had regular annulations, a sub-circular cross-section, and sometimes a median groove. The diameters of the specimens ranged from 1.5 to 6 cm, which is unusually large for *Arthrophycus* (but see Nogueira *et al.* 1999). The photographs are somewhat blurry and include only a blurry coin as an indication of scale, so the claims of exceptional size cannot be verified. The lack of palmate structures or bundling may indicate an assignment to *A. brongniartii* rather than *A. alleghaniensis*, but the specimens can be placed in *Arthrophycus* based on their regular annulations, cross-section, branching, median groove, and general shape, regardless of which ichnospecies designation might be more appropriate.

Conrad (1837) noted *F. alleghaniensis* from the Silurian of New York, probably of the Medina Group. He did not include a figure or description, so this record is not fully confirmed. In 1838, Conrad referred to the ichnospecies as *F. harlani*. In 1839, Conrad again referred to *F. harlani*, expanding his report to

Pennsylvania and Virginia. Both of these records are also not completely confirmed, lacking good descriptions or figures.

Dalloni (1934) observed *Harlania* in the Silurian sandstones of Chad. He observed the annulations, median groove, constant diameter of individuals, and rectangular cross-section; his figured specimens also show bundling. These specimens conform to the definition of *Arthrophycus* based on both the description and figured specimens.

Downey (1980) described specimens of *A. alleghaniensis* from the Lower Silurian Tuscarora Sandstone of Pennsylvania. His specimens exhibit the annulations, median groove, general shape, bundles and branches common to *Arthrophycus*. He noticed an iron "stain" on the edges of the traces that he suggested could represent the remnants of ancient hemoglobin secreted by the trace-maker, which he thought might be a worm similar to *Agaophamus circinata*, a segmented marine annelid. Downey further suggested that asexual reproduction in the annelids could explain the branched and bundled patterns of *Arthrophycus*. Regardless of that speculation, these fossils conform to the definition of *A. alleghaniensis* based on the annulations, median groove, general shape, bundles, and branches.

Eschard *et al.* (2005) reported *Harlania* from the Lower Ordovician "Vire du Mouflon" of Algeria. Their report consisted of one sentence regarding the ichnospecies, observing it as part of the *Cruziana* ichnofacies present in the sandstones. This occurrence is therefore unverifiable.

Fenton and Fenton (1958) mentioned *A. alleghaniensis* from the Silurian Medina Sandstone of eastern North America. Their work was an elementary catalog rather than a technical publication, but the figured specimens are confirmable as *A. alleghaniensis* for their simple shape, regular annulations, and bundled forms.

Fernandes (1999) reported *A. alleghaniensis* from the Silurian-Devonian of Brazil. This work is really just a compilation of work that had been published earlier on four Brazilian formations, and *Arthrophycus* was reported from two (earlier reports from a third formation rejected) with no figures or specific description.

Fernandes (2001) reported *A. alleghaniensis* again in the Silurian-Devonian of Brazil. Like the previous work, the author listed the ichnogenus again in several formations of Silurian-Devonian age in Brazil, but he also saw some differences between the Brazilian Silurian and Devonian forms and suggested that differences in behavior might reflect nutrient availability. Because Fernandes included no description or figures, this report is regard as providing no additional confirmation beyond what had been published earlier.

Fernandes *et al.* (1995) mentioned *A. alleghaniensis* in the Silurian Vila Maria Formation of Brazil, along with *Paleophycus*. In this report, the first of many by the same authors, they used the presence of *Arthrophycus* to understand the paleoenvironment of the Vila Maria Formation, which they interpreted as shallow marine from the presence of the *Cruziana* ichnofacies. As the authors included no figures, this report is not verifiable.

Fernandes and Borghi (1996) noted *A. alleghaniensis* in the Ordovician-Devonian (?) of Brazil. The authors included no figures, but rather discuss the history and distribution of *Arthrophycus*, with particular attention to Brazil. Their stratigraphic resolution is somewhat confused, because they mentioned *Arthrophycus* in the

Ordovician and possibly early Devonian, but then in their conclusion the authors stated that the ichnospecies is restricted to the Silurian. However, with regard to assessing their taxonomy, these authors seem to have considerable experience in dealing with *Arthrophycus*, so their report here depends upon the strength of their other publications.

Fernandes *et al.* (2000) described *A. alleghaniensis* from the Silurian-Devonian Furnas Formation of Brazil. The figured specimen shows annulations, straight form, and bundling, while the description mentions a sub-circular cross-section and sporadic faint median groove. The authors noted some differences in branching between various formations; this may indicate the presence of both *A. alleghaniensis* and *A. brongniartii*. This material conforms to *A. alleghaniensis* based primarily on the illustration, but also on the written description.

Fernandes *et al.* (2002) described several ichnospecies of *Arthrophycus*, including *A. alleghaniensis*, in the Trombetas Group and the Nhamunda, Vila Maria, and Furnas Formations, of Ordovician-Devonian (?) age in Brazil. The figures of *A. alleghaniensis* show bundled structures twisting about in three dimensions, with annulations and typical shape and size expected for *Arthrophycus*. These specimens conform to *A. alleghaniensis* on the basis of annulations, shape, and bundling.

Fritel (1925) remarked upon *Harlania* from the Silurian of Chad. He used the ichnogenus to assist him in dating the formations, noting that the "Ennedi formations" should correlate to the Medina Sandstone. He included no figures and described the fossils only as "slightly flattened cylinders" that "intersect in every direction." Crimes

(1981) seemed to support this report, but without figures or a detailed description, its assignment cannot be confirmed.

In his review of the strata of Brazil, Grahn (1992) mentioned *A. harlani* in the Silurian. However, his report is only a collection of published reports and cannot be evaluated on its own merit. It is included in the counts of the biostratigraphic and geographic records herein because several of the source reports were not otherwise included.

Grove (1960) reported *Harlania* in the Silurian of Chad, from the sandstones of Tibesti. He did not provide figures or a description, and wrote that even the assigned age of Silurian was uncertain (but probable). This report is an unverifiable record, as it lacks figures or written description.

Gubler *et al*. (1966) reported *Harlania* from the Ordovician of Algeria. Their figure shows regular annulations, a simple form, and multiple occurrences of pseudo-branching in high relief. The rather straight and independent shapes are reminiscent of *A. brongniartii*, but the traces are much closer together than is typical for that ichnospecies, and at least one group of traces may be coalescing into a bundle. The authors' description stated that bundles did occur, and that a single individual could be traced for over 1 m in length. The fossils conform to *A. alleghaniensis* based on the multitude of characters presented above from both the figure and the written description.

Janvier and Melo (1988) noted *A. harlani* from the Silurian-Devonian Trombetas Formation of Brazil. Their report was concerned mostly with fossil acanthodians, but the authors found specimens of *Arthrophycus* in certain portions of the field sites as well. Lacking figures or descriptions of the traces, this record is unverifiable.

Kumpulainen *et al.* (2006) found *A. alleghaniensis* in the Adi MaEkheno Member of the Adigrat Formation of Eritrea. The authors noted the presence of confirmable *Arthrophycus* in strata from the Ordovician to the Devonian in different parts of the world, but they dated the occurrence in Eritrea as Ordovician only. Regardless of potential problems in dating the fossils, the traces themselves displayed regular annulations, subquadrate cross- sections, pseudo-branching, simple shape, and mass aggregation of individuals. The authors also noted an occasional faint median groove and some palmate fans. These specimens conform to the definition of *A. alleghaniensis*, based on from the many features common to *Arthrophycus* and observable in the excellent figures.

Lesley (1889) included *A. harlani* from the Silurian White Medina of Pennsylvania in his encyclopedia of fossils. Oddly, he included a separate, shorter entry for *Harlania halli*, calling *A. harlani* a junior synonym, but contradicted this synonymy by placing most of the information and figures under the entry for *A. harlani*, which he regarded as a fossil seaweed. His specimens display the regular annulations, simple form, and frequent palmate fans and narrower bundles common to *Arthrophycus*, so they conform to the standard concept of *Arthrophycus*.

Lessertisseur (1955) discussed *Harlania* (using both *H. alleghaniensis* and *H. harlani* on the same page) in an early support of Sarle's (1906) suggestion of a burrowing "program" to explain the traces. Lessertisseur's work is encyclopedic in nature, discussing the ichnogenus *in toto* rather than any particular ichnospecies or specific occurrence. His figured specimens show regular annulations, a simple shape, and palmate branching, and conform to *Arthrophycus*.

Liñán (1984) described *A. alleghaniensis* from the Cambrian Julia Member of the Torrearboles Formation of Spain. The single figure shows only a few traces (perhaps three – the image is indistinct) with regular annulations and some branching; the description mentions an intermittent median groove and a sub-rounded cross-section. These traces are among the smallest described as *A. alleghaniensis* (2.5-4.0 mm wide), but are within the size range for the ichnogenus. These specimens conform to the standard concept of *A. alleghaniensis*, although the paucity of preserved traces on the slab is problematic, as any *Arthrophycus* ichnospecies is typically a gregarious trace. Mángano *et al.* (2005a) were also concerned because of the fragmentary nature of the material, but suggested that the specimen could be included in *A. minimus* instead of *A. alleghaniensis*, based primarily on the lack of bundles necessary for designation as *A. alleghaniensis*.

Metz (1998) discussed *A. alleghaniensis* from the Silurian Shawangunk Formation of New Jersey. His figured specimen shows regular annulations and a simple shape, with very few preserved traces. However, the fossils' very low relief could indicate erosion of pre-existing layers of other *Arthrophycus* traces; the faint outlines of traces in the corner of the figure indicated that other *Arthrophycus* individuals lie below the surface. The text indicated that the author found 63 specimens on only 6 slabs. In his description, Metz noted constant diameter, an occasional faint median groove, and structure-less internal fill. Lack of bundles or palmate fans may indicate an assignment of *A. brongniartii* rather than *A.*

alleghaniensis, but the fossils conform to *Arthrophycus* regardless of ichnospecies designation.

Metz (2006) also reported *A. alleghaniensis* from the Silurian Lizard Creek Member of the Shawangunk Formation of New Jersey. However, this report was only included in a meeting abstract, showed no figures or details, and therefore is unverifiable.

Miller *et al.* (2009) documented a remarkable occurrence of *A. alleghaniensis* from the Silurian Tuscarora Formation of Virginia. The preserved slab of sandstone is 30 cm thick on average, with a surface area of 3.4 m^2 across the main surface, with hundreds of specimens of *Arthrophycus* preserved across the bedding. Though the photographs are blurry, these specimens show regular annulations, retrusive spreiten, subquadrate cross-section, and both pseudo-branching and palmate fans. There are also some rather unusual orientations, including loops of the same type as in a similarly-sized slab at Yale Peabody Museum (Figure 2.18). The authors interpreted the orientations as a result of avoidance behavior on the part of the trace-makers, perhaps using a chemical signal. The traces conform to *Arthrophycus* based on the list of characters and on the fact that Seilacher reviewed the manuscript and found no problems with the assignment.

Moneda (1963) used both the names *A. alleghaniensis* and *A. harlani* (in the same sentence) to describe fossils from Argentina. The author gave no stratigraphic position, description of the fossils, or figures, so the report cannot be confirmed.

Moreira *et al.* (1998) recorded *A.* aff. *alleghaniensis* from the Silurian to (?) Early Devonian of Brazil. The authors noted some differences between their specimens and *A. alleghaniensis*, notably smaller size and in the annulation size and spacing. However, these may reflect only small changes in the trace-maker and are not enough for a different ichnospecies designation. Without a detailed description or any figures, this record cannot be confirmed.

Moreira and Borghi (1999) identified *A. alleghaniensis* from the Silurian Furnas Formation of Brazil. The ichnospecies is mentioned only as a part of the *Cruziana* ichnofacies found in the study, without further description, and the single photograph showing *Arthrophycus* is too blurry to see well. Because these authors have been reliable in the past, this occurrence was considered unverifiable because it is neither a good specimen nor is it truly questionable.

Neto de Carvalho *et al.* (2003) found *A. alleghaniensis* in the Ordovician Armorican Quartzite of Portugal. The authors observed subcircular cross-section, regular annulations, constant diameter, and near-vertical spreiten. They emended the ichnospecies diagnosis as "burrows in tridimensional bundles with protrusive or retrusive backfill structures, which may ramify from a single point in a palmate fashion or bend asymmetrically" (English theirs). The included photograph is too blurry for confident assignment, but the description is very promising, so these specimens conform to the standard concept of *A. alleghaniensis*.

Nogueira *et al.* (1999) described specimens of *A. alleghaniensis* from the Lower Silurian Nhamunda Formation of Brazil. The specimens were very large (2-6 cm wide, up to 1 m in length) and possessed large regular annulations (but not large relative to the width of the traces), a subquadrate to elliptical cross-section, and a median groove. The figures were too dark to see any of the described features, so the large reported size cannot be confirmed. However, based on the strength of the description, the specimens conform to *A. alleghaniensis*.

Pickerill *et al.* (1984) collected *A. alleghaniensis* from the Ordovician Armorican Quartzite of Spain. The traces were subquadrate in cross-section, with regular annulations and an occasional faint median groove. No branching was observable, but the single figure included depicted a rather small piece of rock with traces very close to one another; a more complete or larger sample might have exhibited better orientations. These traces conform to *Arthrophycus* based on the annulations, groove, and cross-section.

Poiré *et al.* (2003) described *A. alleghaniensis* from the Cambrian-Ordovician Balcarce Formation of Argentina. Their figure shows specimens with regular annulations, a median groove, simple shape, dense aggregations, and both bundles and relatively independent individuals, and the description concurs. These specimens conform to *A. alleghaniensis* based on those characters.

Prouty and Swartz (1923) described *A. alleghaniensis* from the Silurian Tuscarora Formation of Maryland. They illustrated both bundled (*A. alleghaniensis*) and independent (*A. brongniartii*) forms, placed Harlan's two species in synonymy, and observed annulations, occasional median groove, subcylindrical cross-section, simple shape, and lack of tapering at the ends. These specimens conform to *Arthrophycus* based on the characters listed, though divided between *A. alleghaniensis* and *A. brongniartii*.

Romano (1991) noted *A. alleghaniensis* in the Ordovician Armorican Formation of Spain and Portugal. The paper did not include a written description or figure, but only noted *Arthrophycus* as present as part of the Cruziana ichnofacies. Although the small sketch of *Arthrophycus* is very promising (it includes regular annulations, a faint median groove, and some branching of finger-like shapes), the record cannot be verified.

Schuchert (1916) noted "*A. alleghaniense*" in the Silurian of New York, Pennsylvania, and New Jersey. He listed the ichnospecies as common in the Silurian formations of those states, but his only figure is at much too large a scale to see details. The record cannot be confirmed because it lacked a written description or figured specimens.

Seilacher (1997) included *A. alleghaniensis* from the Silurian of Libya in his book Fossil Art. The figured specimen displays regular annulations, simple shape, and many bundles among a mass aggregate of traces. These specimens conform to *A. alleghaniensis* based on those traits.

Seilacher (2000) also described *A. alleghaniensis* from the Ordovician-Silurian of formations around the world. He emended the ichnospecies diagnosis to "Arthropycid (*sic*) burrows, 5-15 mm in diameter, which explore the sediment mainly in a horizontal fashion." Curiously, he did not invoke any branching pattern to distinguish the ichnospecies from *A. linearis*, which was defined in the same paper. However, his figures of *A. alleghaniensis* do show prominent palmate forms, along with typical regular annulations, finger-like shape, and retrusive spreiten. These specimens conform to *A. alleghaniensis* based on the characters in the figured specimens.

Seilacher *et al.* (2003) observed *A. alleghaniensis* in the Ordovician-Silurian Balcarce Formation of Argentina. The authors did not include a detailed description, but their figured specimens show regular annulations, a simple form, and many instances of bundling. These specimens conform to *A. alleghaniensis* based on the characters in the figured specimens.

Seilacher (2007a) included *A. alleghaniensis* in his arthrophycid group. The figures display regular annulations, a simple form, bundles and palmate forms, and faint median grooves. The specimens conform to *A. alleghaniensis* based on those characters.

Selley (1970) noted *Harlania* from the Ordovician Um Sahm Formation of Jordan. He did not include a description, but the illustrated specimens possess regular annulations, simple forms in high relief, and both pseudo-branching and bundling. These specimens conform to *Arthrophycus* based on those features.

Selley (1972) mentioned *Harlania* in the Ordovician Graptolite Sandstone of Jordan. He did not include a description or any pictures of the fossils, but only mentioned them as being in the informal "*Harlania* Shale Member" and included the ichnogenus in his stratigraphic columns. Without any further evidence, the record remains unverifiable.

Shimer and Schrock (1944) mentioned *A. alleghaniensis* and *F. harlani* in the Silurian Tuscarora and Clinch Formations of eastern North America. The authors described the ichnospecies as "simple or apparently branching, rounded or subangular ridges with median groove and closely set transverse grooves," which includes the most important and common characters of *Arthrophycus*. The drawings included were some of Hall's originals, so this is not a newly reported occurrence but merely an encyclopedic entry.

Taylor (1834) mentioned *F. alleghaniensis* from the Silurian of Pennsylvania, near the area where Harlan's original specimens may have originated. Taylor's sketch reveals regular annulations, simple shape, pseudo-branching, and palmate bundles; his specimens conform to *Arthrophycus* based on those characters.

Taylor (1835) again mentioned *F. alleghaniensis* from the Silurian of Pennsylvania, in different sites than in his earlier (1834) report. However, this time Taylor did not include a detailed description or figure, his report cannot be confirmed.

Turner and Benton (1983) reported *A. alleghaniensis* from the Cambrian-Ordovician, Silurian, and Early Devonian in several formations of Libya. The fossils have regular annulations, simple form, and intersect each other at all angles in high relief. The authors also wrote that the specimens had a circular to elliptical cross-section, and that bundles do exist. These specimens conform to *A. alleghaniensis* based on the characters in the figure and those mentioned in the description.

Turner *et al.* (2005) noted *Harlania* in the Late Ordovician Tubeiliyat Formation of Jordan. The authors did not include a description of the fossils, and the single figure purported to show *Harlania* is very small and includes numerous brachiopods. The brachiopods are visible, but the trace fossils are not discernible, so this report remains questionable.

Wolfart (1961) reported *A. alleghaniensis* from the Devonian of Paraguay. He described the fossils as subcylindrical, branched, with a constant diameter, annulations, and possibly a median groove (translation unclear). However, the single figure is blurry and entirely unconvincing as *Arthrophycus*, so this record is hesitantly classified as questionable. The description is fine, but the figure remains problematic.

Finally, Young (1955) observed *A. alleghaniensis* in the Silurian Keefer Sandstone of Virginia. He considered *Arthrophycus* to be a possible "guide fossil," but suggested that the stratigraphic definition not be limited to the Medinan (Lower Silurian). The figured specimen shows regular annulations, simple form, and a typical branching pattern, so these specimens conform to *A. alleghaniensis*.

In addition to the above accounts, some specimens reported only as *Arthrophycus* isp. may actually be *A. alleghaniensis*. These include Abel (1935), Becker and Donn (1952), Pflüger (1999), and Seilacher and Alidou (1988, Fig. 1e and ?1f) and are discussed below.

A. harlani and *Harlania halli*

A. harlani Conrad 1838 was, as mentioned in the history of *Arthrophycus*, erected by Conrad in 1838 as *Fucoides harlani* in place of *F. brongniartii* with no explanation. Hall (1852) then retained Conrad's specific name when he renamed the genus *Arthrophycus*, but there was no reason to drop Harlan's original name of *alleghaniensis* for the first (and for Hall, only) ichnospecies (James 1893a). As there are no differences between the two ichnospecies, *A. harlani* is a junior synonym to *A. brongniartii*. The name *A. harlani* does not come up often in the literature; only Schimper and Schenk (1879-1890) Lesley (1889), Janvier and Melo (1988), and Grahn (1992) have used that name since Hall (1852), and all of these authors used the name *A. harlani* in a sense that certainly meant *A. alleghaniensis*. However, labels persist through museum catalogs: the Yale Peabody Museum, the American Museum of

Natural History, the New York State Museum, the Science Museum of Buffalo, and the Paleontological Research Instititution among the museums visited for this study used the name *A. harlani*.

Harlania halli Göppert 1852 is a junior synonym to *A. alleghaniensis*, as determined by James (1893a) and by popular consent in the literature. All specimens originally designated in published reports as either *A. harlani* or *H. halli* are included under the discussion of *A. alleghaniensis*; thus, they need not be critiqued further.

<u>*A. brongniartii*</u>

A. brongniartii Harlan 1831, named less than a year after *A. alleghaniensis*, is perceived as largely forgotten in the literature. However, this is not entirely the case. The first description of the ichnospecies was by Harlan as *F. brongniartii* (1832) and featured a written description but did not include a figure. Harlan described his new species as "*Fronde elongata, sub-quadrangularis, canliculata, transverse rugosa; ramulis inequalis, sparsis, remotis, compressis, rugatis, recurvis, nudis*," which translates to "frond elongate, sub-quadrangular, channeled, transversely ribbed, unequal branches, sparse, distant (from each other), compressed, wrinkled (ribbed), recurved, naked." The important features of *A. brongniartii* that place it in *Arthrophycus* are the subquadrate cross-section, annulations, and branching, but *A. brongniartii* is distinct from *A. alleghaniensis* in the relatively independent or "distant" nature of the individuals and in the lack of bundles, having only pseudo-branching.

Taylor (1835) provided the next mention of the ichnospecies and what may be the first figured specimen (Figure 3.2) and Harlan referred to the name again in his 1836 paper. Conrad (1837) noted *F. brongniartia* (spelling his) as particularly abundant in the Medina of New York. Hall (1852) and Göppert (1852) placed *F. brongniartii* in synonymy with *F. alleghaniensis* in *Arthrophycus* and *Harlania*, respectively, without further explanation, and James (1893a) mentioned both forms in his history of the ichnogenus but considered them to be forms of the same ichnospecies. Prouty and Swartz (1923) mentioned *A. brongniartii* but included it within *A. alleghaniensis*. The figures of Prouty and Swartz (1923) clearly indicate which specimens they considered to be the *A. brongniartii* form, but Hall (1852) and Göppert (1852) were not so precise. The specimens of both Taylor (1835) and Prouty and Swartz (1923) are accepted as *A. brongniartii* for their annulations, median groove, simple shape, and independent form. Conrad (1837) did not include a description or figure and Hall (1852) and Göppert (1852) were unclear, so the specimens of those three authors cannot be assessed.

After 1923, the name *A. brongniartii* was not mentioned until Rindsberg and Martin (2003), who found abundant specimens of the ichnospecies in the Silurian Red Mountain Formation of Alabama. Their specimens possess annulations and independent orientations, as well as retrusive spreiten. A new feature is the "stellate" shape of multiple traces coming together at wide angles (palmate forms have acute angles); this may be considered a compound trace. Although Mángano *et al.* (2005a) had some doubts as to the assignment of these traces, these traces conform to *A. brongniartii* for their annulations, orientations, and retrusive spreiten.

Kumpulainen *et al.* (2006) have also used the name *A. brongniartii* for specimens from the Adi MaEkheno Member of the Adigrat Formation of Eritrea. The authors were not certain of their assignment, but their figured specimens share the annulations and independent nature of *A. brongniartii*, and even have retrusive spreiten. Their specimens are certainly worthy of inclusion in *A. brongniartii*.

The eighty-year hiatus between 1923 and 2003 does not violate the rules of the ICZN, otherwise few fossils would retain their original names. However, this lapse may explain why Seilacher (1997, 2000) introduced the name *A. linearis*, which is almost certainly a synonym of *A. brongniartii* (Rindsberg and Martin 2003). Because of the eighty-year gap and the many authors' combinations of *A. alleghaniensis* and *A. brongniartii*, many specimens identified as *A. alleghaniensis* may actually be *A. brongniartii*. The main morphological difference between the two ichnospecies is in the morphology of the bundling: *A. alleghaniensis* is more typically bundled and *A. brongniartii* has individual branches that do not bundle but are more independent of one another. Specimens of *A. brongniartii* may appear to branch, but that is probably a result of over-crossing and not true branching.

In addition to those specimens that the authors originally described as *A. brongniartii*, there are a number of *A. alleghaniensis* specimens that might more properly be assigned to *A. brongniartii*. These include specimens figured in Bender (1963 and 1968), Borghi *et al.* (1996), Borrello (1966, only Plates III, V, VI, and XI), Burjack and Popp (1981), Downey (1980, only Fig. 6), Metz (1998), and Poiré *et al.* (2003, only Fig. 5C and 5D).

Moreover, some specimens originally designated only as *Arthrophycus* isp. might be more properly assigned to *A. brongniartii*. These specimens include those in Durand (1985), Pemberton and Risk (1982), and Seilacher and Alidou (1988, Fig. 1d), and are discussed below.

The actual stratigraphic and geographic ranges for *A. brongniartii* may include some reports of specimens that were under the name *A. alleghaniensis*. However, considering only those described by the authors as *A. brongniartii*, the stratigraphic range is Ordovician to Devonian and the geographic range includes the country Eritrea and the American states New York, Pennsylvania, and Alabama. The specimens originally described as *A. linearis* by other authors (e.g. Fernandes *et al.* 2002, Aceñolaza and Aceñolaza 2003) extend the geographic range of *A. brongniartii* to Argentina, Brazil, Portugal, Jordan, and to additional parts of North Africa, and extend the stratigraphic range into the Cambrian.

A. linearis

A. linearis Seilacher 1997 was first named by Seilacher in his book Fossil Art, in the caption for a small sketch (Figure 3.3), but he did not formally describe *A. linearis*. From this sketch, it can be seen that the traces have regular annulations and some kind of median structure, and that the traces are independent of one another. Seilacher and Alidou (1988) mentioned *Arthrophycus* specimens from the Kandi Sandstone of Benin and in one of the figures, the authors referred informally to a linear form of *Arthrophycus*. However, they did not describe a new ichnotaxon, and were apparently unaware of the previous name *A. brongniartii*.

Seilacher (2000) subsequently described *A. linearis* more fully, with more images (Figure 3.4) and descriptions, and divided the ichnospecies into two subspecies based on two different modes of backfill (protrusive and retrusive). He reported the stratigraphic range of the ichnospecies to be Ordovican to Silurian and the geographic range to include North Africa, North America, and Jordan.

A. linearis possesses the standard features of *Arthrophycus*: annulations, a median groove, subquadrate cross-section, and general shape. As already noted, individual traces tend to weave more independently of one another than in *A. alleghaniensis*, showing only pseudo-branching as they cross over one another and never coalescing into bundles or palmate fans. Both protrusive and retrusive forms of backfill are present (Seilacher 2000). Given these characteristics, the inclusion of *A. linearis* in *Arthrophycus* is supported.

Fernandes *et al.* (2002) referred to *A. linearis* in their <u>Guide to Ichnofossils of Invertebrates of Brazil</u>, though without an image, so the report could not be evaluated.

Seilacher *et al.* (2002) mentioned *A. linearis* in Ordovician Hawaz Formation sandstones of Libya. The authors did not include a detailed description of the specimens, and the only photograph of *Arthrophycus* is labeled as *A. simplex*, so the report could not be evaluated.

Seilacher *et al.* (2003) mentioned *A. linearis* in the Balcarce Formation of Argentina in a study that focused on correlating rocks based on their trace fossils (chiefly *Arthrophycus* and *Cruziana*). There is no description and only one figure, which is dark and indistinct. However, given that one of the authors of the paper is the same person who erected the ichnospecies, there is no reason to doubt the assignment of the specimens.

Aceñolaza and Aceñolaza (2003) found *A. linearis* in the Cambrian-Ordovician Balcarce Formation of Argentina. The authors did not include a description in the text, but the small figure of *A. linearis* appears to conform to *A. linearis*. The specimens are annulated and show both the characteristic shape of *Arthrophycus* and the independence of *A. linearis*.

Neto de Carvalho *et al.* (2003) described specimens of *A. linearis* from the Armorican Quartzite of Portugal in detail. They noted the independent shape of the traces, a lack of true branching, and the two types of backfill that Seilacher (2000) had described. Unfortunately, the quality of most of the figures is rather poor, and most features are indistinct, but there are enough features there to identify the specimens as *A. linearis*, especially when coupled with the description. The clearest of the figures is the most intriguing, for it shows a circular three-dimensional spiral that may indicate circling behavior similar to that of *Cruziana semiplicata*. This specimen deserves further study, but such will not be attempted here.

No one except Seilacher (2007a) has described *A. linearis* since Rindsberg and Martin (2003) pointed out its synonymy with *A. brongniartii*.

A. montalto

A. montalto Simpson 1888 was referred to by Lesley (1889), who included a sketch of a specimen by Simpson (Figure 3.5) but did not provide a detailed description or full bibliographic information. The original specimen was found, in a scenario eerily similar to Harlan's (1831) find of *A. alleghaniensis* in a tavern stone, in the wall of a sawmill in Pennsylvania. It allegedly came from a quarry of sandstone above the Cambrian Potsdam Formation, but the quarry did not yield any more specimens.

The only description of *A. montalto* Simpson 1888 available for study is Lesley (1889), which reproduces Simpson's original figure. The specimen illustrated, presumably of the primary type material, appears similar to *A. brongniartii* with slightly curving, rather independent individuals with apparent branching by overcrossing, and regular annulations. A line down the middle of some portions is also present. Lesley (1889) compared the specimens to crinoid stems, which they may indeed be, or they may be specimens of *A. brongniartii*. Alpert (1975) mentioned their similarity to *Planolites virgatus*, but did not place Lesley's specimens in that ichnospecies; this possibility may merit further investigation. No other authors have mentioned *A. montalto* except in lists of ichnospecies in *Arthrophycus*. There is not enough evidence to separate this material from *A. brongniartii*.

<u>*A. siluricus*</u>

The origins of *A. siluricus* Schimper 1890 remain a mystery. In their volume of Zittel's encyclopedic work <u>Handbook of Paleontology</u>, Schimper and Schenk (1879-1890) mentioned *A. harlani* as an algal form and then noted *A. siluricus*. Their "description" was one sentence long and is translated here: "A second thinner and shorter species (*A. siluricus* Sch.) occurs in the lower Silurian [Cambrian] formations from which I possess the same from Sardinia [Italy], where they were greenish micaceous shale heaps is the same as the preceding species in the Medina sandstone." The authors did not describe the ichnospecies any further, did not include a figure, and did not include any reason for the new name. The fossil presumably had some kind of similarity to *A. alleghaniensis*, in order to justify the placement in *Arthrophycus*, but this supposed similarity is unknown. Schiller (1930) listed *A. siluricus* in a list of synonyms of *A. alleghaniensis*, perhaps indicating that he thought *A. siluricus* was not a valid ichnospecies by itself. Because of the lack of description and figure, *A. siluricus* is designated a *nomen nudum*.

A. elegans

A. elegans Herzer 1901 has not appeared in print since its original description, with the exception of Rindsberg and Martin (2003) who included it only in a list of *Arthrophycus* ichnospecies. Herzer (1901) described his new ichnospecies as similar to *A. alleghaniensis*, but denser in aggregate, slimmer, and with deeper "furrows," apparently referring to transverse markings rather than to a median groove. Some sections of his described slab preserve groups of individual traces that run parallel to one another, but this is not part of the larger pattern. The delicate nature of *A. elegans* is also seen in the size of the reported specimens (1/16 to 3/16 of an inch in width) and in the dense transverse markings. Herzer did not include a photograph, but made a sketch of the specimen (Figure 3.6).

The slightly-curving shape, annulations, and consistent width are compatible with *Arthrophycus* and the lengths of parallel behavior with the shared walls are intriguing, but there is not enough evidence to consider *A. elegans* as a separate ichnospecies from *A. brongniartii*. *A. elegans* is judged as a possible synonym of *A. brongniartii*, but the report conforms to *Arthrophycus* for the purpose of biostratigraphy and biogeography. Herzer was not specific about the stratigraphic position of *A. elegans*, referring it only to "Coal Measures," and Rindsberg and Martin (2003) listed the ichnospecies as Carboniferous in age. The ichnospecies has been reported only from Ohio, USA.

A. corrugatus

A. corrugatus (Fritsch 1908) was originally described as *Radix corrugatus*. Mikuláš (1992) referred Fritsch's description and figure to *Arthrophycus*. No other discussions of the ichnospecies are known; it has only been included in lists of *Arthrophycus* ichnospecies. Fritsch described the ichnospecies as branching and knotty, with transverse wrinkles, but the specimen appears rather wavy with an inconsistent diameter and irregular rings, lacks the median groove, and is a singleton.

Fritsch (1908) also wrote that the specimen could be similar to a stolon (a stem or a runner) belonging to a plant such as *Lepidotruncus*, which was found in the same layer. The main text referred to Fritsch's original figure (Figure 3.7) as *R. corrugatus*, but the caption for the figure is for *Radicites rugosus*, with no explanation for the apparent discrepancy.

Mikuláš (1992) figured the same specimen as Fritsch (1908) and mentioned an irregular swelling of the trace and irregularly-developed annulations along with an oval cross-section, which are not characteristic of *Arthrophycus*. Therefore, this ichnospecies assignment to *Arthrophycus* is questionable. Uchman (1998) questioned the placement into *Arthrophycus* and Mángano *et al*. (2005a) considered the name a *nomen nudum*, without explaining why. *Radix corrugatus* cannot be considered a *nomen nudum* because it has both a verbal description and an illustration, but *Radicites rugosus* (Fritsch 1908, plate 6 figure 8) lacks a verbal description. *Radicites rugosus* appears to be both an objective synonym and a *nomen nullum* of *Radix corrugatus*. This ichnospecies has only been reported from the Ordovician and Silurian quartzite band of "Repor d5" of the Czech Republic.

A. flabelliformis

A. flabelliformis Hundt 1940 was named in a paper primarily devoted to a discussion of the new ichnospecies of *Keckia* and *Palaeonereis*, leaving very little room for a description of *A. flabelliformis*. Hundt described *A. flabelliformis* as somewhat similar to *A. alleghaniensis*, with a fan-shaped structure of tubes. His figure of "*Arthropkycus* [sic] *flabelliformis*" (Figure 3.8) is rather dark and unrevealing, with a different fan shape from the palmate form of *A. alleghaniensis*, and no other descriptive information is provided. An attempt to contact two professors at the University of Köln with regard to specimens of *A. flabelliformis* received no reply. Hundt's specimens came from the Ordovician upper quartzite of Germany.

The only other mention of *A. flabelliformis* comes from Benton (1982), who referred Hundt's (1940) specimen to *Dictyodora zimmermanni* Hundt, as part of the vertical wall of *D. zimmermanni*. Hundt (1940) had compared his specimen to *Dictyodora manni*, but found insufficient similarity. Benton's figure showing the vertical wall of *D. zimmermanni* does show "rippled" structures that Hundt (1940) could have interpreted as individuals of *Arthrophycus* converging into a fan (Benton 1982). On the basis of Benton's suggestion and the lack of positive evidence that Hundt's specimens belong in *Arthrophycus*, there is no reason to include *A. flabelliformis* in the ichnogenus.

A. krebsi

A. krebsi Hundt 1941 was first described as "striated tubes" from the Ordovician quartzite of Germany. Hundt recognized the "sweeping" nature of the structure and suggested that it resulted from a burrowing method similar to that suggested by Sarle (1906a) for *A. alleghaniensis*, but gave no other details about the ichnospecies. The single photograph (Figure 3.9), is far too dark and provides no diagnostic criteria. Attempts to track down the specimens at the University of Köln have not yielded results, and Hundt was the only person to describe or recognize *A. krebsi*. Without any positive evidence that this is *Arthrophycus*, these specimens are removed from the ichnogenus and there is insufficient support for the ichnospecies concept.

<u>*A. minoricensis*</u>

A. minoricensis Bourrouilh 1973 was originally named in an unpublished PhD thesis from France. This does not satisfy the current requirements for publication distribution for the ICZN, but in 1973, those rules did not apply to trace fossils. Since then, this ichnospecies has been redescribed twice, by Orr (1994) and Llompart and Wieczorek (1997). Fernandes and Borghi (1996) also included a small discussion of the ichnospecies in their paper, without describing specimens. There is some disagreement as to the spelling of the name: Orr (1994) and Llompart and Wieczorek (1997) used *A. minoricensis*, but Fernandes and Borghi (1996) referred to *A. minorcensis*. According to Orr (1994), Bourrouilh may have originally described the ichnospecies as *Harlania minoricensis*. *A. minoricensis* has been reported only from the Carboniferous of the Balearic Islands, specifically from the island of Menorca (or Minorca) (Orr 1994 and Llompart and Wieczorek 1997).

In his 1994 paper, Orr also described *A. minoricensis* as associated with *Nereites*. His specimens have elliptical cross-sections, no inner fill, and have either "radial" or "arborescent" (branching) forms (Figure 3.10a). The radial forms are similar to the palmate orientation of many *A. alleghaniensis* specimens, but the palm structure is much larger and the individuals are not as condensed into the palmate form as in *A. alleghaniensis*. Orr did report fine striations, but they may be only on the external wall and the figures are not clear enough or large enough to make this determination.

Llompart and Wieczorek (1997) did not include a formal description of their *Arthrophycus* specimens, and their figure (Figure 3.10b) is not convincing. The specimens cover the rock densely and evenly, with no apparent overlap or bundling, which seldom, if ever, occurs in *Arthrophycus*. The traces do have a constant width and a slightly weaving shape, but no median groove or annulations are apparent and it is not possible to determine the cross-section.

Llompart and Wieczorek (1997) described *A. minoricensis* from the Carboniferous Culm siliciclastic sequence of Minorca Island, the same locality studied by Bourrouilh (1973). They described specimens from the *Nereites* ichnofacies of a turbidite, which includes ichnogenera such as *Palaeodictyon* and is generally understood to be a deep-water ichnofacies, whereas *Arthrophycus* is usually placed in the *Cruziana* ichnofacies, a shallow-water ichnofacies (Seilacher 1964a, Bromley 1990). Llompart and Wieczorek suggest that the presence of the shallow-water *Skolithos* ichnofacies directly above their specimens indicated a difference in energy, and not necessarily water depth, but in their conclusion the authors appear to have decided on the deep-water interpretation.

On the basis of the above characters, there is no reason to include the specimens of either of the above works in *Arthrophycus*. Uchman (1998) placed the inclusion of Orr's specimens in *Arthrophycus* under question and described *A. minoricensis* as a *nomen nudum* for the insufficient diagnosis, but did not mention Bourrouilh's specimens specifically (he had probably not seen them). He also did not mention the work of Llompart and Wieczorek (1997), but it is likely that the publication dates made this impossible. Mángano *et al.* (2005a) agreed that *A. minoricensis* should be considered a *nomen nudum*.

A. annulatus

A. annulatus Książkiewicz 1977 was the first of the three new ichnospecies of *Arthrophycus* defined by Książkiewicz. No one else has used the name since to describe new occurrences. Książkiewicz (1977) described *A. annulatus* as occurring in aggregates with occasional branching (probably pseudo-branching); the individuals are mostly straight with a circular or oval cross-section. The specimens have wide annulations (2.0-2.5 mm for 1 cm of width) and no median groove (Figure 3.11). The type specimens are Lower Eocene Ciężkowice Sandstone, but Książkiewicz (1977) reported other, narrower specimens from the Cretaceous Inoceramian Beds. Both are from Poland.

Książkiewicz (1977) discussed differences between *A. annulatus* and *Ophiomorpha*, but Mángano *et al.* (2005a) suggested that *A. annulatus* be placed there and Uchman (1998) suggested that *A. annulatus* should be placed in *Ophiomorpha* under the specific name *O. annulata* (Książkiewicz). The case to include *A. annulatus* within *Arthrophycus* is not particularly strong, based on the lack of positive evidence.

A. strictus

A. strictus Książkiewicz 1977 was the second of the three new ichnospecies of *Arthrophycus* described by Książkiewicz. In her specimens of *A. strictus*, Książkiewicz (1977) noted dense striations, some branching, and mostly straight and small (1.5-2.0 mm wide) burrows in the Cretaceous Lgota and Ropianka Beds of

Poland (Figure 3.12). She also noted another variety of *Arthrophycus*, placed in the same ichnospecies, that was larger (2.5 mm wide), with more pronounced transverse markings, a point at one end, and a radial arrangement. Neither variety of *A. strictus* had a median groove and was three times more narrow than specimens of *A. alleghaniensis*.

Pacześna (1996) provided a short description of material similar to the holotype form of *A. strictus*. The specimens are straight traces with annulations, but they taper at the ends and are not very common on the sample of rock – the sole figure shows only one branched structure. This specimen may not belong in *Arthrophycus* because of the tapered ends and small number of traces figured. Uchman (1998) removed Pacześna's specimen from *Arthrophycus*. Mángano *et al.* (2005a), however, tentatively suggested placing the specimens in *A. minimus*.

Uchman (1998) analyzed the Książkiewicz specimens of *A. strictus* further. He noticed differences even within her second morphotype and assigned some of those to *A. tenuis*, but accepted the holotype specimen as *Arthrophycus*. Mángano *et al.* (2005a) rejected the holotype specimen as *Arthrophycus* because of the cylindrical cross-section and the simplicity of the general shape of the trace. *A. strictus* (holotype) is tentatively considered as *Arthrophycus* herein, but Książkiewicz's second morphotype does not conform to the ichnogenus because the radial arrangement and pointed terminus do not resemble the blind endings and general form of *Arthrophycus*.

A. dzulynskii

A. dzulynskii Książkiewicz 1977 is the third new ichnospecies of *Arthrophycus* that Książkiewicz designated from Poland. She was unsure of the ichnogeneric assignment, noted that the straight specimens possessed transverse ribs (Figure 3.13), but also observed an odd curvature of the ribs and thought that there was a difference between the ventral and dorsal sides. The specimen is a singleton, with a depression in the center and a knob at one end, neither of which is characteristic of *Arthrophycus*, and the annulations are not consistent in size, but narrow toward the outer edges of the trace. No other authors have described occurrences of *A. dzulynskii*, so it remains known only from the Oligocene Krosno Beds of Poland.

Książkiewicz (1977) placed her specimens in *Arthrophycus* due to the presence of the annulations and the general shape of the trace, but also suggested that the specimens could be placed in *Climactichnites* in view of the ending knobs. Uchman (1998) suggested that specimens of *A. dzulynskii* be placed in *Protovirgularia* under the specific name *P. dzulynskii* (Książkiewicz), and Mángano *et al.* (2005a) agreed. *A. dzulynskii* is rejected herein as an ichnospecies of *Arthrophycus* due to the single occurrence, central depression, terminal knob, and curvature of the ribs, but which, if either, of these other assignments is preferable has not been determined.

<u>*A. tenuis*</u>

A. tenuis (Książkiewicz 1977) was first described by Książkiewicz as *Sabularia tenuis*, from the Oligocene Krosno Beds of Poland. Her original description of *S. tenuis* included delicately annulated burrows, pseudo-branched, with one or both ends pointed (Figure 3.14). She noted the very small size (0.5 to 0.7 mm wide) of the short and straight burrows, which occur in large numbers on the slab. The specimens have no median groove and one or both ends of each individual trace are pointed. Uchman

(1998) subsequently assigned the specimens to *Arthrophycus* under the ichnospecies name *A. tenuis* (Książkiewicz).

Uchman (1998) has since referred other specimens to *A. tenuis*. Alexandrescu and Brustur (1984) described specimens of *S. tenuis* from the Oligocene-Miocene Tarcau unit of Romania that are slightly wider (1-2 mm) and occurred in dense accumulations, but cross one another in only a few places, are pointed on one end, and do not have transverse annulations. Uchman (1998) suggested that such fine markings might not always be preserved and that thus the absence of annulations was not important, and placed the specimens in *A. tenuis*.

Uchman (1999) also placed traces from a turbiditic sequence from the Cretaceous Flysch-Gault Quartzitseries of Germany into *A. tenuis*. These specimens show some branching and are similar in size to Książkiewicz's material (0.6-0.7 mm wide), but do not have transverse annulations. They rather resemble impressions of small twigs. Uchman and Demircan (1999) described similar specimens from a deep-sea fan fringe from the Miocene Cingöz Formation of Turkey, but were unsure of their placement in *Arthrophycus*. The specimens in the figure resemble those in the figure in Uchman (1999), except for one intriguing larger individual. This specimen was not specifically discussed in the paper. Though interpreted as a deeper water formation, the authors noted seventeen species of three different ichnofacies (*Skolithos*, *Cruziana*, and *Nereites*).

All of the specimens in *A. tenuis* should be removed from *Arthrophycus*. The primary types are the only ones with annulations, though other specimens assigned to this ichnospecies may have had annulations that were subsequently eroded. More problematic are the pointed ends of the traces, tiny size, and lack of median groove or any other character common in *Arthrophycus*, and few other specimens of *Arthrophycus* are reported from deep water sequences. Mángano *et al.* (2005a) also did not consider the holotype of *S. tenuis* as belonging to *Arthrophycus*, citing the odd branching pattern and typical lack of annulations. It is therefore suggested that *Sabularia tenuis* be excluded from *Arthrophycus*, and that the specimens that Uchman referred to *A. tenuis* return to *S. tenuis*. Uchman (1998) proposed that the ichnogenus *Sabularia* is a subjective synonym of *Ophiomorpha*, but this proposal is not accepted herein.

The original specimens of *A. tenuis* were known from the Oligocene of Poland (Książkiewicz 1977); Alexandrescu and Brustur (1984) noted *S. tenuis* in the Oligocene to Miocene of Romania. Uchman (1999) noted *A. tenuis* in the Cretaceous of Germany, while Uchman and Demircan (1999) referred Miocene material from Turkey to *A. tenuis*. The entire reported range of the ichnospecies is thus Cretaceous to Miocene, in parts of Turkey and eastern Europe.

<u>*A. qiongzhusiensis*</u>

A. qiongzhusiensis Luo 1994 was the first ichnospecies of *Arthrophycus* to be described from China, but no new occurrences of the ichnospecies have been recognized by any other authors since. Luo *et al.* (1994) described *A. qiongzhusiensis* as branching, slightly curved, with both transverse ridges and fine striae in between the ridges, and a circular cross-section. The median groove is not present, and the figures show very few individuals. Neither of the two figures (Figure 3.15) included are of high enough resolution to reveal these finer striae and my efforts to contact the authors were fruitless. The ichnospecies is known only from the Cambrian Yu'anshan Member of the Chiungchussu Formation of China.

The placement of these specimens in *Arthrophycus* is problematic because of the small number of individuals, the very small size (1-2 mm wide), and the "wriggly" appearance of the traces. This last observation is something more than just a curving shape, but something that is not straight either. Mángano *et al.* (2005a) questioned the placement of *A. qiongzhusiensis* in *Arthrophycus* because of the circular cross-section and poorly-defined annulations. Those authors also found the specimens to be too isolated from any others to be *Arthrophycus*. Uchman (1998) questioned the placement of the specimens in *Arthrophycus* and suggested that they were reminiscent of "internal sediment pads" of *Torrowangea* Webby, but Mángano *et al.* (2005a) considered *Torrowangea* to be quite different from *Arthrophycus* (they did not address the possible resemblance of *A. qiongzhusiensis* and *Torrowangea* specifically).

A. tarimensis

A. tarimensis Yang 1994 was also described from China and is known only from the Ordovician Ulikeztag Formation. Yang (1994) described the new ichnospecies as somewhat curved, with annulations, but with a rounded cross-section and no median groove, and the traces are rather small (3-4 mm in width). The individuals are in a dense aggregate and truncate each other, but the only figure included in the paper (Fig. 3.16) is too blurred, small, and dark to reveal details. Efforts to contact the author and locate the specimen were unsuccessful. There is not enough evidence to include the specimens in *Arthrophycus* or to accept this ichnospecies.

A. hunanensis

A. hunanensis Zhang *et* Wang 1996 is a third ichnospecies of *Arthrophycus* described from China, and is currently limited to the Silurian Xiaoheba Formation. Zhang and Wang (1996) described the new ichnospecies as somewhat curved, occasionally overlapping but not branching, on the surface of the beds, and with annulations (Figure 3.17). The specimens have a similar width range (8-10 mm) compared to the typical size range of *Arthrophycus* and have a rounded or elliptical cross-section. No other authors have reported new specimens of *A. hunanensis*.

The placement of this ichnospecies in *Arthrophycus* is problematic because of the rippled appearance of the traces, particularly the one on the left in the figure. However, Mángano *et al.* (2005a) and Uchman (1998) both considered the possibility that these specimens were synonymous with *A. alleghaniensis*.

A. unilateralis

A. unilateralis Seilacher 1997 was first mentioned by Seilacher in his book Fossil Art. It is featured in the figure caption of a small sketch, without further description (Figure 3.3). In his 2000 work, Seilacher included the name in the synonymy of his ichnospecies *A. lateralis*, making the name *A. unilateralis* a ***nomen nullem*** and an objective synonym of *A. lateralis*. However, the name *A. unilateralis* has priority over the name *A. lateralis* by three years.

A. lateralis

A. lateralis Seilacher 2000 incorporated the sketch that his earlier work (1997) had labeled as *A. unilateralis*. In the description, *A. lateralis* possesses the typical subquadrate cross-section, annulations, median groove, and general shape of

Arthrophycus. The new ichnospecies is rather similar to *A. alleghaniensis*, but the individuals in the dense bundles "bend only to one side" (Figure 3.18) (Seilacher 2000). Seilacher has also remarked upon the backfill, which is horizontal as opposed to vertical, revealing how the trace-maker had burrowed.

In the work of Fernandes *et al.* (2002), the authors observed the asymmetrical fan shape of *A. lateralis* and also noted that the traces were somewhat smaller than those of *A. alleghaniensis*. The specimens of both authors conform to *Arthrophycus*, as they share the important characters that are diagnostic of the ichnogenus. The stratigraphic range of *A. lateralis* is Ordovician to (Early?) Devonian, with a geographic range that currently includes only Brazil and Libya (Seilacher 2007a, Fernandes *et al.* 2002).

A. lateralis is recognized herein as an ichnospecies of *Arthrophycus*, but it may more properly be a subspecies of *A. alleghaniensis*. Neto de Carvalho *et al.* (2003) supported the latter view, including *A. lateralis* in their synonymy for *A. alleghaniensis*; their report may extend the geographic distribution of *A. lateralis* to Portugal, but the figure is too blurry for confident assignment. Mángano *et al.* (2005a) considered *A. lateralis* to be a valid ichnospecies, but noted that polished sections are essential to reveal the burrowing program.

If *A. lateralis* is indeed a valid ichnospecies of *Arthrophycus*, and if the main diagnostic character (without sectioning) is the asymmetrical palmate form, then it may be possible to extend the geographic range further. Specimens at the Yale Peabody Museum (Grimsby Sandstone, Figure 3.19a), the Science Museum at Buffalo (not illustrated), and Paleontological Research Institution (Tuscarora Sandstone, Figure

3.19b) also appear to show this asymmetry, though the Buffalo specimen is palmate in the vertical dimension rather than horizontal. If these specimens fit the concept of *A. lateralis*, then they would extend the range of the ichnospecies to the Silurian of New York. If the "vertical" Buffalo specimen is *A. lateralis*, then perhaps the odd stacked specimen in Legg (1985) is also *A. lateralis*, which would extend the range of *A. lateralis* to the Cambrian of Spain.

<u>*A. simplex*</u>

A. simplex Seilacher 2002 is something of a mystery (Figure 3.20). It was first mentioned in a figure caption by Seilacher *et al.* in 2002 (their Fig. 4); the text of the paper reported *A. linearis* in the Hawaz Formation (Middle Ordovician) and *A. simplex* in the same formation, but in the figure caption only. The only other authors to report the ichnospecies are Konate *et al.* (2003). In their paper, they referred to "*Arthrophycus simplex* or *Harlania*-type galleries (linear)" in the Late Ordovician Ka Member of the Kandi Formation in a figure caption and used the terms *Arthrophycus* or *Harlania* in both the Ka and Kb Members of the Kandi Formation in the text, with no specific names or detailed discussion. *A. simplex* thus has no formal description, though it resembles *A. brongniartii* from the two figures in which it is noted. The name *A. simplex* may have been included in the first paper in error and then copied into the paper by Konate *et al.* If that is the case, the name appears to be a *nomen nullum*, and an objective synonym of *A. linearis*. The ichnospecies is reported from the Middle Ordovician of Libya (Seilacher *et al.* 2002) and the Late Ordovician of Niger and Benin (Konate *et al.* 2003).

A. minimus

A. minimus Mángano 2005 was first reported from the Cambrian Alfarcito Member of the Santa Rosita Formation of Argentina. Some of the same authors reported a new occurrence of the ichnospecies later that year (Mángano *et al.* 2005b) but *A. minimus* has not been noted since. Mángano *et al.* (2005a) described *A. minimus* as small, long, and narrow structures with annulations and a median groove, with a subquadrate cross-section and a slightly curving shape. The figures reveal dense accumulations and pseudo-branching but do not have the palmate forms typical of *A. alleghaniensis* (Figure 3.21) (Mángano *et al.* 2005b).

The specimens of *A. minimus* are small (1.8-4.8 mm in width), but are within the typical size range of *A. alleghaniensis* and other ichnospecies of *Arthrophycus* (Tables 2.3 and 2.4). *A. minimus* has all the hallmarks of *Arthrophycus*, even including retrusive spreiten as backfill. The inclusion of the *A. minimus* specimens in *Arthrophycus* is accepted herein on the basis of the many shared characters. Seilacher (2007a) suggested that the specimens be included in *Phycodes*, based partly on the small size of both *Phycodes* and *A. minimus*, but typical *Phycodes* morphology is more bundled than the independent structures seen in *A. minimus*.

The only remaining question regarding this ichnospecies is whether the specimens of *A. minimus* are too similar to *A. alleghaniensis* or *A. brongniartii* to warrant a new ichnospecies name. Mángano *et al.* addressed this question in their 2005(a) paper, noting that their specimens were exceptionally straight, with hardly any curving at all, and that the annulations were less evident. The size of the specimens is notably small, and some workers do support size as a criterion for dividing ichnospecies (e.g. Magwood 1992, Pickerill 1994). Small size may also reflect a response to stress in the environment (MacEachern *et al.* 2005); it is reasonable to accept this difference in body dimension as an ichnospecific character. Although the size range of *A. minimus* is actually within the lower bounds reported for *A. alleghaniensis* (Table 2.3), the smallest on the list (Liñán 1984) may actually be *A. minimus* (as suggested by Mángano *et al.* 2005a), leaving only the report of Metz 1998, which overlaps only slightly. If one accepts size as an acceptable ichnospecific criterion, then *A. minimus* is distinct from the ranges of *A. alleghaniensis* and *A. brongniartii*. *A. minimus* is therefore accepted as a valid ichnospecies of *Arthrophycus* based mainly on the unusually straight form and the small size.

A. parallelus

A. parallelus Brandt *et al.* 2010 was first described from float material determined to have come from the Grand River Formation of Michigan. As it is the most-recently described ichnospecies of *Arthrophycus*, there has not been sufficient time for a reaction in the literature. The notable features of *A. parallelus* include the regular annulations, median groove, pseudo-branching, small size (3.5-4.5 mm wide with relatively short lengths), and predominantly parallel orientation of the traces (Figure 2.20) (Brandt *et al.* 2010). Currently, the ichnospecies is known only from the Late Pennsylvanian of Michigan.

A. parallelus resembles *A. minimus* in its small size, but *A. parallelus* has a more restricted size range. *A. parallelus* also has annulations that are more pronounced, much wider (0.9-1.9 mm), and are clearly visible to the unaided eye, in contrast to the annulations of *A. minimus* that are "most visible under magnification"

(Mángano *et al.* 2005a). The *A. parallelus* material conforms to *Arthrophycus* based on the annulations, median groove, and general structure of the specimens. It is a valid new ichnospecies on the basis of the small size, unusual behavior producing parallel traces, and the coplanar nature of the traces.

Another specimen from the Devonian of New York may be a new occurrence of *A. parallelus* (Figure 3.22). These traces share the characteristics of *A. parallelus*: small size, annulations and a faint groove present, straight shape, and parallel orientation. The specimen, which was discovered in the collections of the New York State Museum, was in a cabinet labeled only "Devonian of New York" with no other data. The stratigraphic range of *A. parallelus* is therefore extended to the Devonian and its geographic range to New York.

A. isp.

Many specimens have been assigned simply to *Arthrophycus* isp., with no further designation. Often, even the original author is not confident of placement in the ichnogenus. As Mángano *et al.* (2005a) also noted, many of these authors seem to have placed specimens in *Arthrophycus* purely on the basis of annulations or other transverse markings.

Abel (1935) mostly discussed *A. alleghaniensis* that others had found in the Medina Sandstone of New York (for this reason, it was not included in the above discussion of *A. alleghaniensis*). However, he did mention an intriguing *Arthrophycus* isp. specimen from upper Austria that may have come from the upper Oligocene ("oberoligozänen"). Abel marked the date with a question mark, but did not explain the reason for the uncertainty. The specimen shows the regular annulations and palmate structure of *A. alleghaniensis*.

Aceñolaza and Aceñolaza (2003) mentioned *Arthrophycus* isp. from the Cambrian-Ordovician Balcarce Formation of Argentina. The figure for *Arthrophycus* isp. is similar to a figure of *A. linearis* in the same paper, but appears more weathered and indistinct. This specimen conforms to *Arthrophycus* for the regular annulations, simple shape, and possible bundle toward the bottom of the sample in the figure.

Aceñolaza and Heredia (2008) noted *Arthrophycus* in the Ordovician of Argentina. The authors mentioned the ichnogenus in the context of ichnostratigraphy, but did not appear to use it in that manner (they used *Cruziana* for the ichnostratigraphy). As there was no description or figure of *Arthrophycus*, the record remains unverifiable.

Akpan and Nyong (1987) mentioned *Arthrophycus* from the Cretaceous Eze-Aku Formation of Nigeria. The traces are described as "common" in the rocks, but the one figured (and presumably the others) is a single unbranched annulated trace. Even the authors questioned the placement of their specimens in *Arthrophycus*, and the placement is questioned herein as well. The subject of the figure resembles a fossil polychaete more than it does a trace fossil.

Alpert (1975) mentioned *Arthrophycus* in the Cambrian of California. He noted the ichnogenus only in a list without further discussion or any figures, so the record cannot be confirmed.

Alpert (1977) again mentioned *Arthrophycus* in the Cambrian of California. In this paper, he reported *Arthrophycus* from several formations of Early Cambrian age and placed it in a group of trace fossils that he found to be "indicative of early Cambrian age." He did not include a detailed description or figures, so this record cannot be confirmed either.

Banerjee (1982) referred specimens from the Cretaceous Eze-Aku Formation of Nigeria to *Arthrophycus*. The author described the specimens as tapered, with transverse markings, and about the right size for *Arthrophycus* (1 cm wide, 10 cm long). The paper does not include a photograph of a specimen, only a sketch, which shows a single trace that is pointed on one end, runs at an angle to bedding, has irregular annulations, and has some kind of scratch-like marks along the outer margin. This specimen should be removed from *Arthrophycus* based on the pointed end, irregular annulations, and non-diagnostic outer markings.

Becker and Donn (1952) reported *Arthrophycus* from the Silurian Tuscarora Formation of Pennsylvania. Their figure shows a large slab with many traces, most of which form narrow bundles with regular annulations and simple shape of individuals. Becker and Donn interpreted the trace as the remains of a fossil plant, which in itself does not invalidate their assignment of the specimen to *Arthrophycus*, as trace "producer" is not a valid ichnotaxabase (Bertling *et al*. 2006). This report conforms to *Arthrophycus* and it is further suggested that the specimens be placed under *A. alleghaniensis*.

Bhargava *et al*. (1984) noted *Arthrophycus* from the Silurian Manchap Formation of India. The authors discussed the ichnospecies but did not describe any of its features, other than the presence of annulations and a "gently meandering" form. The sole figure shows a single fossil with a somewhat wavy form and transverse markings. This specimen is excluded from *Arthrophycus* for the lack of sufficient evidence to place the fossil in the ichnogenus.

Bhargava and Bassi (1988) observed *Arthrophycus* in the Silurian Takche Formation of India. Their description mentions branching and bundling, along with annulations and a sub-circular cross-section, but the figure is too grainy to reveal any features of the specimens. Therefore, this report is considered questionable.

Bjerstedt (1987) found an *Arthrophycus* specimen from the Devonian-Mississippian Oswayo Member of the Price Formation of West Virginia. The description included a simple shape with some curve and annulations, without a median groove. The single figure is small and not very convincing, as it shows only one definite specimen. However, after examining this specimen at the Cleveland Museum of Natural History (Figure 3.23), the specimen may conform to *Arthrophycus* because there is more than one trace present, and all have faint annulations and the general shape of *Arthrophycus*.

Chiplonkar and Ghare (1975) reported *Arthrophycus* from the Bagh Beds of India and referred to Maberry (1971, questioned by several authors including myself) for their comparison with *Arthrophycus*. The authors never specifically mentioned an age for their formation, but Ghare and Kulkarni (1986) indicated that a previous report from the Bagh Beds of India was Cretaceous in age, and their reference list included the paper by Chiplonkar and Ghare. The authors' choice of Maberry's Cretaceous specimens for comparison also points to a Cretaceous age for the Indian fossils. The Indian specimens were variously described as "round, elliptical or flattened in cross section" and tapered toward the end. Annulations, median groove, interior structure, branching, and other characteristic features of *Arthrophycus* were not mentioned and the single figure is too dark to discern anything. These specimens are therefore excluded from *Arthrophycus*, as Uchman (1998) and Mángano *et al.* (2005a) also suggested.

Correia Perdigao (1964) mentioned *Arthrophycus* from the Ordovician of Portugal. The author listed *Arthrophycus* among a group of questionable specimens and noted that the putative *Arthrophycus* was even more questionable. The specimen resembled *Arthrophycus*, but without ornamentation; the meaning of this is unclear. The single figure is grainy and shows only a linear feature at high relief. There is no positive evidence for this report, so it is recorded as questionable.

Cotter (1983) reported *Arthrophycus* from the Silurian Tuscarora Formation of Pennsylvania. He did not include a description, but the figure shows specimens with regular annulations, simple form, and both the independent pattern of *A. brongniartii* and the bundling of *A. alleghaniensis*. The specimens conform to *Arthrophycus*, probably as a gradation between those two ichnospecies or as an example of co-occurrence.

Crimes (1981) recorded *Arthrophycus* from the Silurian-Devonian of North Africa. He mentioned that the ichnogenus is indicative of shallow marine sequences and is cosmopolitan in its geographic distribution, but did not discuss specific occurrences, so his report is unverifiable.

De Alvarenga *et al.* (1998) reported *Arthrophycus* from the Silurian Vila Maria Formation of Brazil. The ichnogenus is mentioned only once in the text and in a figure of stratigraphic correlations. In the absence of pictures and specimen descriptions, the record cannot be confirmed.

Duimovich (1963) noted *Arthrophycus* in Argentina. He did not provide a date for his specimens and recorded only that *Arthrophycus* was present with *Cruziana*, with no figures or description, so the record cannot be confirmed.

Durand (1985) reported *Arthrophycus* from the Ordovician Armorican Sandstone of France. He described his fossils as cylindrical to subcylindrical, with some branching or overlap of gently-curving shapes, and in the two figures, some annulations are visible as well. Durand suggested that the fossils might be *A. harlani*, but that many were too weathered for a confident ichnospecific designation. The size is rather large (2-3 cm wide), but it is suggested herein that the specimens be included in *Arthrophycus* for their annulations and general shape, and in *A. brongniartii* for their rather independent orientation and lack of bundles or palmate fans.

Dutta and Chaudhuri (2005) observed *Arthrophycus* from the Permian of India. Their paper did not give an age for the fossils, but the Manendragarh Beds of the Talchir Formation are listed as Permian by Ghosh (2003) (and Maejima *et al.* 2001 list the entire formation as Carboniferous-Permian). The description included a circular cross-section, annulations, the occasional median groove, possible retrusive spreiten, and a slightly curved shape. Some annulations are at an angle rather than parallel, and some seem to occur in pairs. The figure is small and blurred, but on request, Dutta and Chaudhuri supplied a better photograph. This photograph shows several traces in one sample, with rather odd scratch-like transverse markings. The specimens do not have the ring-like appearance of the more typical "annulations" and the markings seem to crisscross in some places. These specimens do not conform to *Arthrophycus*.

Eagar *et al.* (1985) reported *Arthrophycus* from the Carboniferous Fletcher Bank Grit of England. The authors noted a subquadrate cross-section, tapered ends, annulations, a median groove, some branching, and a rather small size (3-12 mm wide, with a mode of 7 mm). The tapered ends are odd, as is the angle of branching (80°). Mángano *et al.* (2005a) were hesitant to accept the report because of the faint annulations and odd branching angle, but the traces are tentatively placed in *Arthrophycus* based on the strength of the other characters.

Frey (1970) noted *Arthrophycus*-like burrows from the Cretaceous Fort Hays Limestone Member of the Niobrara Chalk of Kansas. The author described the fossils as simple, sometimes branched, cylindrical, and with annulations in some specimens. One of the two figures is at too large of a scale to show details; the other does not show enough. The figured structure is single and may have annulations, but nothing else about it is reminiscent of *Arthrophycus*. It is therefore recommended, with support from Uchman (1998) and Mángano *et al.* (2005a), that this material be removed from the ichnogenus.

Frey (1972) also noted *Arthrophycus*-like burrows from the Cretaceous Fort Hays Limestone Member of the Niobrara Chalk of Kansas. *Arthrophycus* is included only in a list on one page and in a block diagram (originally from Frey and Howard 1970). The diagram shows a single branched structure with regular annulations, but the orientation to the substrate is odd and there is not enough evidence to place the specimen in *Arthrophycus*. Uchman (1998) and Mángano *et al.* (2005a) also disputed the report.

Frey and Howard (1970) noted *Arthrophycus* from the Cretaceous Fort Hays Limestone Member of the Niobrara Chalk of Kansas and the Star Point Formation of Utah. All of the traces from Utah were generally better preserved than those from Kansas, but the block diagram of the alleged *Arthrophycus* specimen (originally in Howard 1966) shows only a single branch with annulations. The description of the Utah specimen indicates that a median groove is present in some specimens, and that the branching point was slightly enlarged. The block diagram of the Kansas trace shows annulations and an odd bulge at the branching point, but no other features of *Arthrophycus*. The description for that specimen, which even the authors question, also indicates that the diameter of the trace was inconsistent. It is recommended herein that both of these reports be removed from the ichnogenus for their odd bulges at the nodes and for the lack of enough evidence to designate them as *Arthrophycus*. Most other workers support this view (e.g. Häntzschel 1975, Uchman 1998) and Mángano *et al.* (2005a) suggested that this and similar specimens belong in *Thalassinoides*.

Ghare and Kulkarni (1985) reported *Arthrophycus* from the Jurassic Khadir Formation of India and are the only authors to report *Arthrophycus* from the Jurassic. Their description noted an oval cross-section, tapered ends, annulations, and a curved shape without branches. They concluded that the difference in cross-section was due to differences in the consistency of the substrate and was therefore not a taxonomic difference or concern. The single figure shows a few blurred traces with the described simple shape and annulations, along with some possible pseudo-branching. This material should be removed from *Arthrophycus* based on the lack of enough positive evidence, as Mángano *et al.* (2005a) also suggested.

Gong Yiming (1999) described specimens of possible *Arthrophycus* from the Carboniferous Julideneng Formation of China. The author described the specimens as annulated and unbranched, with a faint median groove and subquadrate cross-section. The specimens were uncommon in the formation and not well preserved, and the poor quality of the figure prevents confidence in the ichnogenus assignment. This record is tentatively classified as *Arthrophycus* based mostly on the strength of the description.

Greb and Chesnut (1994) discussed possible *Arthrophycus* from the Pennsylvanian Breathitt Formation of Kentucky. The authors did not include a description and questioned the taxonomic placement themselves. The sole figure of "*Arthrophycos*" shows a slightly curving tube-like structure with relatively thick transverse ribs, an inconsistent diameter, and no branches. This material should be removed from *Arthrophycus* based on the inconsistent diameter and the thickness of the annulations, as Mángano *et al.* (2005a) also suggested.

Howard (1966) reported *Arthrophycus* from the Cretaceous sandstones of Utah. His description and block diagram present a "segmented trace" with occasional branches with a bulge at the point of branching, a round or oval cross-section, and sometimes a median groove. This material should be removed from the ichnogenus because of its odd bulge and branching pattern, and most other workers agree with this position (e.g. Häntzschel 1975, Mángano *et al.* 2005a).

Kern (1978) observed possible *Arthrophycus* specimens from the Cretaceous (Sievering Formation) to Eocene (Greifenstein Sandstone) flysch of Austria. He described the fossils as mostly straight cylindrical tubes with annulations, though with a small diameter (1-6 mm); the description mentions branching but the traces are pseudo-branched in the sketch. Mángano *et al.* (2005a) did not accept this report; Uchman (1998) expressed doubt that it belonged in *Arthrophycus*.

Książkiewicz (1970) mentioned *Arthrophycus* from the Cretaceous flysch of Poland. She described the specimens as straight and unbranched, with annulations. The tiny sketch shows transverse markings on a very simple structure that does not have nearly enough evidence for an assignment to *Arthrophycus*. Uchman (1998) placed the specimen in *A. strictus*, but it is recommended herein that the material be removed from *Arthrophycus*.

In a very intriguing report, Laird (1981) noted *Arthrophycus* from the Ordovician Camp Ridge Quartzite of Antarctica. Unfortunately, this mention was merely a note in a list of ichnogenera that included *Daedalus*, and the author did not provide any further information, so the record cannot be confirmed.

Legg (1985) reported *Arthrophycus* from the Cambrian Oville Formation of Spain. He included annulations and a faint median groove in the description and noted possible indications of spreiten. The figure shows noticeable annulations that angle toward the middle of the trace, a feature not previously described for *Arthrophycus*, and the median groove is not apparent. This fossil is in much higher relief than normal for *Arthrophycus* and may be a vertical stack of traces. Mángano *et al.* (2005a) questioned the assignment of these specimens because of their vertical nature and suggested further analysis to determine if the specimens belong to *Arthrophycus* at all.

The assignment was classified as questionable herein because of the isolation, atypical annulations, and verticality.

Li (1993) mentioned two unnamed *Arthrophycus* types (A and B) from the Ordovician Gongwusu Formation of China. The author described the traces as branching, with annulations and a simple shape ("twig-shaped"), but these characteristics are not necessarily evident in the photographs. Specimen A is a singleton, is irregular in diameter, does not branch, and annulations are only faintly present. Specimen B shows the annulations more clearly and has branches, but the angle of branching (possibly true branching rather than pseudo-branching) is unusual for *Arthrophycus*. Mángano *et al*. (2005a) questioned the placement of the specimens in *Arthrophycus* based on their indistinct morphology and Uchman (1998) questioned them both, particularly Specimen B. Neither specimen belongs in *Arthrophycus*, based on the many problems with Specimen A and the unusual branching in Specimen B.

Lin *et al*. (1986) mentioned *Arthrophycus* in the latest Precambrian Gaojiashan Formation of China. Their description included a circular cross-section, annulations, and orientation of the traces as parallel to the bedding. Of the two included figures, one is an odd J-shaped trace with an uneven diameter and is therefore not *Arthrophycus*. The other figure is a single trace with a rather wavy shape but more consistent diameter, but the annulations are somewhat lumpy and irregular. It is not quite enough for a confident designation as *Arthrophycus*.

Lopez and Roy (2002) noted *Arthrophycus* in the Silurian Spragueville Formation of Maine. However, this report was an abstract from a meeting, in which

Arthrophycus is part of a list of ichnospecies found in the *Cruziana* ichnofacies in this stratigraphic unit, so the record remains unverifiable.

Maberry (1971) described *Arthrophycus* from the Cretaceous Blackhawk Formation of Utah. His description included annulations, branching with a bulge at the node, and an oval cross-section. However, the two figures do not depict anything that resembles *Arthrophycus*. The photographed specimen seems to run perpendicular to the bedding and is a singleton with an inconsistent diameter. The sketched specimen is also vertical rather than horizontal and has irregular walls and annulations; it resembles a badly-stacked column of coins. It is recommended that this material be removed from *Arthrophycus*, as did Uchman (1998) and Mángano *et al.* (2005a).

Manca (1986) discussed *Arthrophycus* in the Cambrian Campanario Formation of Argentina. The specimens are short, mostly straight cylindrical tubes with annulations. In the figure, the traces are quite short and rather lumpy, so the occurrence was classified as questionable herein.

Mergl and Massa (2000) mentioned *Arthrophycus* in the Silurian Akakus Formation of the Djado Basin (SW Libya or NE Niger). *Arthrophycus* is "characteristic" of the Silurian Akakus Formation there, but is not found in the overlying and otherwise similar beds. The authors did not provide a description or figure, therefore their record cannot be confirmed.

Moore (1933) mentioned *Arthrophycus* as an index fossil of the Silurian of the Appalachian region of the United States. He did not include a description, but the sketch looks like the typical *Arthrophycus* with its annulations, median groove, simple shape, and pseudo-branching.

Mukherjee *et al.* (1987) reported *Arthrophycus* in the Proterozoic Gulcheru Quartzite of India. The authors described their fossils as simple, horizontal, and both branched or not branched. The single figure shows structures that are labeled only as lebensspuren and does not show enough detail for an ichnogeneric assignment. The authors referred to Pettijohn and Potter (1964) for their assignment, but Kulkarni and Borkar (2002) stated that the structures in Pettijohn and Potter's (1964) work were inorganic sedimentary structures and thus refuted the Mukherjee *et al.* traces. It is recommended herein that the traces be removed from *Arthrophycus* based on the absence of positive evidence to place them there.

Peeples *et al.* (1997) noted *Arthrophycus* in the Middle Ordovician Swan Peak Sandstone of Idaho. They indicated that *Arthrophycus* was abundant in their study, but the report is only a meeting abstract and so could not be confirmed.

Pemberton and Risk (1982) mentioned *Arthrophycus* from the Silurian Thorald Sandstone of New York and Ontario. They described typical *Arthrophycus* specimens with subquadrate cross-section, faint median groove, annulations, and branching. The authors included a simple sketch rather than a figure, but their specimens conform to *Arthrophycus* (possibly *A. brongniartii*) based on the description.

Perez and Salazar (1978) observed *Arthrophycus* in the Cretaceous Dura Formation of Colombia. The authors described their specimens as "ringed, sometimes forked, folded" and as part of the *Cruziana* ichnofacies, but the plate that they included is small and blurry. It depicts a single, irregular, ridged structure that does not resemble *Arthrophycus*.

Pettijohn and Potter (1964) mentioned *Arthrophycus* from the Silurian Tuscarora Quartzite of Pennsylvania. The single plate that shows *Arthrophycus* depicts a network of branched traces without much structure or any other discernible features. The traces could have been weathered enough to erase all structure, or the "traces" could actually be inorganic sedimentary structures, as was proposed by Kulkarni and Borkar (2002). The traces cannot be accepted as *Arthrophycus* because of the lack of annulations, median groove, appropriate cross-sectional shape, or other features common to *Arthrophycus*.

Pflüger (1999) reported *Arthrophycus* from the Silurian Acacus Sandstone of Libya. He did not describe the occurrence in detail, but the figured specimens have regular annulations, simple structure, and many instances of bundling. This record conforms to *Arthrophycus* based on those characters and it is furthermore suggested that the specimen be designated as *A. alleghaniensis*.

Pickerill *et al.* (1991) noted *Arthrophycus* from the Cambrian-Ordovician Beach Formation of Newfoundland. The authors noted that the fossil was straight and simple in shape with annulations but no branches or intersections, as only one trace was present. The figure emphasizes the poor preservation and lack of very many features. The lack of diagnostic features and presence of only a single trace means that this report should be termed merely *Arthrophycus*-like.

Poiré *et al.* (2003) mentioned both *A. alleghaniensis* and *Arthrophycus* isp. from the Cambrian-Ordovician Balcarce Formation of Argentina. They did not describe the two separately or give any reasons for listing more than one, and included figures only of *A. alleghaniensis*, so their claim of any specimens that may be different from *A. alleghaniensis* cannot be evaluated. The report itself is classified as accepted based on the *A. alleghaniensis* specimens.

Romano (1991) also noticed both *A. alleghaniensis* and *Arthrophycus* isp. in the same paper, from the Ordovician Armorican Formation of Spain and Portugal. He did not include descriptions or figures of either *Arthrophycus*, so it cannot be determined what he perceived as different about some of his specimens. His claim therefore cannot be evaluated.

Roniewicz and Pienkowski (1977) reported *Arthrophycus* from the Eocene-Oligocene Podhale Flysch of Poland. However, this was only in a list of "transversely ornamented knobbly and ridge-like forms," so the validity of this claim cannot be assessed.

Sarle (1906) referred to many specimens of *Arthrophycus* in the Silurian Medina Sandstone of New York. However, his focus was on determining the burrowing programs of *Arthrophycus* and *Daedalus*, not on documenting a particular occurrence.

Schiller (1930) discussed an occurrence of *Arthrophycus* from the Cambrian of Argentina. However, as already discussed above, he found the specimens to be tectonic in origin and removed them from *Arthrophycus*, and his interpretation is accepted herein.

Seilacher and Alidou (1988) described *Arthrophycus* specimens from the Ordovician-Silurian Kandi Formation of Benin. The authors mentioned three different forms of *Arthrophycus*: linear, palmate, and deeply-scooping palmate. They did not describe these forms fully, but it is logical to presume from the photographs and drawings that the linear form is *A. brongniartii* and that one or both of the palmate forms are *A. alleghaniensis*. All the figured specimens have annulations, simple shape, and branching, so they conform to *Arthrophycus*.

Silva (1951) mentioned "*Arthrophycis*" in the Silurian of Brazil. The paper did not include a description or figure, so the record cannot be evaluated.

Stanley and Feldman (1998) found possible *Arthrophycus* specimens in the Ordovician Deadwood Formation of South Dakota. The authors claimed that the specimens were bilobate and annulated, but not branched, and the single figure depicts a single specimen with no apparent annulations or groove. The authors questioned the placement of the specimens in *Arthrophycus*, noting that their material was fragmentary. Mángano *et al.* (2005a) rightly removed these specimens from *Arthrophycus*.

Terrell (1972) mentioned a possible *Arthrophycus* specimen from the Permian Elephant Canyon Formation of Utah. He did not include a figure or describe the structure specifically, but noted only that it was similar to *Arthrophycus*. The Utah specimens described by Howard (1966), Frey and Howard (1970), and Maberry (1971) did not conform to *Arthrophycus*, Terrell's (1972) specimen to be doubted herein, but without a figure or description, the record cannot be confirmed.

Wagner (1978) noted *Arthrophycus* from the Silurian of Tennessee and Pennsylvania. The report was only a meeting abstract, so it cannot be confirmed, but at least one of the two formations cited in the paper (the Tuscarora Sandstone of Pennsylvania) has produced *Arthrophycus* in the past.

Webby (1977) observed *Arthrophycus* in the Cambrian-Ordovician quartz-rich clastics of New South Wales, Australia. As this is the only report of *Arthrophycus* from Australia, it is rather intriguing, but it is a meeting abstract and thus is not part of the peer-reviewed literature and so cannot be confirmed.

Wolfart (1981) mentioned *Arthrophycus* in the Silurian "Worm Burrows Sandstone" of Jordan. He did not discuss or figure any specimens of *Arthrophycus*, so his claim cannot be evaluated.

Yang *et al*. (1996) mentioned *Arthrophycus* in the Late Triassic Zhuwo Formation of China. They are the only authors to report the ichnogenus from the Triassic, but they did not include a description. The single figure is far to dark to reveal any details, and the traces come from black silts that may be deep marine flysch, which is highly unusual for *Arthrophycus*. There is no positive evidence to include this material in *Arthrophycus*, so it must be recommended that the material be removed from the ichnogenus, as did Mángano *et al*. (2005a).

Taxonomic Conclusions

After reviewing the publications, five ichnospecies were accepted herein as valid *Arthrophycus*: *A. alleghaniensis*, *A. brongniartii* (= *A. linearis*), *A. lateralis*, *A. minimus*, and *A. parallelus*. This evaluation was based on the major morphologic characters including annulations, simple form, branches, bundles, shape of cross-section, median groove, and internal structures. Table 3.2 summarizes these assessments of ichnospecies and provides some suggestions of synonyms from other authors.

The review of *Arthrophycus* literature revealed five characters in addition to those given by the authors of the primary literature on *Arthrophycus* (Harlan 1831, Hall 1852, Göppert 1852, Häntzschel 1975) in assigning specimens to *Arthrophycus*. The review also documented variability in some characters, such as the inconsistency of the median groove, definitions of annulations, presence of bundles and/or branches, and the question of singletons, and inconsistency in applying diagnostic characters (i.e. the ones listed by the primary authors).

With so many variable characters, the question arose as to how many of them are necessary for designation as *Arthrophycus*, and if a lack of a single character might be enough for rejection of a specimen or proposed ichnospecies. Condensing so many characters for so many taxa is difficult to do qualitatively, but a quantitative approach may help to reduce all of the information in an objective manner.

These issues and the plethora of both specimens and ichnospecies referred to *Arthrophycus* make precise definitions of *Arthrophycus* and its diagnostic characters difficult, and highlight the desirability of applying more objective, reproducible techniques in making taxonomic decisions.

Table 3.1: Published ichnospecies of *Arthrophycus*.

Ichnospecies	Date	First Author	Reported Time	Reported Place	Rock Type
alleghaniensis	1831	Harlan	Sil	New York	ss[1]
brongniartii	1832	Harlan	Sil	New York	ss
harlani	1838	Conrad	Sil	New York	ss
montalto	1888	Simpson	Camb	Pennsylvania	ss
siluricus	1879/1890	Schimper	Camb	Italy	sh[2]
elegans	1901	Herzer	Penn	Ohio	ss
corrugatus	1908	Fritsch	Sil	Czech Rep.	qztit[3]
flabelliformis	1940	Hundt	Ordo	Germany	qztit
krebsi	1941	Hundt	Ordo	Germany	qztit?
minor(i)censis	1973	Bourrouilh	Carb?	Minorca Is.?	sand-mud?
annulatus	1977	Książkiewicz	Cret-Eo	Poland	ss
strictus	1977	Książkiewicz	Cret	Poland	ss
dzulynskii	1977	Książkiewicz	Oligocene	Poland	ss
tenuis	1977	Książkiewicz	Oligocene	Poland	ss
qiongzhusiensis	1994	Luo	Camb	China	sh, ss, siltss[4]
tarimensis	1994	Yang	Ordo	China	not spec.
hunanensis	1996	Zhang	Sil	China	ss
linearis	1997	Seilacher	Ordo-Sil	several	ss?
unilateralis	1997	Seilacher	Sil?	Libya?	ss?
lateralis	2000	Seilacher	Ordo-Sil	Libya	ss
simplex	2002	Seilacher	Ordo	Libya	ss
minimus	2005	Mángano	Camb	Argentina	mudss[5], ss
parallelus	2010	Brandt	Carb	Michigan	ss
Arthrophycus	**1852**	**Hall**	**Sil**	**New York**	**ss**
(Harlania)	1852	Goeppert	Sil	New York	ss

[1] ss = sandstone
[2] sh = shale
[3] qztit = quartzite
[4] siltss = siltstone
[5] mudss = mudstone

Table 3.2: Guide to assessments regarding the status of each proposed ichnospecies of *Arthrophycus*.

Ichnospecies	Date	First Author	Reported Time	Reported Place	Rock Type	Assessment	Suggested Synonym
alleghaniensis	1831	Harlan	Sil	New York	ss	good	
brongniartii	1832	Harlan	Sil	New York	ss	good	
harlani	1838	Conrad	Sil	New York	ss	junior	*A. alleghaniensis*
montalto	1888	Simpson	Camb	Pennsylvania	ss	bad	*? Planolites virgatus*
siluricus	1879/1890	Schimper	Camb	Italy	sh	*nomen nudum*	
elegans	1901	Herzer	Penn	Ohio	ss	bad	*? A. alleghaniensis*
corrugatus	1908	Fritsch	Sil	Czech Rep.	qztit	bad	*? Radicites*
flabelliformis	1940	Hundt	Ordo	Germany	qztit	bad	*D. zimmermanni*
krebsi	1941	Hundt	Ordo	Germany	qztit?	bad	
minor(i)censis	1973	Bourrouilh	Carb?	Spain?	sand-mud?	*nomen nudum*	
annulatus	1977	Książkiewicz	Cret-Eo	Poland	ss	bad	*? Ophiomorpha annulata*
strictus	1977	Książkiewicz	Cret	Poland	ss	bad	
dzulynskii	1977	Książkiewicz	Oligocene	Poland	ss	bad	*Protovirgularia dzulynskii*
tenuis	1977	Książkiewicz	Oligocene	Poland	ss	bad	*Sabularia tenuis*
qiongzhusiensis	1994	Luo	Camb	China	sh, ss, siltss	bad	*? Torrowangea*
tarimensis	1994	Yang	Ordo	China	not spec.	bad	
hunanensis	1996	Zhang	Sil	China	ss	bad	
linearis	1997	Seilacher	Ordo-Sil	several	ss?	junior	*A. brongniartii*
unilateralis	1997	Seilacher	Sil?	Libya?	ss?	*nomen nullem*	*A. lateralis*
lateralis	2000	Seilacher	Ordo-Sil	Libya	ss	good	
simplex	2002	Seilacher	Ordo	Libya	ss	bad naming	*? A. brongniartii*
minimus	2005	Mangano	Camb	Argentina	mudss, ss	good	
parallelus	2010	Brandt	Carb	Michigan	ss	good	
Arthrophycus	**1852**	**Hall**	**Sil**	**New York**	**ss**	**good**	
(Harlania)	1852	Goeppert	Sil	New York	ss	junior	*Arthrophycus*

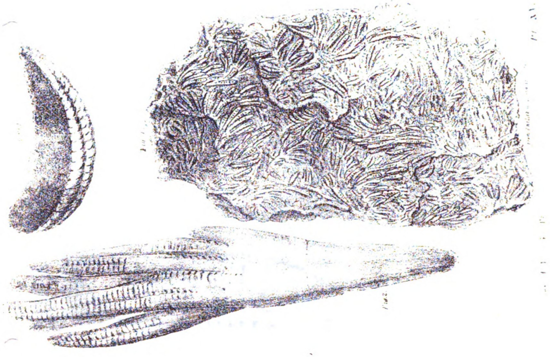


Figure 3.1: Drawings of *Fucoides alleghaniensis* from Harlan's original work (1831). Silurian of Pennsylvania, found in a tavern wall. No scale given.

Figure 3.2: The first known drawing of *F. brongniartii*, from Taylor (1835). Silurian of Lewiston, PA. No scale given.

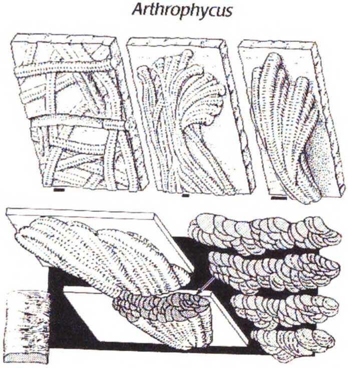


Figure 3.3: Seilacher's original drawings of *A. linearis* (top left) and *A. unilateralis* (bottom) (1997). No locality information or scale given.

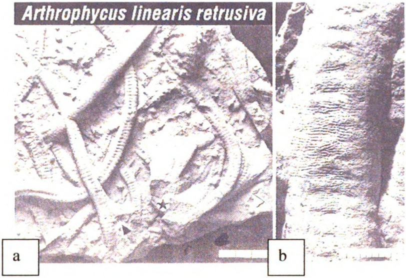


Figure 3.4: *A. linearis* in Seilacher (2000), along with a figure of wrinkles on that specimen. Silurian of Rochester, NY, Medina Sandstone. Scales represent 3 cm for (a), 10 mm for (b).

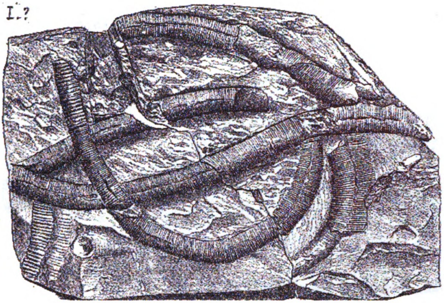


Figure 3.5: *A. montalto* from Lesley (1889). Cambrian of Pennsylvania, found in a sawmill wall. No scale given.

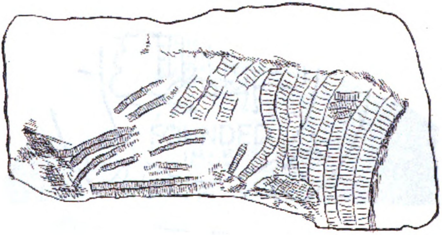


Figure 3.6: *A. elegans* from Herzer (1901). Carboniferous of Marietta, OH. Thinner traces are approximately 1/16" wide, wider traces are approximately 3/16" wide.

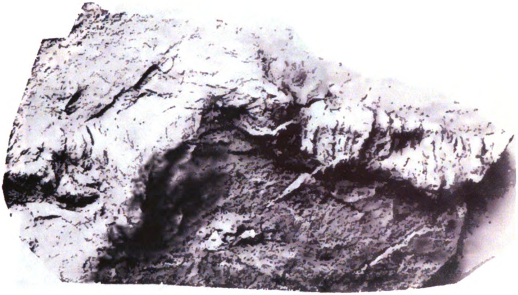


Figure 3.7: *A. corrugatus* (as *Radicites rugosus*) from Fritsch (1908). Silurian of Czech Republic. No scale given.

Figure 3.8: *A. flabelliformis* from Hundt (1940). Ordovician of Wuenschendorf ad Elster, Germany. No scale given.

Figure 3.9: *A. krebsi* (arrow with base line) from Hundt (1941). Ordovician of Wuenschendorf ad Elster, Germany. No scale given.

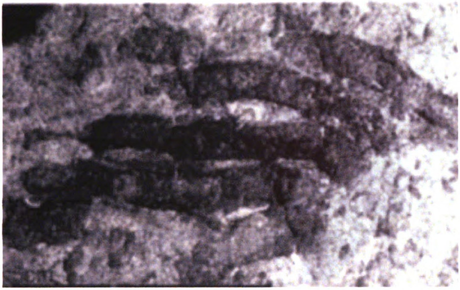


Figure 3.10a: *A. minoricensis* from Orr (1994). Lower Carboniferous of Menorca Island. Traces are approximately 1 cm wide.

Figure 3.10b: *A. minoricensis* from Llompart and Wieczorek (1995). Carboniferous of Minorca Island, Culm siliciclastic sequence. No scale given.

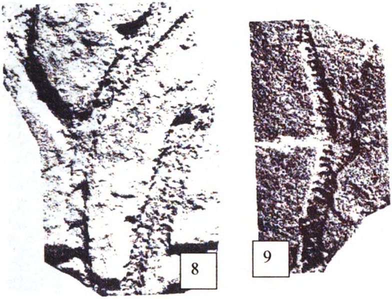


Figure 3.11: *A. annulatus* from Książkiewicz (1977). Lower Eocene of Poland, Ciężkowice Sandstone (8) and Turonian, Inoceramian Beds (9). Traces are approximately 1 cm wide.

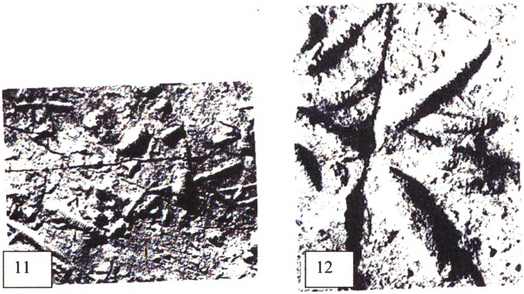


Figure 3.12: *A. strictus* from Książkiewicz (1977). Cretaceous of Poland, Lgota Beds (11), Ropianka Beds (12). Traces are 1.5 to 2.0 mm wide.

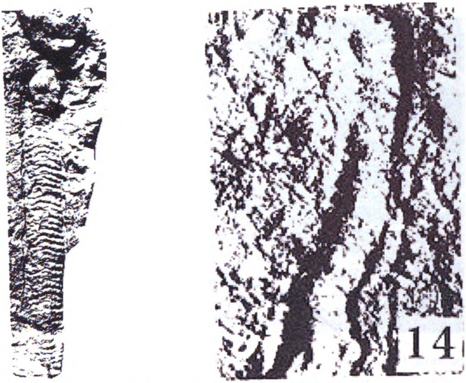


Figure 3.13: *A. dzulynskii* from Książkiewicz (1977). Oligocene of Poland, Krosno Beds. Traces are approximately 1 cm wide.

Figure 3.14: *A. tenuis* (as *Sabularia tenuis*) from Książkiewicz (1977). Oligocene of Poland, Krosno Beds. Traces are 0.5 to 1.0 mm wide.

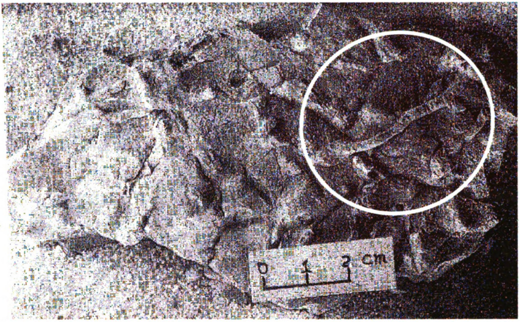


Figure 3.15a: *A. qiongzhusiensis* from Luo *et al*. (1994). Early Cambrian of China, Yu'anshan Member of the Chiungchussu Formation. It was not clear from the paper which structure is *Arthrophycus*; the most likely candidate is circled.

Figure 3.15b: *A. qiongzhusiensis*, also from Luo *et al*. (1994). Early Cambrian of China, Yu'anshan Member of the Chiungchussu Formation. No scale given.

Figure 3.16: *A. tarimensis* from Yang (1994). Lower Ordovician of the Tarim Basin, China, Ulikeztag Formation. No scale given.

Figure 3.17: *A. hunanensis* from Zhang *et al*. (1996). Silurian of China, Xiaoheba Formation. Traces are approximately 1 cm wide.

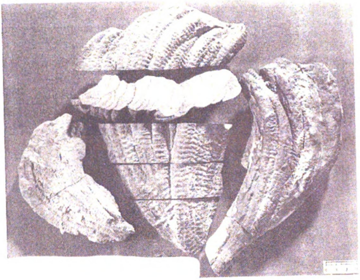


Figure 3.18a: *A. lateralis* from Seilacher (2000). Lower Silurian of Libya, Akakus Sandstone. Scale bar in corner represents 3 cm.

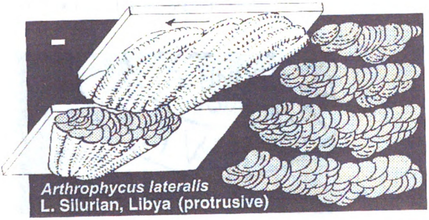


Figure 3.18b: Sketch of *A. lateralis* from Seilacher (2000).

Figure 3.19a: Loop of *Arthrophycus* showing asymmetry of the bundling toward the bottom of the photograph. Silurian of Rochester, NY, Grimsby Sandstone. YPM207001. Scale bar represents 2 cm.

Figure 3.19b: Asymmetrical bundle in an *Arthrophycus* specimen, labeled as *A. harlani* but possibly representing *A. lateralis*. Silurian of Tyrone, PA, Tuscarora Sandstone. PRI, unnumbered specimen. Scale bar is in cm.

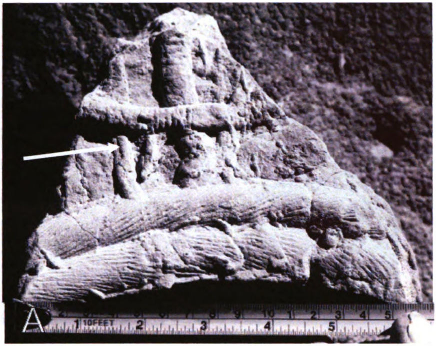


Figure 3.20: *A. simplex* (arrow) from Seilacher *et al.* (2002), with specimen of *Cruziana goldfussi*. Ordovician of the Kufra Basin, Libya, Hawaz Formation.

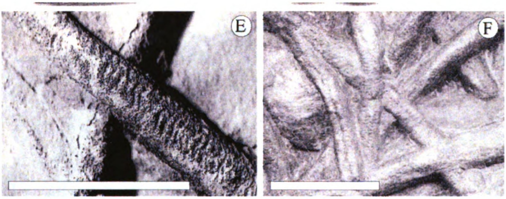


Figure 3.21: *A. minimus* from Mángano *et al.* (2005a). Upper Cambrian of Argentina, Alfarcito Member of the Santa Rosita Formation. Scale bars represent 1 cm.

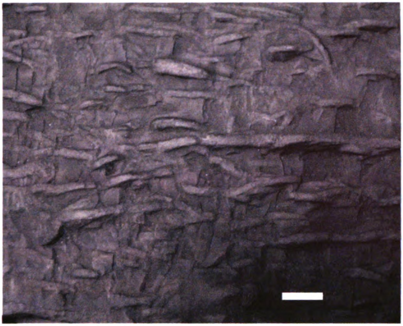


Figure 3.22: Unnumbered specimen referred herein to *A. parallelus*, from the New York State Museum. Devonian of New York, possibly Hamilton Group. Scale bar represents 1 cm.

Figure 3.23: *Arthrophycus* isp. Late Devonian to Early Mississippian, Rowlesburg, WV, Oswayo Member of the Price Formation. CMNH8340. Scale bar represents 1 cm. Specimen is the same as that figured in Bjerstedt (1987).

Chapter IV. Definition of *Arthrophycus*, Part III.: numerical ichnology

Previous Use in Ichnology

Although most techniques for evaluating ichnotaxa are wholly or partially qualitative, some quantitative methods have been used. In a study of vertebrate trackways, Demathieu and Demathieu (2002) used a system of measured characters (e.g. width of digit, stride and pace lengths) to analyze different ichnospecies and estimate potential for overlap in the definitions of the ichnotaxa. Lockley (1998) also attempted to evaluate the use of measurements for vertebrate trackways but met with mixed results and difficulty of standardization, while Trewin (1994) attempted to standardize arthropod trackway identification with character states coded as numerical data. In *Arthrophycus*, the only attempt at quantitative data comes from Neto de Carvalho *et al.* (2003), who published a single small graph comparing diameter measurements of *A. brongniartii* (as *A. linearis*) and *A. alleghaniensis* specimens. No other quantitative attempts in ichnotaxonomy are known.

Basic Methods

In the statistical program PAST (Hammer *et al.* 2001), a simple clustering diagram, or dendogram, is a way of showing hierarchical distance relationships among groups. Taxa that are more similar to each other will group together, with more-dissimilar taxa placed farther away. As with cladistics, all nodes in the dendogram can be rotated; left and right placements have no particular meaning.

The first step is the creation of a data matrix of numerically coded character states for each character. In the data matrix, OTUs (operational taxonomic units, in this case equal to ichnospecies with some exceptions) are in rows and characters are in columns. Each character has a number of different character states (e.g. groove: absence and presence), which are each designated by a number (e.g. absence of a groove = 0, presence = 1). PAST then uses these data to construct the dendogram or cladogram.

There are three different algorithms available in PAST for cluster diagrams, and twenty-two different similarity measures, not all of which can accept more than two states per character. Ward's method was the algorithm chosen for this study, because it is suitable for studying morphological data and permits the use of multistate characters. Ward's method assumes Euclidean distance as the similarity measure, so no additional decision among the similarity measures is necessary.

The characters chosen were based on those that are common in the literature describing *Arthrophycus*. These characters are median groove, shape of annulations, shape of cross-section, proximity to other traces, overall shape, palm shape, radial shape, branching pattern, parallel behavior, orientation to the substrate, internal structure, wrinkles, shape of the ends of the trace, smoothness of the walls, and width. This list includes the common characters from Harlan (1831), Hall (1852), Göppert (1852), and Häntzschel (1975); the others are those that recur in published descriptions and that were noted during examination of specimens during this study.

In order to code the character states for each ichnospecies, the original description and figure (drawing or photograph) were examined wherever possible. If the image and the specimen did not agree, the character state was coded based on the image or one of the intermediate states for the character was chosen, if intermediate states were available and not contradicted by the image, because intermediate states minimize the degree of uncertainty. In cases with more than one report of the ichnogenus (widespread for *A. alleghaniensis*, common in *A. brongniartii/linearis*), all available photographs and written descriptions were inspected. If the specimens were correctly diagnosed in these descriptions, then the codings from both should match. This was usually the case; the only notable exceptions were the measurements for width, as detailed below. In the case of *A. alleghaniensis*, it is possible that some specimens designated as *A. alleghaniensis* should be *A. brongniartii*, so Harlan's (1831) sketch and/or a simple majority of all available illustrated material were used in case of any discrepancies. The entire data matrix may be found in Appendix III.

Character States

Annulations were initially coded as either present or absent. All of the proposed ichnospecies of *Arthrophycus* have annulations present, so this was an uninformative character. However, on closer inspection, differences in shapes of the annulations were apparent and this character became more interesting. The states for annulations are now coded as ring-like (0), concavo-convex (1), chevron-like (2), or biconvex (3) (Figure 4.1).

The median groove, internal structure, and wrinkles are all coded as either present (1) or absent (0).

Cross-section is the second multistate character. The three states are subquadrate (0), cylindrical (1), and elliptical or oval (2).

Closeness is an attempt to code how gregarious the traces are. The traces may be singletons (0), few traces (1), somewhat close (2), or dense (3).

Overall shape was difficult to code because the states grade into one another. The burrows may be predominantly curving (0), predominantly straight (2), or intermediate between the two (1). For this character in particular, both the published descriptions and all available figures were used to assess the shape as accurately as possible.

Palm shape refers to traces that form bundles. The states are: not bundled (0), asymmetrically palmate (1), and symmetrically palmate (2).

Radial shape refers to traces that form a radial pattern from a single point, rather than a bundle with an axis. The states are not radial (0) or radial (1).

Branching pattern was difficult to code because the degree of branching of traces can be difficult to quantify. For this character, the published descriptions were the primary sources of information ("extensive" means whatever the original authors meant), as well as the images. For the purposes of this coding, pseudo-branching and true branching are regarded as the same character state. The states are: no branching (0), some branching (1), and extensive branching (2).

Parallel behavior is coded as not parallel (0) or traces predominately parallel to one another (1).

Planar relationships refer to the orientation of the traces with respect to one another in three dimensions. They are either in a single plane (0) or in several (1).

Ends refer to the nature of the termini of the traces. They are termed blunt (0), pointed (1), or knobby (2). Traces that are bundled are still considered to have blunt ends unless the unbundled end is pointed. Traces in which one or both ends are not observable because the trace goes off the edge of the sample or descends beneath the surface were coded as blunt (0) because it is the most common character state.

Diameter refers to the variability of the diameter: the trace is either largely variable along its length (0) or consistent (1). As with the trace terminus, bundled individuals are not examined at the bundled end and traces that extend beyond the slab are examined only where observable. The width of the ends of the trace, where applicable, is part of the "end" character above and is not included here.

Smooth refers to the condition of the surface of the sides of the trace: smooth (0) or rough and irregular (1). Only one OTU was coded as exhibiting character state 1.

As noted above, width was the only notable character for which there was variation among the reports of the different ichnospecies. All reported width measurements for each ichnospecies were recorded and a range of measurements for each ichnospecies was compiled. Table 4.1 is a diagram of these ranges and is divided into three size classes: 0-5 mm (0), 5-10 mm (1), and greater than 10 mm (2). All of the ichnospecies with width measurements fell nicely into these three categories, with three exceptions: *A. alleghaniensis*, *A. brongniartii*, and *A. linearis*. *A. brongniartii* has a reported range of 5-14.1 mm, with the greater sizes being more typical, so I used an approximate midpoint of 11. *A. alleghaniensis* has a very large reported range of width measurements, but most of them fall between 5 and 15, with a larger tail toward the higher end, so a midpoint of 11 was suitable here. *A. linearis* also has a large reported range (mostly from Neto de Carvalho *et al.* 2003), but nearly all of its width measurements are over 10 mm.

Missing Data

As is often the case in paleontology, there are a number of instances of missing data in the data matrix, despite efforts to be complete. Some of the illustrations available were not sufficiently clear for confident assignment of a particular character's state, while many of the written descriptions also did not provide enough information. Because PAST cannot run the cluster analysis with missing information, the state that would minimize error for each empty cell was chosen.[6] For characters that are either present or absent, "absent" may be assumed to mean "absent or unobservable."

However, some ichnospecies had excessive missing data. *A. siluricus*, which had no available drawing or photograph and essentially no description (Schimper and Shenk 1879-1890), did not furnish any data at all. *A. krebsi* (Hundt 1941) and *A. flabelliformis* (1940) both had photographs and some description, but far too little to fill in the data matrix with any confidence. These three ichnospecies are therefore eliminated from the analysis. *A. unilateralis* and *A. harlani* are also absent from the analysis, because their synonymy with other ichnospecies of *Arthrophycus* has been clearly established and accepted, and thus their inclusion was not necessary.

Conversely, one ichnospecies had to be divided into three OTUs for this analysis. *A. strictus* has been described in two reports, that of Książkiewicz (1977) in the Cretaceous and Paczeŝna (1996) in the Cambrian. Such a broad stratigraphic range, with no occurrences in between, suggested that the two should be considered

[6] Groove: *A. minoricensis* = 0. It is better to infer absence than presence.
Cross-section: *A. montalto*, *A. elegans*, *A. corrugatus* = 1. Cylindrical is the closest to an intermediate state for this character, reducing potential error either way.
Shape: *A. strictus* (second Książkiewicz type) = 2. Książkiewicz noted that the second type was similar to the first type she described, which is coded as 2 herein.
Width: *A. montalto* = 1. *A. montalto* had no size descripton and the figure had no scale. Character state 1 was chosen because it is the width most often found in "typical" *Arthrophycus* specimens and because 1 is the intermediate state.

separately; if indeed similar, they should plot together on the dendogram. In addition, Książkiewicz described two similar morphotypes of *A. strictus* in her original description (1977). They were of different sizes and had different types of branching, so I chose to code them separately (Uchman (1998) also supported the idea of two different morphotypes in Książkiewicz's work). Again, if truly similar in spite of those differences, the morphotypes (designated *strictus* K1 and *strictus* K2) should plot together.

Cluster Analysis Results

The cluster diagram produced by PAST is in Figure 4.2. The numbers along the y-axis represent the Euclidean distances between clusters; higher numbers indicate groups of ichnospecies that are not very similar to one another, while lower numbers indicate more similar groupings.

Depending on the level of similarity desired, the cluster diagram can be divided into several groups. The cluster on the left side is composed of only six ichnospecies: *A. alleghaniensis*, *A. brongniartii*, *A. linearis*, *A. lateralis*, *A. minimus*, and *A. parallelus*, and the rest of the ichnospecies fall into a separate cluster. It is striking that these six ichnospecies should cluster together, and be so distant from the other ichnospecies, because they are all ichnospecies previously supported as conforming to *Arthrophycus* in the qualitative section.

Within the cluster of six ichnospecies, *A. linearis* and *A. brongniartii* plot very closely together, which would be expected if they are indeed synonyms as Rindsberg and Martin (2003) suggested. In fact, the only difference in the coding between *A. linearis* and *A. brongniartii* is that the branching pattern of *A. linearis* is "some branching" and that of *A. brongniartii* is "no branching" – these are probably quite similar orientations and possibly an artifact of the illustrations. The analysis therefore supports the synonymy of *A. linearis* with *A. brongniartii*.

Also within the same cluster, *A. lateralis* and *A. alleghaniensis* clustered more distantly, which was a surprise because these two ichnospecies appeared very similar except for the direction of their palmate forms. However, *A. lateralis* has less curvature, which is probably related to the difference in the shape of the palm fan. As *A. lateralis* was named only within the last decade, a lack of study and few occurrences could explain the apparent absence of wrinkles and the narrower range of widths (which is, however, within the lower bounds of *A. alleghaniensis*). *A. lateralis* is most similar to *A. minimus*, another unanticipated result, as *A. minimus* is more similar to *A. brongniartii* and *A. linearis* in its shape. *A. parallelus*, similar to *A. minimus* in size, differs in other characters (e.g. shape of annulations, parallel behavior), but still plots with the other five ichnotaxa determined previously to be *Arthrophycus*.

The remaining putative ichnospecies of *Arthrophycus* all plot into one large cluster on the right of Figure 2. Therefore, none of these is considered to be *Arthrophycus*: they should be removed from the ichnogenus and, where applicable, be placed in other ichnogenera as other authors have suggested (see Chapter III). All three of the morphotypes of *A. strictus* fell into the same sub-cluster of this analysis, indicating that they may be the same morphotype.

The position of *A. simplex* within the outer cluster was unexpected. The conclusion from the qualitative analysis was that *A. simplex* was actually *A. brongniartii* (=*A. linearis*), because *A. linearis* was the only ichnospecies of

Arthrophycus mentioned in the text of the initial paper that mentioned *A. simplex* (Seilacher *et al.* 2002). It is possible that some of the coding choices for *A. simplex* were in error because there were so few photographic images and no published written descriptions to draw from.

Width may not be a reliable character, due to the large ranges and overlaps in sizes of ichnospecies, and because size is not usually considered a valid ichnotaxobase (Bertling 2007). To determine the impact of width, the analysis was run with the same parameters as before, but without the width data (Figure 4.3). The six taxa that were supported as belonging to *Arthrophycus* are still together, but some of the internal relationships changed: *A. parallelus* and *A. alleghaniensis* were each outsiders to the subgroup that includes the other four OTUs.

The positions of most of the OTUs within the larger cluster changed, preserving few of the previous sub-clusterings. Notably, the three morphotypes of *A. strictus* no longer fell in the same sub-cluster: the Cambrian specimens described by Pacześna (1996) are more similar to the holotype of *A. strictus* (*strictus* K1) than the two Cretaceous morphotypes described by Książkiewicz (1977) are to each other.

In order to discover which characters the software used to group taxa, PAST was used to make a two-way cluster diagram, with OTUs on one side (Q-mode analysis) and characters on the other (R-mode analysis) (Figure 4.4). The data matrix between the two dendograms indicates the character state for each OTU for each character, and non-zero numbers are indicative of an impact on the groupings. For the cluster containing the six *Arthrophycus* ichnotaxa, there is no distinct cluster in the R-mode analysis of important characters; the contributing characters are scattered in the dendogram. The characters contributing to the group of six ichnotaxa are diameter, shape, shape of annulations, width, internal structure, plane, median groove, and closeness as the most important. These eight characters should therefore be a major part of any definition of *Arthrophycus*.

Principal Coordinates Analysis (PCO)

The PAST software can also produce a "map" of the character data to identify patterns in how the OTUs are grouped together. Principal coordinates analysis reduces the data to the primary axes of variation, which are plotted in two-dimensional space (Legendre and Legendre 1983). As in the cluster analysis, closely-related taxa should cluster closer together in the plot space. For consistency, the Euclidean similarity index was used in the principal coordinates analysis as well as in the cluster analyses. The first three axes were the most important, comprising 58.545%, 20.852%, and 10.649% of the variance, in descending order. The OTUs conformable to *Arthrophycus* are represented by the + symbols and the other OTUs are represented by dots.

Figures 4.5 and 4.6 show the results of this analysis with coordinates 1 and 2 and coordinates 1 and 3, respectively. The groups identified earlier in the cluster diagrams are still present as entities in both PCO diagrams, as they group together and do not overlap, though one of the *Arthrophycus* points (*A. parallelus*) plots further toward the middle than the others do. Coordinate 1 provides the separation of the clusters in both diagrams, while Coordinate 3 separates them to some degree but Coordinate 2 does not at all. As Coordinate 1 has most of the weight (58.545%), it is the most important axis. PCO analysis thus supports the results of the cluster analysis and the conclusion that the "true *Arthrophycus*" cluster is real and distinct from the other OTUs.

Cladistic Analysis

A cladistic analysis requires the choice of an outgroup. It is possible to take the oldest member of the ingroup and code it as the outgroup, but there are several potential problems with this. One is that some doubt remains over which, if any, of the oldest ichnospecies of *Arthrophycus* are true representatives of the ichnogenus: *A. qiongzhusiensis*, *A. strictus*, and *A. minimus* are all Cambrian, and the assignments of the first two are particularly questionable. Another problem is that preconceived ideas of the evolution of *Arthrophycus* may not be consistent with the oldest representatives known as being necessarily the most "primitive," meaning that they should belong toward the base of the cladogram.

The other possible outgroup is a non-*Arthrophycus* ichnospecies from an ichnogenus that is thought (e.g. Seilacher 2000) to be related to *Arthrophycus*, such as *Daedalus*. Many of the characters used to describe *Arthrophycus* are applicable to *Daedalus*, but there is still the problem of which ichnospecies of *Daedalus*, or any other proposed ichnogenus, to code for use as an outgroup. The ichnospecies of *Daedalus* are different from each other (Durand 1985), just as the species of *Arthrophycus* are, and thus the selection of any particular ichnospecies of *Daedalus* could greatly change the results of the cladogram generated. By its very nature, the selection of an outgroup will polarize the character states of each character, since whatever state is present in the outgroup will be presumed to be primitive.

A cladistic analysis was performed using PAST to test the efficacy of the technique with ichnological data. The Cambrian occurrence of *A. strictus* (*strictus* P) was chosen as the outgroup because it was one of the Cambrian reports of *Arthrophycus*, although its conformity to *Arthrophycus* is questionable. The first appearance datum (FAD) and last appearance datum (LAD) for each OTU were also included in order to calculate the stratigraphic consistency index (SCI) for the cladograms, using the same midpoint ages as for the size graph in Chapter II (Figure 2.24).

The heuristic algorithm was used for all of the cladograms because there are too many OTUs for the other algorithms (even branch and bound works better for fewer than fifteen OTUs). The tree bisection and reconnection (TBR) rearrangement was used because it can usually find shorter trees than can the other heuristic options (Hammer and Harper 2005). The Fitch optimization, which allows the sequence of characters to be reversible and unordered (all steps have equal length in any direction: 1→2 = 0→2 = 2→1 and so on), involves the fewest assumptions and is therefore preferable (Hammer and Harper 2005).

The first cladistic analysis produced three most parsimonious trees (Figures 4.7 and 4.8). The same cladistic analysis with a different Cambrian ichnospecies, *A. qiongzhusiensis*, as the outgroup, produced nineteen most parsimonious trees (Figure 4.9).

The cladograms revealed a similar but different story from the cluster diagrams, which is due to the different assumptions present in the cladistic techniques, chiefly that of an outgroup, which forces one OTU to be on its own and unconnected with any others; none of the OTUs were isolated in the cluster diagrams.

There were some parallels between the phenetic and cladistic analyses. With the Cambrian *A. strictus* as the outgroup (Figures 4.7 and 4.8), the six verified *Arthrophycus* ichnotaxa remain together, though not in the same order, and the other OTUs group away from them. This provides further support for the idea that this cluster represents a real grouping of ichnospecies that properly belong in *Arthrophycus*. The remaining OTUs have sub-groupings different from either of the cluster diagrams.

The length of the cladogram in Figure 4.7 is 49, which means that 49 steps were necessary to map all the character states. The cladogram's ensemble consistency index (CI) is 0.5417, which means that the levels of homoplasy in its characters are not too high (45.83%, or about half). The ensemble retention index (RI) is 0.6857, which is also a fairly good indicator of lack of homoplasy. The stratigraphic consistency index (SCI) is 0.3889 for the third tree, which implies many gaps and ghost ranges. This last is obvious even when considering only the three Cambrian occurrences: one is the outgroup and the other two are embedded in "crown" sections.

In the other cladistic analysis, *A. qiongzhusiensis* was used as the outgroup, which resulted in nineteen most parsimonious trees with a length of 49 (Figure 4.9 contains Tree #1). These trees have an ensemble CI of 0.5306, and an RI of 0.6761, which are all comparable to those of the first cladogram with *A. strictus* as the outgroup. The SCI is 0.4444, indicating that this cladogram fits the stratigraphic record slightly better than does the one above.

The *Arthrophycus* cluster is still one unit in the middle left of the cladogram, forming a monophyletic group. The other ichnotaxa again have changed their sub-groupings and do not form a monophyletic group. However, it should be noted that as a result of the use of the heuristic algorithm, both of these cladistic analyses can be run many times and yield slightly different results of the same tree length.

Potential Errors

As with the qualitative data, there are a number of possible errors arising from preservation of the trace fossils. The characters were coded based on the available images and descriptions, but if features were present at the time of the trace formation and subsequently eroded, some characters may be coded incorrectly.

Some of the characters are gradational, without clear division between their states. For example, "shape" includes curving, intermediate, and straight. As noted above, the measurement of width involves some overlap of categories and two of the ichnospecies have large reported ranges. In all cases of uncertainty, the codings chosen were those with the greatest potential for minimizing error.

Codings also depend on the accuracy of the translations of foreign-language descriptions. Three of the ichnospecies were originally described in German, but were excluded based on insufficient information. *A. corrugatus* was originally described in French, but a subsequent report was in English. Harlan's original descriptions of *F. alleghaniensis* and *F. brongniartii* were in Latin, but as there are numerous other reports of both ichnospecies, that translation should not be a problem. However, three new ichnospecies were described only in Chinese, and the coding for those ichnospecies (*A. qiongzhusiensis*, *A. tarimensis*, and *A. hunanensis*) rests largely on the translated descriptions because of the poor quality of the figures. Finally, *A. minorcensis* was initially described in French, in an unpublished PhD thesis, so the papers by Orr (1994) and Llompart and Wieczorek (1997) were used to code the character states.

It is entirely possible that some of the specimens assigned to *Arthrophycus* may not be *Arthrophycus* at all. Apart from *A. alleghaniensis* and *A. brongniartii*, originally assigned to *Fucoides* (Harlan 1831 and 1832), *A. corrugatus* and *A. tenuis* were originally assigned to other ichnogenera, and most of the others have been questioned in the previous chapter. One of the reasons in using a phenetic analysis here is to utilize quantitative techniques to sort out misidentifications of this sort. There are also many specimens of *Arthrophycus* identified only to the ichnogenus level. These specimens are not included in the main analysis, but it may be possible to incorporate some of them in future work, in an effort to find which, if any, of the established ichnospecies an unknown specimen most closely resembles.

Numerical Taxonomy Conclusions

The cluster analyses, PCO diagrams, and cladistic analyses converge on a consistent classification of *Arthrophycus* ichnospecies: *A. alleghaniensis*, *A. brongniartii* (= *A. linearis*), *A. lateralis*, *A. minimus*, and *A. parallelus*. The numerical analyses supported the tentative conclusions of the qualitative analysis (Chapter III).

The qualitative analysis had left the placement of a few ichnospecies unresolved: the placement of *A. strictus* and of some ichnospecies considered to be possible junior synonyms of *A. alleghaniensis* (*A. hunanensis*) or *A. brongniartii* (*A. montalto*, *A. elegans*, and *A. simplex*). Based on the cluster diagrams, none of these ichnospecies is actually *Arthrophycus* and none are closely related to one another. These placements could be real, or may be artifacts of the absence of information. The hypothesis that *A. simplex* was mislabeled and is actually *A. brongniartii* may be correct, because the coding differences could have been a result of insufficient illustration or lack of other reports of the ichnospecies.

The clusters of non-*Arthrophycus* OTUs do not represent real taxonomic entities. Although the OTUs within it plotted together in the PCO graphs, the internal relationships did not remain the same throughout the two cluster diagrams or the cladograms. As indicated in Chapter III, other ichnogeneric assignments have been proposed for many of these ichnospecies, so it is likely that they do not represent a single cohesive group. These ichnospecies are simply taxa that have mistakenly been placed in *Arthrophycus* and do not necessarily bear any relationship to one another.

The cluster diagrams, cladograms, and principal coordinates analyses tend to support both one another and the qualitative observations, but there is an important caveat: the coded characters are all based on qualitative observations; even width is broken into three qualitative states. The analyses all support one another, but this may be largely because they were already linked. However, through precise definitions of characters, the quantitative analyses offered a degree of objectivity not available in qualitative descriptions. The difference is that the treatment is rigorously systematic and the subjectivity inherent in qualitative treatments is controlled.

Phenetics should prove to be a useful tool in studies of trace fossil taxonomy. Cluster diagrams provide a more concise visual summary of the data than does a list of features, and PCO compresses many dimensions into a few simple plots. In the case of

Arthrophycus, the cluster diagrams have helped to show that nearly all of the ichnospecies assigned to the ichnogenus were placed there in error. Cladistic analysis proved to be less useful, but may work well for a small sample size that will allow the use of the branch-and-bound algorithm.

An Application of the Method

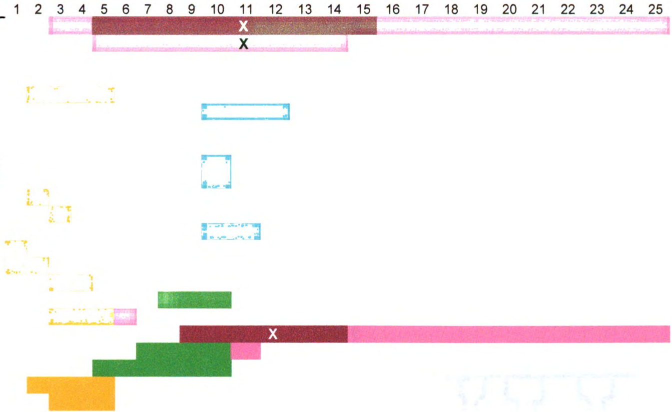
The numerical analyses used herein have potential for evaluating new ichnospecies or specimens that could be *Arthrophycus*. The methods proved useful in two additional trials:

1) The unlabelled specimen from the New York State Museum at Albany, similar in size, shape, and orientation to *A. parallelus*, was added to the cluster analysis as a new OTU. The character states were all identical to those for *A. parallelus*, supporting the hypothesis.

2) The fossil reported by Kern (1978) represents a report whose placement in *Arthrophycus* was uncertain in the qualitative analysis. Therefore, this report was coded as a new OTU and included in separate cluster and principal coordinates analyses. Kern's report plotted well within the non-*Arthrophycus* cluster in both analyses, so this occurrence is rejected as *Arthrophycus*.

Table 4.1: Size range of *Arthrophycus* ichnospecies. Yellow indicates the smallest size, green is intermediate, and blue is the largest size. Blocks in pink indicate an overlap of ranges or, in the case of *A. alleghaniensis*, *A. brongniartii*, and *A. linearis*, a very large range. The maroon color indicates the "more typical" range of widths for that ichnotaxon and the X's mark the approximate midpoints.

Ichnospecies	Width(mm)	
alleghaniensis	2.5-30	
brongniartii	5.0-14.1	
montalto		
siluricus		
elegans	1.6-4.8	
corrugatus	10-12.	
flabelliformis		
krebsi		
minor(i)censis		10
annulatus		10
strictus(K1)	1.5-2	
strictus(K2)	2.5.	
dzulynskii	10-11.	
tenuis	0.5-1.0	
qiongzhusiensis	1-2.	
tarimensis	3-4.	
hunanensis	8-10.	
strictus(P)	3-6.	
linearis	8-27.	
lateralis	7-11.	
simplex	5-10.	
minimus	1.8-4.8	
parallelus	3.5-4.5	



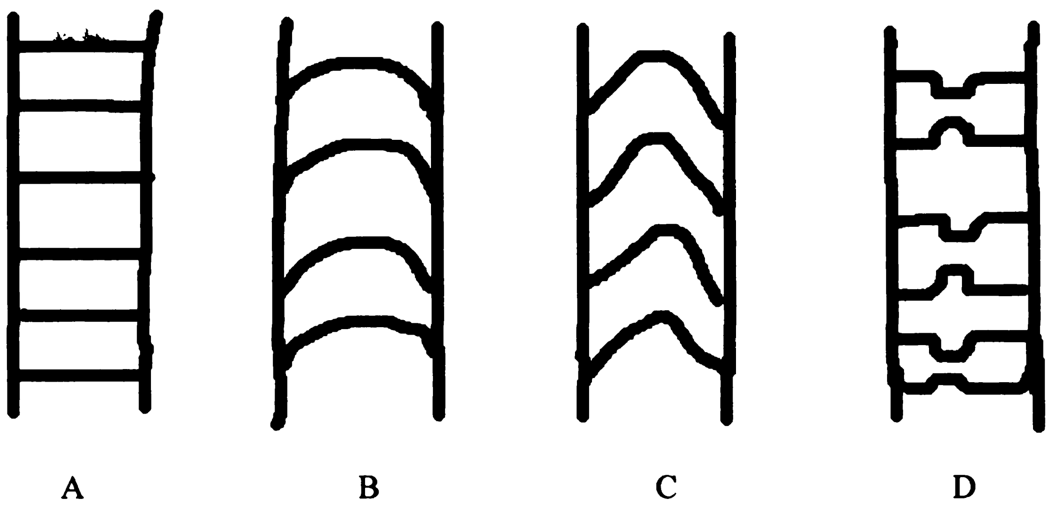


Figure 4.1: Different types of annulations observed in ichnospecies of *Arthrophycus*. A) rings; B) concavo-convex; C) chevrons; D) biconvex.

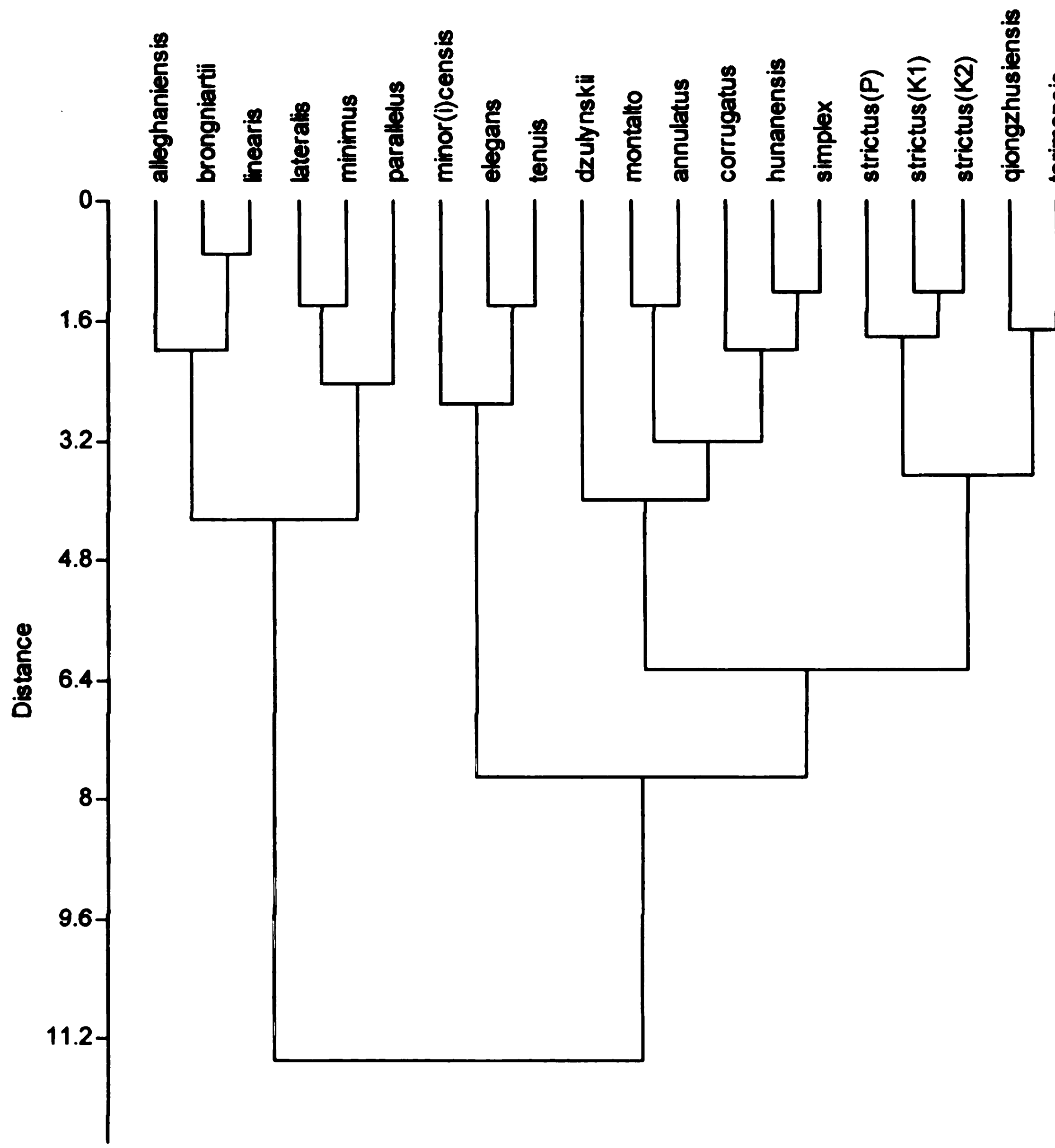


Figure 4.2: Cluster diagram of twenty OTUs of *Arthrophycus*.

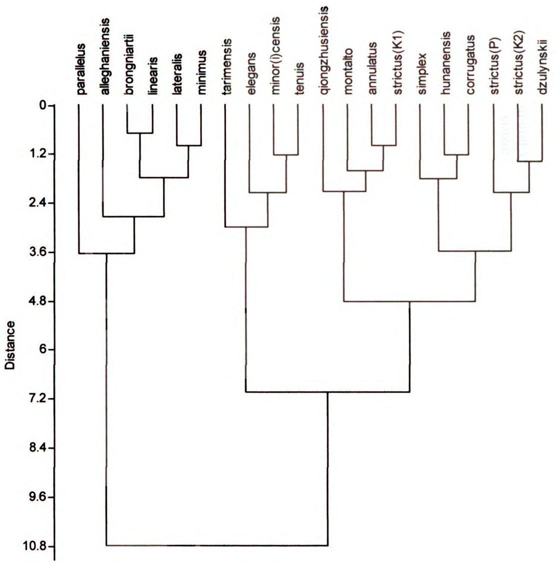
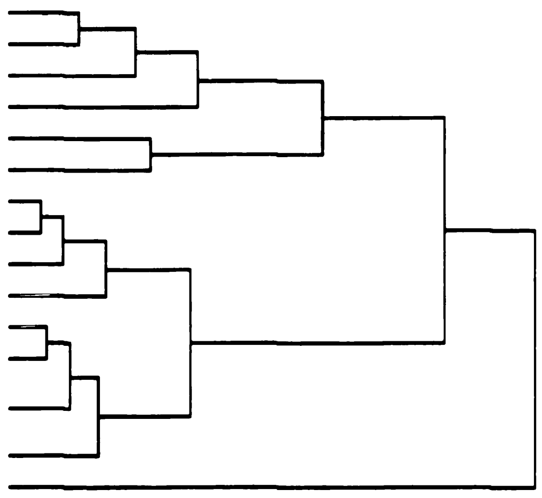


Figure 4.3: Cluster diagram of twenty OTUs of *Arthrophycus*, without the width character.

	al	br	li	la	mi	pa	mr	el	te	dz	mo	an	co	hu	si	sP	sK1	sK2	qi	ta
1	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	2	2
2	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1
3	0	0	0	0	0	0	2	1	2	1	1	1	1	1	0	0	1	1	1	1
4	0	1	1	1	2	2	0	2	1	2	1	2	2	1	1	2	2	2	1	0
5	3	3	3	3	3	2	0	0	0	1	0	1	0	0	0	0	0	0	1	0
6	2	2	2	1	0	0	2	0	0	2	1	2	2	1	1	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
8	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
9	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	1	0	1	0	0
11	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0
16	3	3	3	3	3	3	3	3	3	0	2	1	0	1	1	1	1	1	1	3



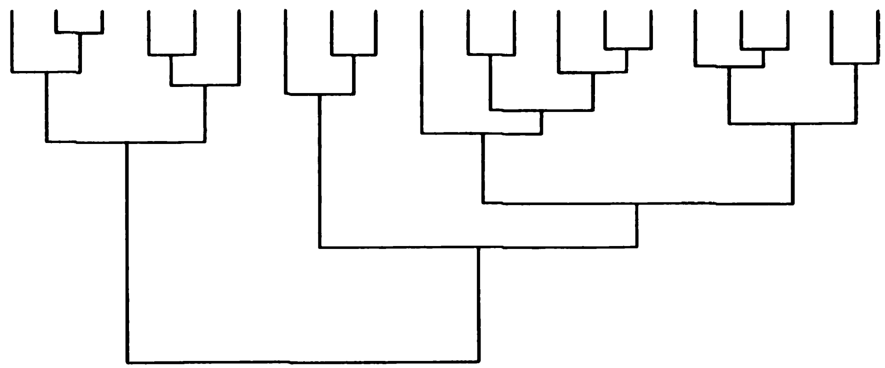


Figure 4.4: Two-way cluster diagram of characters with *Arthrophycus* OTUs. Non-zero numbers in the data matrix indicate which characters are most important for defining clusters of taxa. The vertical line divides the numbers in the matrix into those for the *Arthrophycus* cluster on the left and all others on the right. See key on next page for abbreviations.

Key for Figure 4.4

OTU		Character	
al	*alleghaniensis*	1	Branching
br	*brongniartii*	2	Diameter
li	*linearis*	3	Cross-section
la	*lateralis*	4	Shape
mi	*minimus*	5	Annulations
pa	*parallelus*	6	Width
mr	*minoricensis*	7	Smooth
el	*elegans*	8	Radial
te	*tenuis*	9	Parallel
dz	*dzulynskii*	10	Ends
mo	*montalto*	11	Palmate
an	*annulatus*	12	Wrinkles
co	*corrugatus*	13	Internal
hu	*hunanensis*	14	Plane
si	*simplex*	15	Groove
sP	*strictus*(P)	16	Closeness
sK1	*strictus*(K1)		
sK2	*strictus*(K2)		
qi	*qiongzhusiensis*		
ta	*tarimensis*		

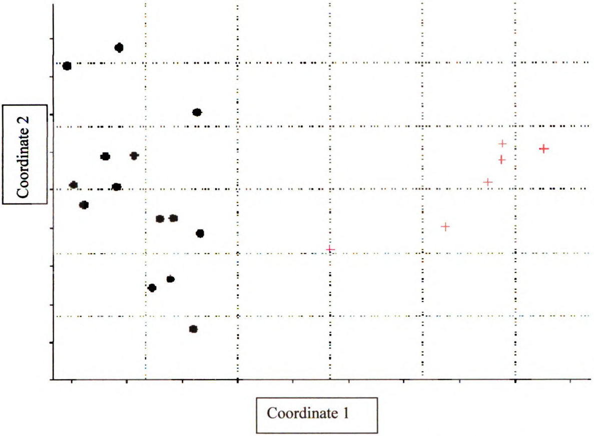


Figure 4.5: PCO graph, coordinates 1 and 2. The cluster of six is represented by the + symbols; all other OTUs are represented by the dots.

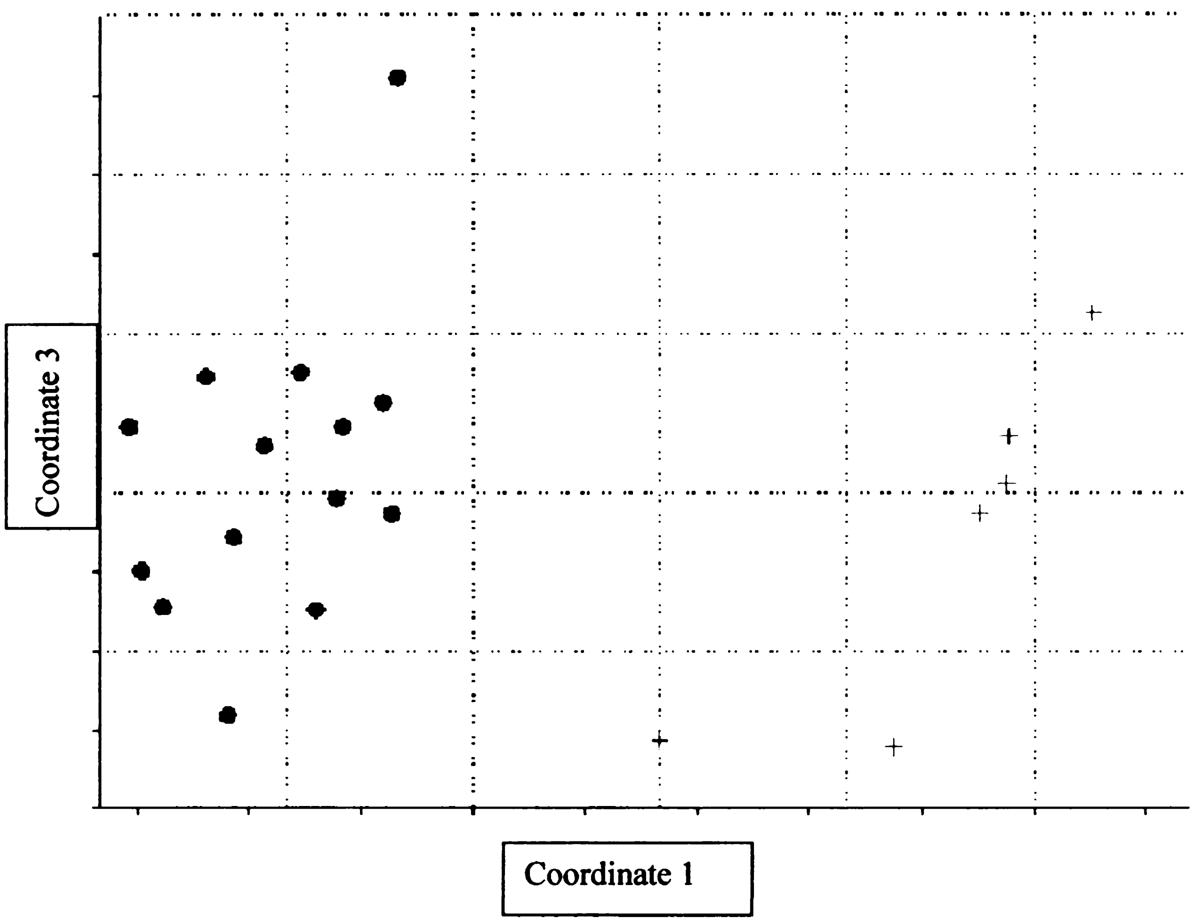


Figure 4.6: PCO graph, coordinates 1 and 3. The cluster of six is represented by the + symbols; all other OTUs are represented by the dots. The dot near the top of the graph represents *A. minoricensis*; this point was not separate from the others in the previous graph.

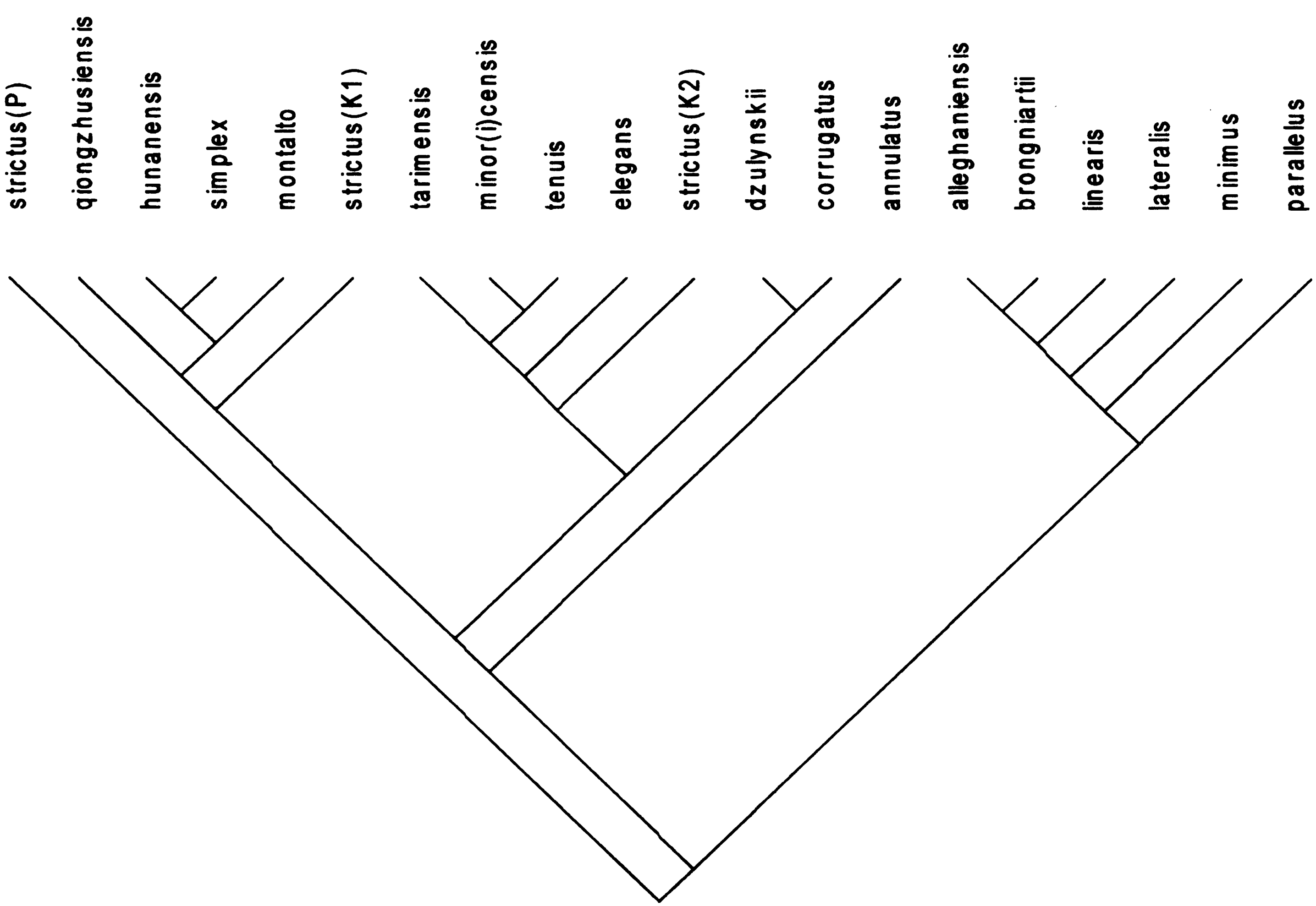


Figure 4.7: Cladogram (third of three most parsimonious trees) of twenty OTUs of *Arthrophycus*, using *A. strictus* (P) as the outgroup.

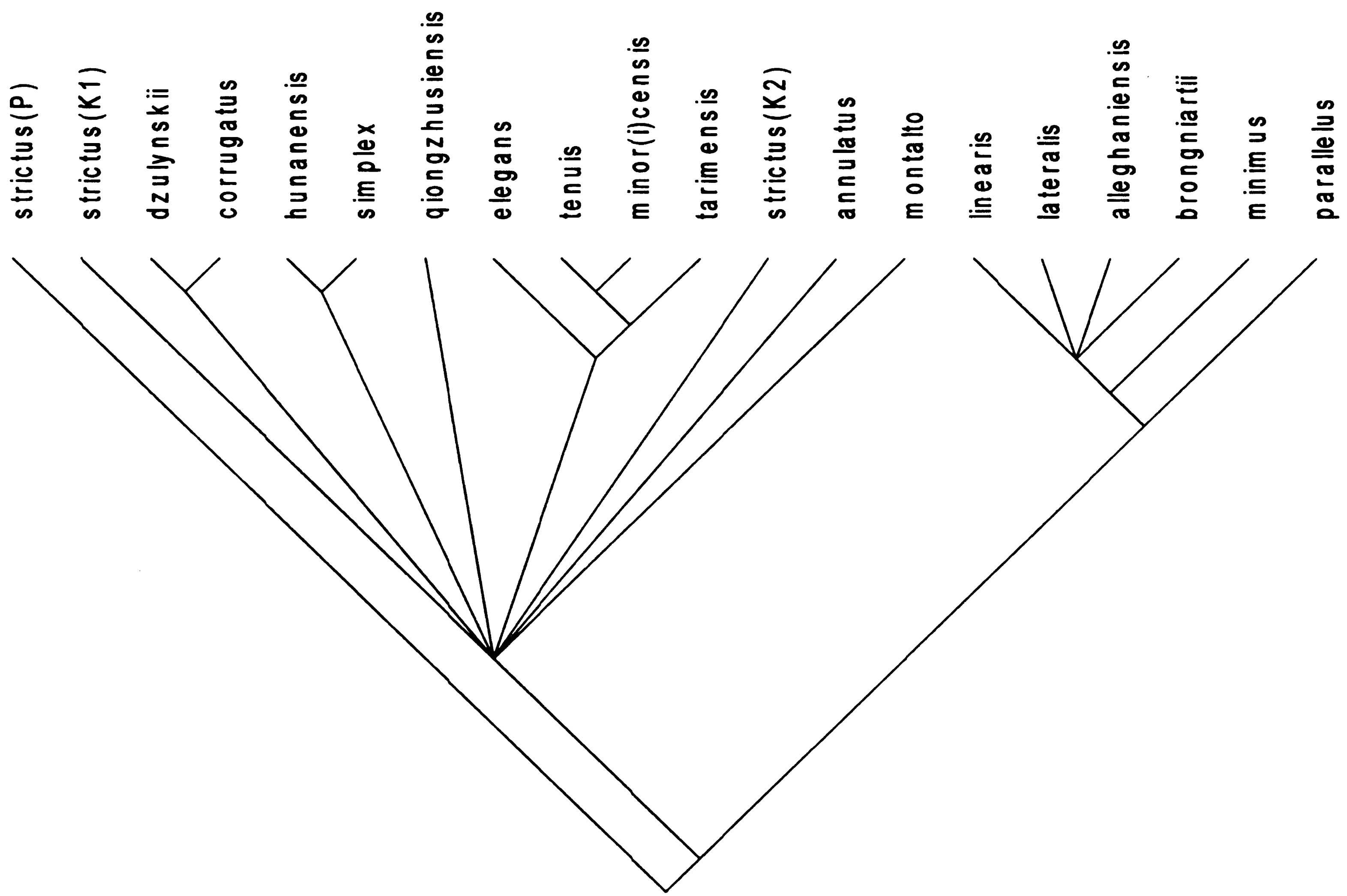


Figure 4.8: Strict consensus cladogram using *A. strictus* (P) as the outgroup.

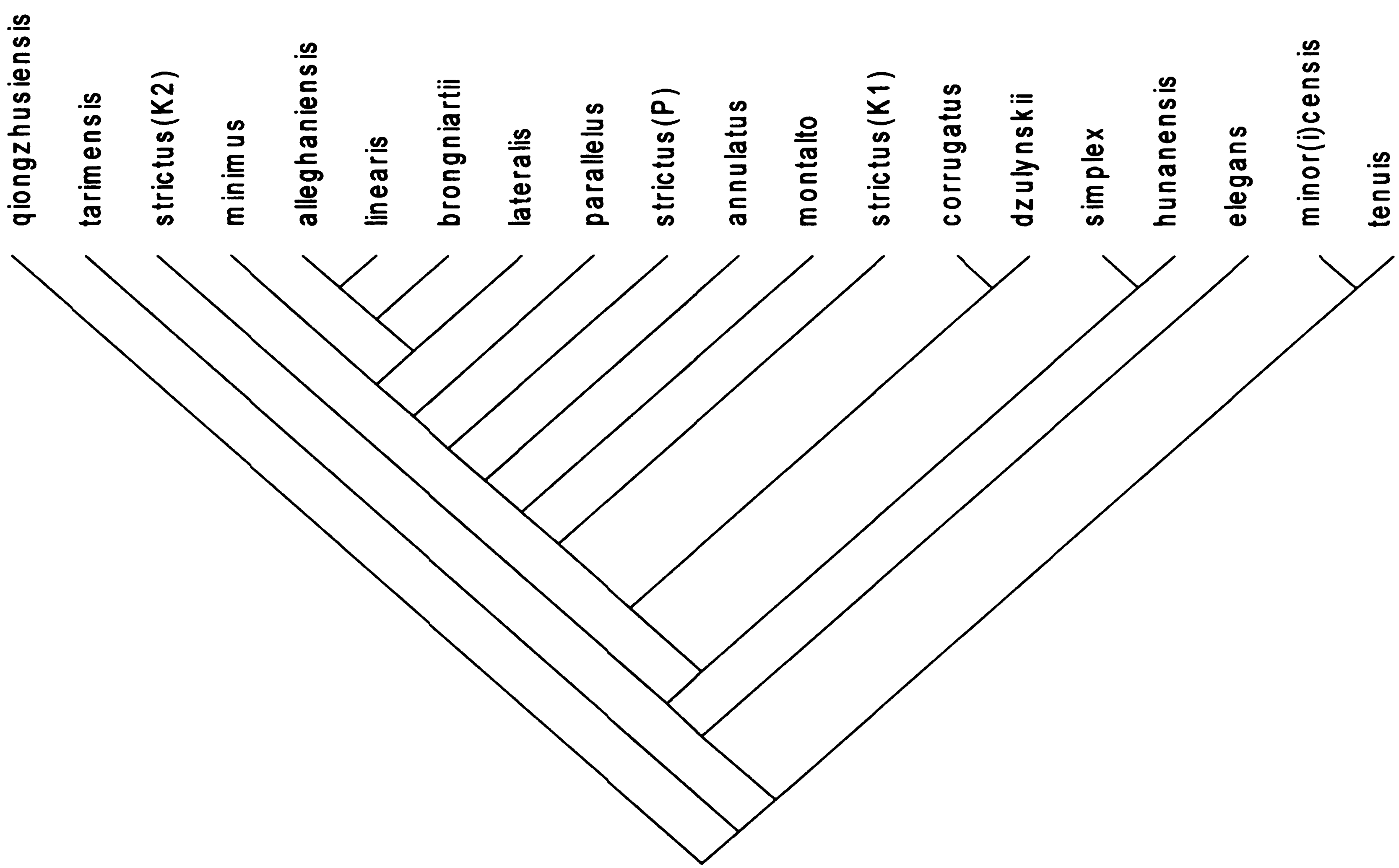


Figure 4.9: Cladogram (first of nineteen most parsimonious trees) of twenty OTUs of *Arthrophycus*, using *A. qiongzhusiensis* as the outgroup.

Chapter V. Systematic Ichnotaxonomy

Ichnogenus *Arthrophycus* Hall, 1852

Generic Synonymy

Arthrophycus Hall, 1852 [*nomen protectum* Rindsberg and Martin 2003]

Fucoides Brongniart, 1822 [*partim*]

Encrinus Andreae 1764 [*partim*]

Crinosoma de Castelnau, 1843 [*nomen oblitum*]

Harlania Göppert, 1852

Synonymy

	1831	*Fucoides alleghaniensis* – Harlan
	1832	*Encrinus giganteus* – Eaton
	1832	*Fucoides brongniartii* – Harlan
non	1834	*Fucoides brongniartii* – Mantell
	1834	*Fucoides alleghaniensis* – Taylor
	1835	*Fucoides alleghaniensis* and *Fucoides brongniartii* – Taylor
?	1837	*Fucoides alleghaniensis* – Conrad
?	1838	*Fucoides alleghaniensis* – Conrad
?	1839	*Fucoides alleghaniensis* – Conrad
	1843	*Crinosoma antiqua* – de Castelnau
	1852	*Harlania halli* – Göppert
	1889	*Arthrophycus harlani* – Lesley
non	1889	*Arthrophycus montalto* – Lesley
non	1890	*Arthrophycus siluricus* n. sp. – Schimper

non	1901	*Arthrophycus elegans* n. isp. – Herzer
non	1908	*Radix corrugatus* and *Radicites rugosa* – Fritsch
?	1916	*Arthrophycus alleghaniense* – Schuchert
	1923	*Arthrophycus alleghaniensis* and *Arthrophycus brongniartii* – Prouty and Swartz
?	1925	*Harlania* – Fritel
	1933	*Arthrophycus* – Moore
	1934	*Harlania* – Dalloni
	1935	*Arthrophycus* – Abel
non	1940	*Arthrophycus flabelliformis* n. isp. – Hundt
non	1941	*Arthrophycus krebsi* n. isp. – Hundt
	1944	*Arthrophycus alleghaniensis* and *Fucoides harlani* – Shimer and Shrock
?	1951	*Arthrophycis* – Silva
	1952	*Arthrophycus* – Becker and Donn
	1955	*Harlania* – Lessertisseur
	1955	*Arthrophycus alleghaniensis* – Young
	1958	*Arthrophycus alleghaniensis* – Fenton and Fenton
?	1960	*Harlania* – Grove
non	1961	*Arthrophycus alleghaniensis* – Wolfart
	1963	*Harlania alleghaniensis* – Bender
?	1963	*Arthrophycus* – Duimovich
?	1963	*Arthrophycus alleghaniensis* and *Arthrophycus harlani* – Moneda
non	1964	?*Arthrophycus* – Correia Perdigao

non	1964	*Arthrophycus* – Pettijohn and Potter
	1966	*Arthrophycus alleghaniensis* – Borrello
	1966	*Harlania* – Gubler *et al.*
non	1966	*Arthrophycus* – Howard
	1968	*Harlania alleghaniensis* – Bender
non	1970	*Arthrophycus* – Frey
non	1970	*Arthrophycus* – Frey and Howard
non	1970	*Arthrophycus* – Książkiewicz
	1970	*Harlania* – Selley
non	1971	*Arthrophycus* – Maberry
non	1972	*Arthrophycus* – Frey
?	1972	*Harlania* – Selley
?	1972	*Arthrophycus* – Terrell
?	1975	*Arthrophycus* – Alpert
non	1975	*Arthrophycus* – Chiplonkar and Ghare
?	1977	*Arthrophycus* – Alpert
	1977	*Arthrophycus alleghaniensis* – Baldwin
non	1977	*Arthrophycus annulatus* n. isp. – Książkiewicz
non	1977	*Arthrophycus strictus* n. isp. – Książkiewicz
non	1977	?*Arthrophycus dzulynskii* n. isp. – Książkiewicz
non	1977	*Sabularia tenuis* n. isp. – Książkiewicz
?	1977	*Arthrophycus* – Roniewicz and Pienkowski
?	1977	*Arthrophycus* – Webby

non	1978	*Arthrophycus* – Kern
non	1978	*Arthrophycus* – Perez and Salazar
?	1978	*Arthrophycus* – Wagner
	1980	*Arthrophycus alleghaniensis* – Downey
	1981	*Arthrophycus alleghaniensis* – Burjack and Popp
?	1981	*Arthrophycus* – Crimes
?	1981	*Arthrophycus* – Laird
?	1981	*Arthrophycus* – Wolfart
non	1982	*Arthrophycus* – Banerjee
	1982	*Arthrophycus* – Pemberton and Risk
	1983	*Arthrophycus* – Cotter
	1983	*Arthrophycus alleghaniensis* – Turner and Benton
non	1984	*Sabularia tenuis* – Alexandrescu and Brustur
non	1984	*Arthrophycus* – Bhargava *et al.*
	1984	*Arthrophycus alleghaniensis* – Liñán
	1984	*Arthrophycus alleghaniensis* – Pickerill *et al.*
	1985	*Arthrophycus* – Durand
	1985	*Arthrophycus* – Eagar *et al.*
non	1985	*Arthrophycus* – Ghare and Kulkarni
non	1985	*Arthrophycus* – Legg
non	1986	*Arthrophycus* – Lin *et al.*
non	1986	*Arthrophycus* – Manca
non	1987	?*Arthrophycus* – Akpan and Nyong

	1987	*Arthrophycus* – Bjerstedt
non	1987	*Arthrophycus* – Mukherjee *et al.*
non	1988	*Arthrophycus* – Bhargava and Bassi
?	1988	*Arthrophycus harlani* – Janvier and Melo
	1988	*Arthrophycus* – Seilacher and Alidou
non	1991	*Arthrophycus* – Pickerill *et al.*
?	1991	*Arthrophycus alleghaniensis* and *Arthrophycus* isp. – Romano
non	1992	*Arthrophycus corrugatus* – Mikuláš
non	1993	*Arthrophycus* A and B – Li
non	1994	*Arthrophycus* – Greb and Chesnut
non	1994	*Arthrophycus qiongzhusiensis* n. isp. – Luo
non	1994	*Arthrophycus minoricensis* – Orr
non	1994	*Arthrophycus tarimensis* n. isp. – Yang
?	1995	*Arthrophycus alleghaniensis* – Fernandes *et al.*
?	1996	*Arthrophycus alleghaniensis* – Borghi *et al.*
	1996	*Arthrophycus alleghaniensis* – Fernandes and Borghi
	1996	*Arthrophycus strictus* – Pacześna
non	1996	*Arthrophycus* – Yang *et al.*
non	1996	*Arthrophycus hunanensis* n. isp. – Zhang and Wang
non	1997	*Arthrophycus minoricensis* – Llompart and Wieczorek
?	1997	*Arthrophycus* – Peeples *et al.*
	1997	*Arthrophycus alleghaniensis, Arthrophycus linearis,* and *Arthrophycus unilateralis* – Seilacher

? 1998 *Arthrophycus* – de Alvarenga *et al.*

1998 *Arthrophycus alleghaniensis* – Metz

? 1998 *Arthrophycus* aff. *alleghaniensis* – Moreira *et al.*

non 1998 *Arthrophycus* – Stanley and Feldman

? 1999 *Arthrophycus alleghaniensis* – Fernandes

1999 *Arthrophycus* – Gong Yiming

? 1999 *Arthrophycus alleghaniensis* – Moreira *et al.*

1999 *Arthrophycus alleghaniensis* – Nogueira *et al.*

1999 *Arthrophycus* – Pflüger

non 1999 *Arthrophycus tenuis* – Uchman

non 1999 *Arthrophycus tenuis* – Uchman and Demircan

2000 *Arthrophycus alleghaniensis* – Fernandes *et al.*

? 2000 *Arthrophycus* – Mergl and Massa

2000 *Arthrophycus alleghaniensis, Arthrophycus linearis,* and *A. lateralis* – Seilacher

? 2001 *Arthrophycus alleghaniensis* – Fernandes

2002 *Arthrophycus alleghaniensis* and *A. lateralis* – Fernandes *et al.*

? 2002 *Arthrophycus* – Lopez and Roy

non 2002 *Arthrophycus simplex* – Seilacher *et al.*

2003 *Arthrophycus alleghaniensis, Arthrophycus linearis,* and *Arthrophycus* isp. – Aceñolaza and Aceñolaza

2003 *Arthrophycus alleghaniensis* and *A. linearis* – Neto de Carvalho *et al.*

2003 *Arthrophycus alleghaniensis* and *Arthrophycus* isp. – Poiré *et al.*

2003 *Arthrophycus brongniartii* – Rindsberg and Martin

2003 *Arthrophycus alleghaniensis* and *Arthrophycus linearis* – Seilacher *et al.*

non 2005 *Arthrophycus* – Dutta and Chaudhuri

? 2005 *Harlania* – Eschard *et al.*

2005 *Arthrophycus minimus* n. isp. – Mángano *et al.*

2005 *Harlania* – Turner *et al.*

2006 *Arthrophycus alleghaniensis* and *Arthrophycus brongniartii* – Kumpulainen *et al.*

? 2006 *Arthrophycus alleghaniensis* – Metz

2007 *Arthrophycus alleghaniensis* – Seilacher

? 2008 *Arthrophycus* – Aceñolaza and Heredia

2009 *Arthrophycus alleghaniensis* – Miller *et al.*

2010 *Arthrophycus parallelus* – Brandt *et al.*

Type Ichnospecies

A. harlani Conrad, 1838, by original monotypy. *F. harlani* Conrad, 1838, which was a junior synonym of *F. brongniartii* Harlan, 1832, as judged by James (1893a) and Rindsberg and Martin (2003), was reassigned as *A. harlani*. Hall (1852) considered both *F. alleghaniensis* and *F. brongniartii* as synonyms of *A. harlani*.

Original Diagnoses

Encrinus giganteus Eaton, 1832: "Branching, red or grey: often compressed, whirls uniform and generally obscure: branches of great length; mostly lying in the direction of the layers, or nearly so."

Crinosoma de Castelnau, 1843: "*Ce corps est tellement different de tous les crinoïdes connus, que, malgré le mauvais état de conservation de l'échantillon, j'ai cru qu'il était nécessaire d'en former un genre distinct.*" (This body is so different from all crinoids known that, despite the poor condition of the sample, I thought it was necessary to form a separate genus.)

Arthrophycus Hall, 1852: "Stems simple or branching, rounded or subangular, flexuous, ascending, transversely marked by ridges or articulations. The species of this genus yet known consists either of simple elongated stems of nearly equal dimensions throughout, or those which divide near the root into several branches and afterwards remain simple."

Harlania Göppert, 1852: (*Frons coriacea simplex cespitose aggregata vel dichotoma, rami in statu iuniori longitudinaliter sulcati; rami adultiores subcylindrici interrupte transversim elevato-striati.*" (Straplike simple turflike aggregate or dichotomous branch, in younger states longitudinally sulcate, branches of adults subcylindrical interrupted transversely by elevated ridges.)

Emended Diagnosis

Dense accumulations of subhorizontal traces with simple smooth-sided form, terminating blindly, annulations typically biconvex, commonly branched and/or bundled into narrow or palmate fans, subquadrate in cross-section, median groove often present, filling chevron-shaped, diameter consistent in individual traces.

Discussion

Chapters II to IV

Included Ichnospecies

A. alleghaniensis (Harlan, 1831)

A. brongniartii Harlan, 1832 (= *A. linearis* Seilacher, 1997)

A. lateralis Seilacher, 2000

A. minimus Mangano *et al.*, 2005

A. parallelus Brandt *et al.*, 2010

Stratigraphic and Geographic Range

Cambrian of Argentina, Spain, and Libya

Ordovician of Argentina, Brazil, Algeria, Libya, Eritrea, Benin, Niger, Jordan, France, Portugal, and Spain

Silurian of Argentina, Brazil, United States, Canada, Chad, Libya, Eritrea, Benin, Niger, Jordan

Devonian of United States, Brazil, Eritrea, and Libya

Carboniferous of United States, China, and England

Chapter VI. *Arthrophycus* in time and space

Biostratigraphy

Dating sedimentary rocks is often difficult to attempt. Lacking radiometric dates, sedimentary rocks must be dated by relative methods, often using fossils that are found within them and correlating with known dates established elsewhere. Index fossils, or those that are relatively short-lived in geologic time, make good tools for this work, and can be used to date formations in which they are found, and many such examples exist, comprising whole books (Shimer and Shrock 1944). As a fossil that might be limited in time to the Ordovician and Silurian (Seilacher 2000), *Arthrophycus* is a possible correlative fossil.

The concept of index fossils is not limited to body fossils; trace fossils have also been used in this manner. Such papers are unusual because most trace fossil have very long geologic time ranges, but trace fossils are potentially useful for the many strata that do not preserve body fossils (Seilacher 1970). Crimes (1968) studied two ichnospecies of *Cruziana* (*C. semiplicata* and *C. furcifera*) in Wales and used them as index fossils to date two formations as upper Cambrian and lower Ordovician, respectively. Seilacher (1970) used many more ichnospecies of *Cruziana* to establish a global ichnostratigraphy. More recently, Aceñolaza and Heredia (2008) used *Cruziana* to date two Ordovician formations in Argentina.

A number of researchers have viewed *Arthrophycus* as limited in time. Conrad (1839) was the first of these, and several others (e.g. Moore 1933, Shimer and Shrock 1944) described *Arthrophycus* as an index fossil to the Ordovician and Silurian. Young (1955) wrote that *Arthrophycus* was easy to recognize, a necessary attribute of a good index fossil, but that it was not as stratigraphically restricted as previous authors thought.

Silva (1951) dated a formation as Silurian rather than Carboniferous, based largely on the presence of *Arthrophycus*. Fernandes and Borghi (1996) considered their formation to be Silurian based on the presence of *A. alleghaniensis*. Seilacher *et al.* (2003) used *Cruziana*, *A. alleghaniensis*, and *Gyrochorte* to correlate sandstones in Argentina and North Africa, concluding that the Argentinean formations were younger than first supposed (Ordovician-Silurian rather than Cambrian-Ordovician). Most recently, Kumpulainen *et al.* (2006) noted a number of trace fossil genera in their formation in Eritrea and dated it as Late Ordovician, based mainly on the presence of *A. alleghaniensis* and *A. brongniartii*.

There are problems with using *Arthrophycus* in ichnostratigraphy. Kumpulainen *et al.* (2006) provided a table of *A. alleghaniensis* occurrences that were Cambrian to Devonian in age, but then used the ichnospecies as evidence of a Late Ordovician (or Early Silurian) age. If the authors used other data to aid them in their decision, they did not make such evidence clear. Fernandes and Borghi (1996) wrote that *A. alleghaniensis* was not exclusive to the Silurian and should therefore be excluded as an indicator of Silurian age, but then proceeded to date their formation as Silurian based on that evidence. Crimes (1981) considered even an Ordovician-Silurian range to be too wide for use in ichnostratigraphy, and Dalloni (1934) wrote that *Arthrophycus* had a geographic range that was too wide for meaningful stratigraphic correlation.

Many researchers (e.g. Turner and Benton 1983, Fernandes 2001) suggest a Cambrian-Devonian age for *Arthrophycus*. Still, Seilacher (2000, 2007a) and other authors (e.g. Mángano *et al.* 2005a, Kumpulainen *et al.* 2006) hold to the idea that *Arthrophycus* has a restricted geologic range and is therefore useful for ichnostratigraphy. Some authors reject any report outside of the Ordovician-Silurian range as *Arthrophycus*, even though most ichnologists reject geologic time as an ichnotaxobase (Bertling *et al.* 2006, Bertling 2007). Ideally, reports of *Arthrophycus* would be verified solely on morphologic characters, independent of stratigraphic or geographic occurrence.

Table 6.1 is an indication of the reported geologic range for each ichnospecies of *Arthrophycus*, with the number of reports that place the ichnospecies into each time period. These data were used to construct a number of histograms in order to assess the utility of *Arthrophycus* as an index fossil.

Figure 6.1 is a histogram of all reports of *Arthrophycus* ichnospecies (or "*Arthrophycus* isp.") reports through time. In order to make this figure and all of the following histograms for geologic time, the reports of *Arthrophycus* were dated as their authors reported, without judgment as to the accuracy of the dating by those authors. Reports that included more than one time period were counted for both periods (e.g. "Ordovician-Silurian" is counted twice, once for each period, "Ordovician-Devonian" is counted thrice) and the x-axis is non-numerical. Any reports that only discussed previous occurrences of *Arthrophycus* (e.g. Moore 1933, Fernandes 2001) or that were additional reports on the same occurrence (e.g. Frey 1972) were not included in this census in order to reduce noise. In a few cases, a complicated report was divided into a number of occurrences to minimize compressing too much information into a single data point (e.g. Lesley 1889, Książkiewicz 1977).

Figure 6.2 provides the results of the geologic range analysis, in which the reports of *Arthrophycus* are divided into the categories of "true" *Arthrophycus*, unverifiable reports, and non-*Arthrophycus* reports based on the earlier taxonomic assessments. Figure 6.1 shows *Arthrophycus* appearing scattered throughout the Paleozoic, with a peak toward the Ordovician-Silurian and only 19 occurrences in the Mesozoic and Cenozoic. However, in Figure 6.2, it becomes evident that this apparent range is distorted by the inclusion of questionable assignments to *Arthrophycus*. Figure 6.2 shows that *Arthrophycus* occurrences peak in the Silurian, with more confirmed occurrences than any other time period even has reports. The Ordovician ranks second, with other Paleozoic periods making small additional contributions. This "corrected" distribution is even more apparent if only confirmed reports are shown (Figure 6.3) or both confirmed and unverifiable reports together (Figure 6.4).

These histograms (Figures 6.1 to 6.4) are for the whole ichnogenus, including all reported ichnospecies of *Arthrophycus*. Because most of those ichnospecies have been eliminated from *Arthrophycus*, it is possible that those invalid ichnospecies were distorting the apparent stratigraphic range of the ichnogenus. To analyze this question, a smaller data set, composed of reports of only those ichnospecies herein considered valid ichnospecies of *Arthrophycus* was compiled (Figure 6.5). This reduced data set did not produce markedly different results, as eliminating invalid ichnospecies removed only 15 reports from the dataset.

To evaluate the effect that reports of "*Arthrophycus* isp." may have had on the distortion of the stratigraphic range of the *Arthrophycus* ichnogenus, a new histogram with only reports of valid ichnospecies with definite ichnospecific assignments (also including those few reports assigned previously herein to either *A. alleghaniensis* or *A. brongniartii*, such as Durand 1985 and Pflüger 1999) was constructed (Figure 6.6). This action reduced the total number of *Arthrophycus* records by 38 and resulted in a different distribution (Figure 6.6). Only three non-*Arthrophycus* results remained and the histogram shows a very high peak in the Silurian, overshadowing its nearest competitor, the Ordovician. As with Figure 6.2, the number of confirmed reports in the Silurian is greater than that for the total of any other period, but in this histogram that difference is much more apparent. The dominance of valid *Arthrophycus* reports from the Silurian, and to a lesser extent, the Ordovician, is real.

However, this dominance of Silurian (and Ordovician) reports might have been a bibliographic artifact of the dominance of the Medina and Tuscarora Sandstones in the *Arthrophycus* literature: perhaps a plethora of reports from those formations overwhelmed single reports from other Paleozoic formations. Figure 6.7 is a histogram of the occurrence of valid *Arthrophycus* through time in which each different *Arthrophycus*-bearing formation is counted once. This graph shows that even after removing the bibliographic effect of multiple reports from a single formation, most *Arthrophycus* reports still come from Silurian strata.

There are confirmed occurrences of *Arthrophycus* in the Paleozoic outside of the Ordovician-Silurian window, in both the unreduced and reduced time analyses (Figures 6.1 to 6.6). However, these reports are not as straightforward as they may appear. In the unreduced analysis (Figure 6.2), there are four confirmed or unverifiable Cambrian reports, four confirmed or unverifiable Cambrian-Ordovician reports, and one confirmed Cambrian-Devonian report. In most of these multiple-period reports, there is no way to determine whether the *Arthrophycus* fossils actually occur in both time periods: they may be from the top of the formation, and thus Early Ordovician, or from the bottom of the formation and thus Late Cambrian. Of the remaining four confirmed or unverifiable reports that are Cambrian only, one is unverifiable (and was questioned by Mángano *et al.* 2005a) and the other three are likely *A. minimus*.

The Devonian presents a similar case of unclear dating. Three of the reports of *Arthrophycus* from Brazil are listed as Ordovician to Devonian (possibly only to Early Devonian). Four other reports give a range of Silurian-Devonian, but three of these are unverifiable. Turner and Benton (1983) had rather vague dating, reporting their fossils from the Cambrian to the Devonian. Mángano *et al.* (2005a) considered this dating to be suspicious and unconfirmed, but the Devonian portion of the range is accepted herein. The only other reports of Devonian *Arthrophycus* are that of Wolfart (1961), assessed here as questionable, and Bjerstedt (1987), which is hesitantly judged conformable to *Arthrophycus* after examining the actual specimen.

Only a few post-Devonian reports of *Arthrophycus* identify the fossils to the ichnospecies level. Of those, only the reports of Brandt *et al.* (2010) and Herzer (1901), both from the Pennsylvanian, may be conformable to *Arthrophycus*. Abel (1935) also reported a specimen of *A. alleghaniensis* from the Oligocene, but this occurrence was questionable. No other reports of *Arthrophycus* from post-Paleozoic rocks were judged herein as acceptable.

The specific behavior represented by *Arthrophycus* may have continued into the Devonian and beyond, but its grip was tenuous, judging by the low number of reports. Five of the nine Cambrian occurrences may not actually be Cambrian, so the Ordovician and Silurian remain as the peak time periods for *Arthrophycus*. *A. minimus* is the only Cambrian ichnospecies accepted herein, and *A. parallelus* the only valid Carboniferous ichnospecies. However, even when considering only *A. alleghaniensis*, an Ordovician-Silurian time range is still rather broad to use for stratigraphic purposes. It is suggested that *Arthrophycus* only be used as supplementary evidence, along with a more reliable indicator such as ichnospecies of *Cruziana*. *A. lateralis* still has ichnostratigraphic potential, as it is known only from the Silurian, but this ichnospecies was named only ten years ago (Seilacher 2000). *A. lateralis* may yet be found in a wider range of geologic time, and given its rather large geographic range, it should not be used in biostratigraphy.

Biogeography

Arthrophycus has been reported on all continents and twenty-seven countries, including sixteen U. S. states, but not all of these reports are judged herein as valid. Figure 6.8 is a histogram showing the geographic distribution of *Arthrophycus*, using the same methods employed to make the stratigraphic histograms. For the sake of simplicity, the regions are reduced to the seven continents, with an additional category for the countries in the Middle East (Jordan and Turkey).

As Figure 6.8 shows, *Arthrophycus* appears to be scattered evenly across the world, with many occurrences in South America, Asia, Africa, and Europe, and only a slightly higher peak for North America. However, in a histogram showing reports divided into the three taxonomic categories of conformable to *Arthrophycus*, unverifiable, and not conformable to *Arthrophycus* (Figure 6.9), North and South America emerge as the prominent regions of confirmed *Arthrophycus* finds, followed by Africa. In a histogram limited to confirmed records (Figure 6.10), North America has the highest peak, as might be expected given that the first records of *Arthrophycus* came from that continent.

Even with the questionable records of *Arthrophycus* removed from the dataset, the ichnogenus still shows a wide geographical distribution. There are confirmed reports from five continents plus the Middle East, including seventeen countries and eight U. S. states. If unverifiable reports are also accepted, two continents, two more countries, and five states are added to the count.

There are some notable gaps in the reported geographic range of *Arthrophycus*. There are many good records from Africa, comprising six countries (plus a seventh indeterminate record), but all of them are from North Africa; no records of *Arthrophycus*, valid or invalid, have come from sub-Saharan Africa.

There is also only one valid report of *Arthrophycus* from Asia (China); the other twelve are judged questionable. Seven of the Asian reports were from China (and three of those proposed new ichnospecies of *Arthrophycus*) while the other six Asian reports were from India. Russia is also missing from the survey, but one author did provide a tantalizing mention of the country. Dalloni (1934) mentioned *Arthrophycus* (as *Harlania*) in a list of places that the ichnogenus had been found in Silurian rocks, but he did not include a reference for that observation, preventing further investigation.

Paleobiogeography

Kumpulainen *et al.* (2006) suggested that *A. alleghaniensis* originated in the seas surrounding the southern continents in the Ordovician Period and then moved north in the Silurian. Figure 6.11 is a plot of *Arthrophycus* distribution in time and space. As in the stratigraphic histograms (Figures 6.1 to 6.10), the repetitive reports or discussion papers were not included, and the reports were categorized as conformable to *Arthrophycus*, unverifiable, and not conformable to *Arthrophycus*. The geographical regions are again the seven continents and the Middle East, and each time period was assigned a numerical code for the y-axis (Table 6.2) rather than using actual ages, because using the numerical ages produced a graph with points much too crowded to be useful. Circle size at each point in Figures 6.11 to 6.13 represents the number of reports at that particular space and time.

Figure 6.11 shows a scatter of *Arthrophycus* reports across time and space. The confirmed records cluster in the Paleozoic and in Africa, South America, and North America, as shown in the histograms. However, there is no concentration of early records in the southern regions: the earliest confirmed records are in South America, but Europe has four Cambrian and Ordovician reports, the Middle East has at least one in the Ordovician, and North America has two early occurrences that are indeterminate.

I then investigated the question of individual ichnospecies of *Arthrophycus* being limited to the southern regions in the Ordovician, with the northern specimens in the Silurian being from different ichnospecies. Figure 6.12 shows the time and space data as in Figure 6.11, but divided into ichnospecies. For this graph, all questionable ichnospecies and records were removed, as well as any "*Arthrophycus* isp." reports.

Reports of *Harlania* are included under *A. alleghaniensis*, but *A. linearis* and *A. brongniartii* were kept separate for clarity. In cases for which there were more than one ichnospecies in the same time and place (e.g. the Silurian of Africa and the Ordovician-Silurian of South America), the circles were offset slightly so that all ichnospecies became visible.

Figure 6.12 shows evidence of early southern occurrences. The only Cambrian occurrences are *A. minimus* and *A. alleghaniensis*, both in South America. *Arthrophycus* is reported from "Cambrian-Ordovician" of Europe and Ordovician strata of Europe and the Middle East. *A. alleghaniensis* and *A. brongniartii* (and *A. linearis*) are widely distributed over time and space and thus are less-sensitive indicators of expansion. Only *A. lateralis* is currently restricted to the Silurian of the southern continents.

Figure 6.13 is a bubble chart with the confirmed and unverifiable "*Arthrophycus* isp." reports included. There are only four confirmed reports of *Arthrophycus* isp., all Silurian or later, but the unverifiable points are scattered over time and space.

Most of the reports from the Ordovician and earlier are from the southern regions and were on the fringes of the glaciers flowing over Africa; at that time the southern continents were centered on the south pole, located in western Africa (Figures 6.14 to 6.16). The *Arthrophycus* trace-maker, therefore, may have been a cold-loving organism.

Facies Control of *Arthrophycus* Distribution

Arthrophycus is typically found on the underside of beds, preserved as convex hyporelief. This is interpreted as infill material that preserved a relic of the original trace, which was made in the beds below and subsequently eroded (Seilacher 1964b, Martinsson 1970). Most *Arthrophycus* specimens are found preserved in sandstone, or occasionally shale (e.g. Bjerstedt 1987); approximately 73% of the reported occurrences reviewed herein are in sandstone, with 10% of the reports not recording lithology (see Appendix I). None of the specimens conformable to *Arthrophycus* come from carbonate rocks; all are from siliciclastic materials.

In the ethological classification introduced by Seilacher (1953), *Arthrophycus* is usually placed in fodinichnia, or feeding traces (e.g. Borghi *et al.* 1996). As the schemes have some overlap, it is also possible to consider *Arthrophycus* to be one of the repichnia, or crawling traces.

Seilacher's (1964a) introduction of the ichnofacies scheme for trace fossils also applies to *Arthrophycus*. Most authors (e.g. Fernandes *et al.* 1995) place *Arthrophycus* in the *Cruziana* ichnofacies, which means that *Arthrophycus* formed in the relatively shallow water of the shelf environment, with medium energy, and typically in sand or silt (Bromley 1990). This area was between the daily and storm wavebases and the fossils found there are typically diverse in both the number of ichnospecies and in the number of ethological categories, but little deep burrowing is present (Bromley 1990).

Judging by the previous reports of *Arthrophycus*, it is likely that the best place to search for *Arthrophycus* is in Paleozoic sandstones from nearshore environments, in the *Cruziana* ichnofacies. Strikingly, *Arthrophycus* is a very facies-dependent fossil, so clastic sequences are crucial. Nearly all of the papers that report valid *Arthrophycus* agree on a nearshore environment, with two minor exceptions. The first is a personal communication from Alidou to Dutta and Chaudhuri (2005), in which Alidou intimated that he knew of a continental *Arthrophycus* from West Africa. In the second, Nogueira *et al.* (1999) reported that Cotter (1983) had interpreted the Tuscarora Formation, which contains abundant *Arthrophycus*, as being from a braided river environment. However, the actual paper by Cotter (1983) reported braided rivers in parts of the Tuscarora, with the typical nearshore environment for the portions of the formation that contained *Arthrophycus*.

The affinity for clastic facies may help explain the northward expansion of *Arthrophycus* from Gondwana to the northern continents as described above. In the Early Silurian, the Iapetus Ocean began to close as continents moved closer together; this may have allowed the maker of *Arthrophycus* to expand its range to the northern continents. As *Arthrophycus* seems to have been a trace fossil of largely deltaic and other shallow-water environments (e.g. Cotter 1983), the trace-maker may not have been able to cross the deeper oceanic waters of the Iapetus until this ocean became narrower and presumably shallower.

Table 6.1: Occurrences of *Arthrophycus* through time by ichnospecies. Number of reports may not equal the total of the row because all periods are counted if a single report spans more than one period (e.g. Ordovician-Silurian). The "Other" column contains reports of uncertain age.

Ichnospecies	Date	First Author	Range	Camb	Ordo	Sil	Dev	Carb	Perm	Tri	Jur	Cret	PreQ	Other	# Reports
alleghaniensis	1831	Harlan	Camb-Dev	6	19	35	8								53
brongniartii	1832	Harlan	Ordo-Dev		1	5	1								6
montalto	1888	Simpson	Camb	1											1
siluricus	1879/1890	Schimper	Sil	1											1
elegans	1901	Herzer	Penn					1							1
corrugatus	1908	Fritsch	Ordo (+Sil?)		1	1									2
flabelliformis	1940	Hundt	Ordo		1										1
krebsi	1941	Hundt	Ordo		1										1
minor(i)censis	1973	Bourrouilh	Carb					2						1	3
annulatus	1977	Książkiewicz	Cret-Eo									1	1		1
strictus	1977	Książkiewicz	Camb-Cret	1								1			2
dzulynskii	1977	Książkiewicz	Oligo										1		1
tenuis	1977	Książkiewicz	Cret-Mio									1	1	2	4
qiongzhusiensis	1994	Luo	Camb	1											1
tarimensis	1994	Yang	Ordo		1										1
hunanensis	1996	Zhang	Sil			1									1
linearis	1997	Seilacher	Camb-Sil	1	5	3								1	7
unilateralis	1997	Seilacher	Sil?			1									1
lateralis	2000	Seilacher	Ordo-Dev		2	2	1								2
simplex	2002	Seilacher	Ordo-Sil		2	1									2
minimus	2005	Mangano	Camb	2											2
parallelus	2010	Brandt	Penn					1							1

Table 6.2: Coding for geologic periods and regions used in the bubble charts.

Time Code	Time	Place Code	Place
1	Proterozoic	1	Africa
2	Cambrian	2	Antarctica
3	Cambrian-Ordovician	3	Australia
4	Ordovician	4	S. America
5	Ordovician-Silurian	5	Asia
6	Silurian	6	Europe
7	Silurian-Devonian	7	Mid East
8	Devonian	8	N. America
9	Carboniferous		
10	Permian		
11	Triassic		
12	Jurassic		
13	Cretaceous		
14	Cretaceous-PreQuaternary		
15	PreQuaternary		

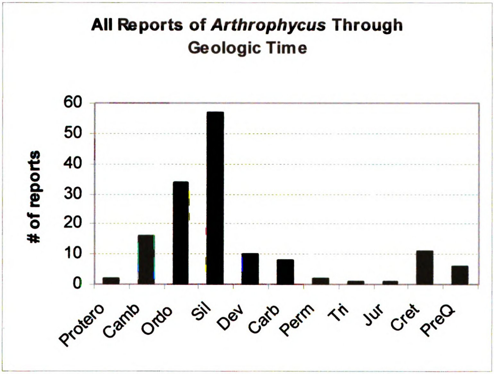


Figure 6.1: Histogram of reported occurrences of *Arthrophycus* through time.

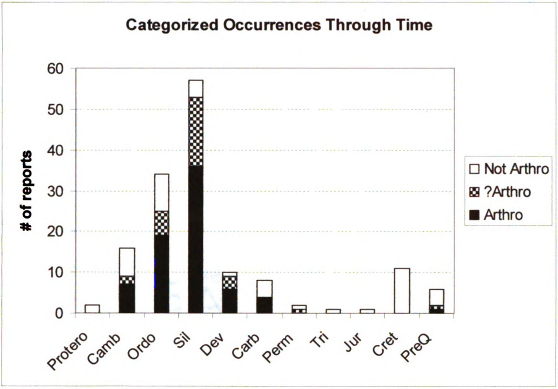


Figure 6.2: Histogram of occurrences of all *Arthrophycus* reports through time, divided into the three taxonomic assessment categories.

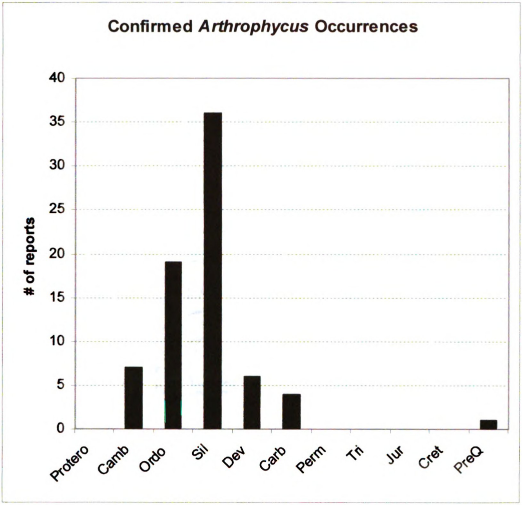


Figure 6.3: Histogram of occurrences of *Arthrophycus* reports through time, confirmed reports only.

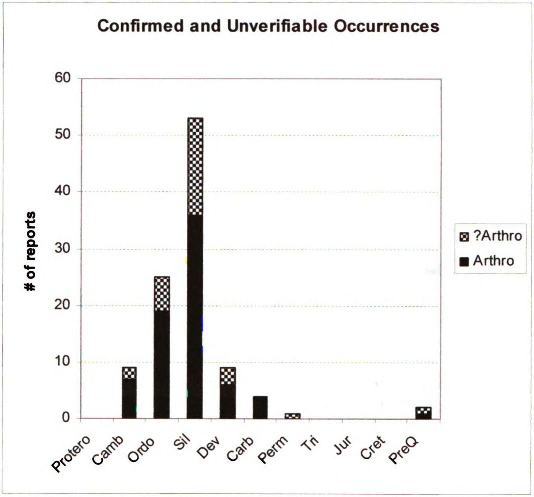


Figure 6.4: Histogram of occurrences of *Arthrophycus* reports in time, confirmed and unverifiable reports only.

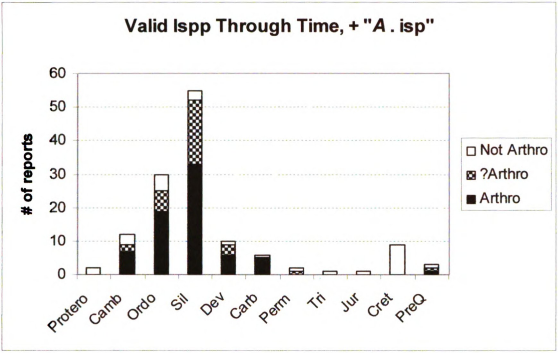


Figure 6.5: Histogram of occurrences of valid ichnospecies of *Arthrophycus* through time, including "*Arthrophycus* isp.," broken into the three taxonomic assessment categories.

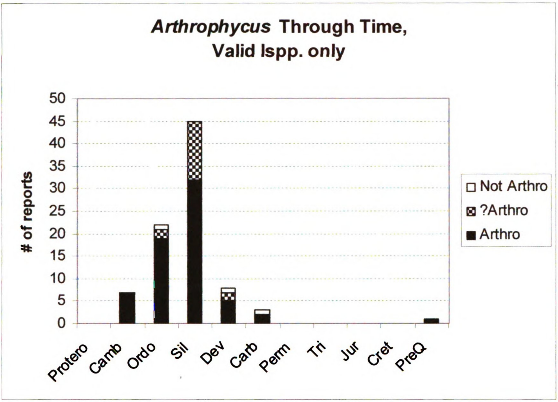


Figure 6.6: Histogram of occurrences of valid ichnospecies of *Arthrophycus* through time, not including "*Arthrophycus* isp.," broken into the three assessment groups.

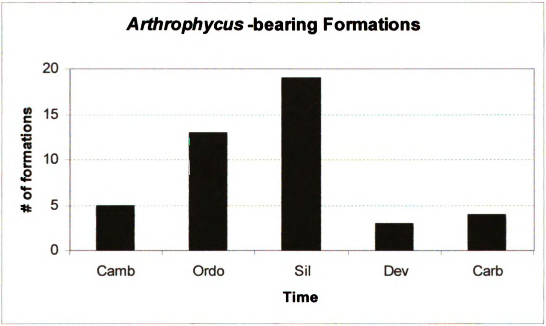


Figure 6.7: Histogram of valid *Arthrophycus*-bearing formations throughout geologic time.

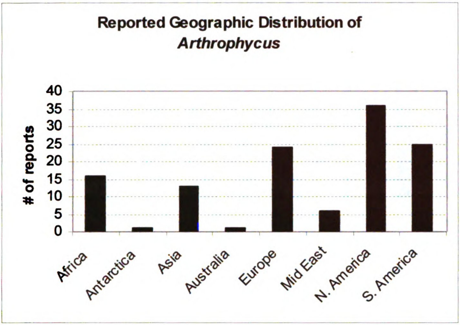


Figure 6.8: Histogram of all *Arthrophycus* occurrences, by geographic region.

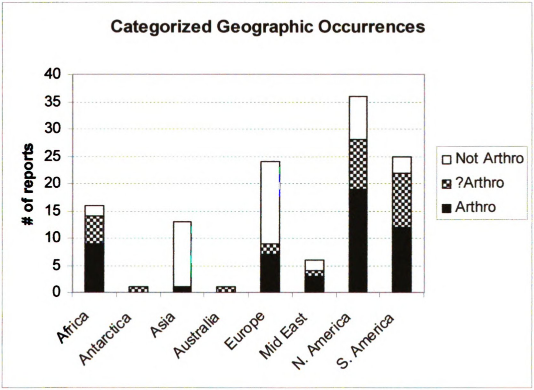


Figure 6.9: Histogram of all *Arthrophycus* occurrences, by geographic region, divided into the three taxonomic assessment categories.

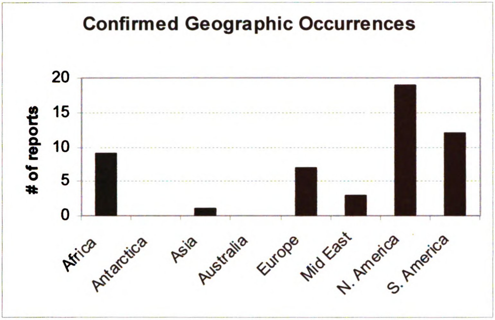


Figure 6.10: Histogram of regions reported for all *Arthrophycus* occurrences, confirmed occurrences only.

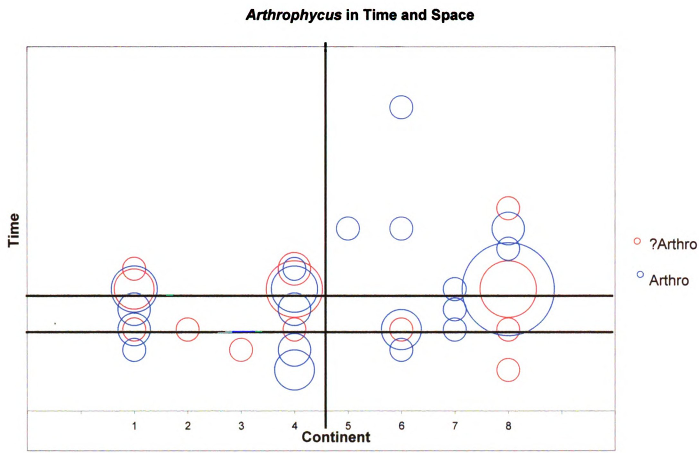


Figure 6.11: Bubble chart of *Arthrophycus* reports over time and space and divided into categories of accepted and present. The vertical line divides the southern and northern regions, the lower horizontal line marks the middle of the Ordovician, and the upper horizontal line marks the middle of the Silurian. The central point of each circle marks the time period in which it belongs and the size of the circle indicates the number of reports at that point in time and space. See Table 6.2 for key to regional identification.

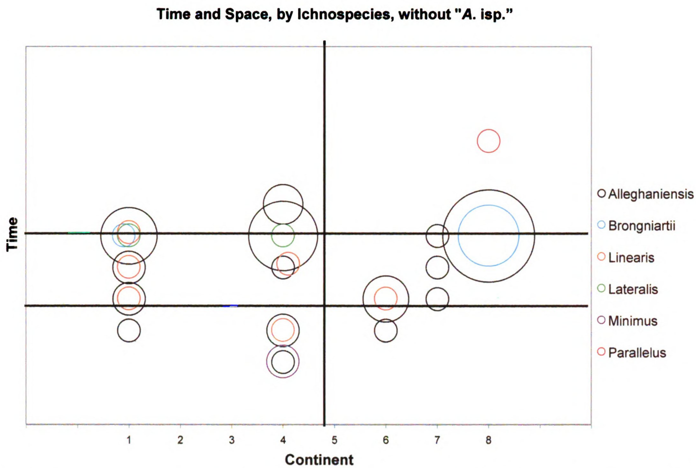


Figure 6.12: Bubble chart of accepted *Arthrophycus* reports over time and space and by ichnospecies. The vertical line divides the southern and northern regions, the lower horizontal line marks the middle of the Ordovician, and the upper horizontal line marks the middle of the Silurian. The central point of each circle marks the time period in which it belongs and the size of the circle indicates the number of reports at that point in time and space. See Table 6.2 for key to regional identification.

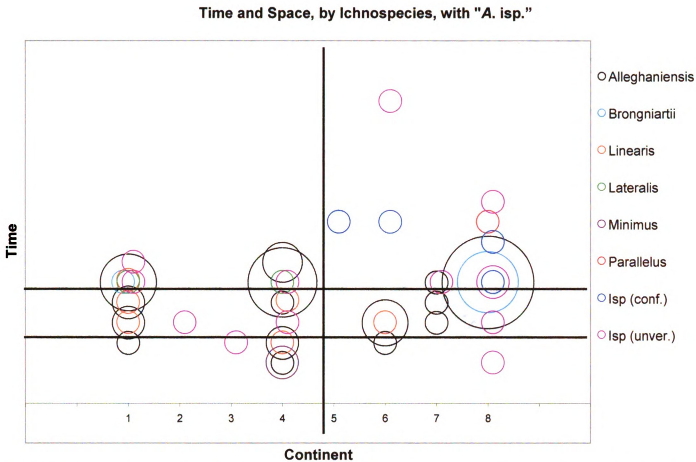


Figure 6.13: Bubble chart of accepted *Arthrophycus* over time and space, by ichnospecies and including "*Arthrophycus* isp." reports. The vertical line divides the southern and northern regions, the lower horizontal line marks the middle of the Ordovician, and the upper horizontal line marks the middle of the Silurian. The central point of each circle marks the time period in which it belongs and the size of the circle indicates the number of reports at that point in time and space. See Table 6.2 for key to regional identification.

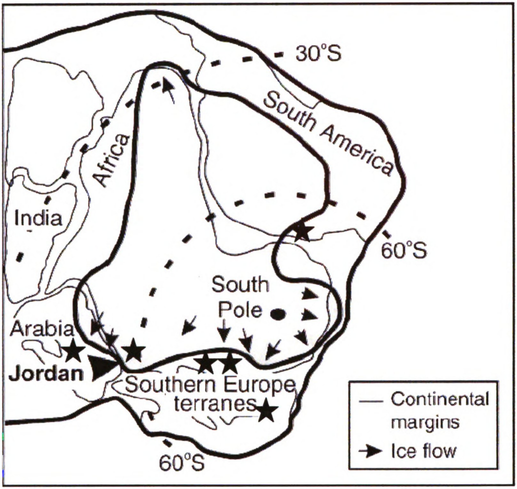


Figure 6.14: Paleogeographic map of the southern continental positions during the Late Ordovician. Ice sheet is shaded and stars represent approximate locations of *Arthrophycus* specimens. From Turner *et al.* (2005).

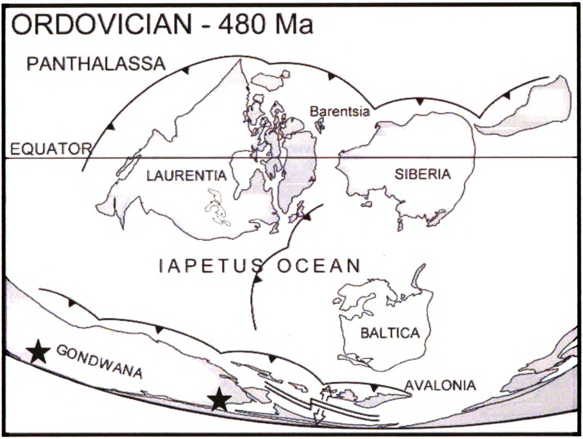


Figure 6.15: Paleogeographic map of all the continental positions during the Early Ordovician. Arrows indicate plate movements and stars represent approximate locations of *Arthrophycus* specimens. From Scotese (2002).

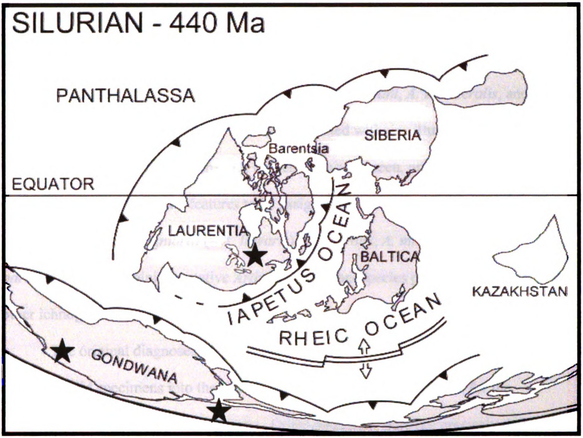


Figure 6.16: Paleogeographic map of all the continental positions during the Early Silurian. Arrows indicate plate movements and stars represent approximate locations of *Arthrophycus* specimens. From Scotese (2002).

Conclusions

Of twenty-three previously named ichnospecies of *Arthrophycus*, at least three names are duplicates of previously-named species (*A. harlani*, *A. unilateralis*, and *A. linearis*) and one (*A. siluricus*) is a name unassociated with any illustrations, descriptions, or known specimens. Of the remaining eighteen, only five ichnospecies possess sufficient diagnostic features to be assigned to *Arthrophycus*: *A. alleghaniensis*, *A. brongniartii* (= *A. linearis*), *A. lateralis*, *A. minimus*, and *A. parallelus*. The remaining putative *Arthrophycus* ichnospecies probably belong in other ichnogenera.

The original diagnoses of *Arthrophycus* were detailed, but subsequent authors placed invalid specimens into the ichnogenus without due consideration for the characteristics set forth in the diagnoses. Other characters were not precisely defined in the original descriptions and thus were easily misinterpreted. The ichnogenus diagnosis is emended herein to "dense accumulations of subhorizontal traces with simple smooth-sided form, terminating blindly, annulations typically biconvex, commonly branched and/or bundled into narrow or palmate fans, subquadrate in cross-section, median groove often present, filling chevron-shaped, diameter consistent in individual traces."

The assertion that small size is characteristic of geologically older *Arthrophycus* (Mángano *et al.* 2005a) is countered by the occurrence of verified small *Arthrophycus* specimens in younger strata. Size differences among ichnotaxa may reflect environmental stress and nutrient availability; therefore, size should not be regarded as an ichnotaxabase.

A numerical phenetic approach using clustering techniques proved useful in clarifying taxonomic affinity of specimens assigned to *Arthrophycus* and has potential for application to other trace fossils. Cluster and principal coordinate analyses based on sixteen characters confirmed the qualitative taxonomic conclusions and forced closer examination and definition of the morphological characters proposed in *Arthrophycus* diagnoses. Trace fossils have numerous characters suitable for coding and these techniques should be transferable to other ichnogenera, as the resulting diagrams are very concise and may make connections clearer that were ambiguous in a more wordy form. Cladistic techniques can also be applied to trace fossils, with the caveat that relationships in the resulting cladograms reflect morphological rather than phylogenetic relationships.

Arthrophycus is most abundant in Ordovician and Silurian strata, but has additional occurrences in the Cambrian, Devonian, and Carboniferous. The conclusion of previous workers that claims of *Arthrophycus* specimens in the Mesozoic and Cenozoic are erroneous, and that post-Devonian Paleozoic records should be treated with caution, is affirmed. However, most ichnospecies of *Arthrophycus* are not useful for biostratigraphic purposes, because they either have long geologic ranges or are known from only a few specimens (e.g. *A. lateralis*, *A. parallelus*). *Arthrophycus* is therefore not suitable for use as an index fossil.

Arthrophycus has a worldwide distribution, present on five continents plus the Middle East, including seventeen countries and eight U. S. states. Notable gaps, such as sub-Saharan Africa and most of Asia, may be real, or may reflect the state of Paleozoic marine paleontology in many of those countries.

The hypothesis that *Arthrophycus* originated in the epicontinental seas of the southern continents and spread north through time (Kumpulainen *et al.* 2006) is supported. However, the timing of the expansion should be emended to Cambrian-Ordovician for the origin in the south, and Late Ordovician-Silurian for the expansion to the northern continents.

Future work may include an investigation into Seilacher's (2000, 2007a) idea regarding the greater taxonomic relationships of *Arthrophycus*, *Daedalus*, *Phycodes*, and the teichichnids. Additional OTUs can be added to the data matrix for the cluster diagrams and PCO plots to determine if additional specimens belong in *Arthrophycus* and the character list may be extended so that additional taxa (such as *Daedalus*) may be studied in the same context. The taxa rejected herein as *Arthrophycus* may be studied further to determine which existing ichnogenus each properly belongs in or if some of the ichnospecies are deserving of their own new ichnogenus, as suggested herein for *Arthrophycus (Sabularia?) tenuis*. The question of the maker of *Arthrophycus* is still unresolved and merits further work as well, as does the question of how dense *Arthrophycus* burrows that presumably were excavated in mud could maintain their shape and whether the *Arthrophycus*-maker used a chemical signal to avoid interference of separate *Arthrophycus* burrow systems as was suggested by Miller *et al.* (2009).

Appendix I: Condensed Data for All Reports of *Arthrophycus*.

Taxa	Date	Author 1	Author 2	Time	Location	Lithology	A/?/n
A. harlani	1852	Hall		Sil	New York	sandstone	A
F. alleghaniensis	1831	Harlan		Sil	Pennsylvania		A
Harlania halli	1852	Goeppert		Sil	E. North Amer.		A
alleghaniensis	2003	Acenolaza	Acenolaza	Camb-Ordo	Argentina	quartzite	A
alleghaniensis	1977	Baldwin		Camb-Ordo	Spain		A
H. alleghaniensis	1963	Bender		Sil	Jordan	sandstone	A
H. alleghaniensis	1968	Bender		Ordo-Sil	Jordan	sandstone	A
alleghaniensis	1996	Borghi	Moreira	Sil	Brazil	sandstone	?
alleghaniensis	1966	Borrello		Ordo-Sil?	Argentina	sandstone	A
alleghaniensis	1981	Burjack	Popp	Sil	Brazil	siltstone	A
F. alleghaniensis	1837	Conrad		Sil	New York	sand/silt	?
F. harlani	1838	Conrad		Sil	New York	sand/silt	?
F. harlani	1839	Conrad		Sil	NY, PA, VA	sandstone	?
Harlania	1934	Dalloni		Sil	Chad	sandstone	A
alleghaniensis	1980	Downey		Sil	Pennsylvania	sandstone	A
Harlania	2005	Eschard	Abdallah	Ordo	Algeria	sandstone	?
alleghaniensis	1958	Fenton	Fenton	Sil	E. North Amer.	sandstone	A
alleghaniensis	1999	Fernandes		Sil-Dev	Brazil	sandstone	?
alleghaniensis	2001	Fernandes		Sil-Dev	Brazil		A
alleghaniensis	1995	Fernandes	Pereira	Sil	Brazil	sandstone	?
alleghaniensis	1996	Fernandes	Borghi	Ordo-Dev?	Brazil	sandstone	A?
alleghaniensis	2000	Fernandes	Borghi	Sil-Dev	Brazil		A
alleghaniensis	2002	Fernandes	Borghi	Ordo-Dev?	Brazil		A
Harlania	1925	Fritel		Sil	Chad	sandstone	?
harlani	1992	Grahn		Sil	Brazil	silt/shale	?
Harlania	1960	Grove		Sil	Chad	sandstone	?
Harlania	1966	Gubler	Bugnicourt	Ordo	Algeria	sandstone	A

App. I, continued.

harlani	1988	Janvier	Melo	Sil-Dev	Brazil	sandstone	?
alleghaniensis	2006	Kumpulainen	Uchman	Ordo-Dev?	Eritrea	sandstone	A
harlani	1889	Lesley		Sil	Pennsylvania	sandstone	A
Harlania	1955	Lessertisseur					A
alleghaniensis	1984	Linan		Camb	Spain	sandstone	A
alleghaniensis	1998	Metz		Sil	New Jersey	sandstone	A
alleghaniensis	2006	Metz		Sil	New Jersey	sand/shale	?
alleghaniensis	2009	Miller	Webb	Sil	Virginia	sandstone	A
alleghaniensis/harlani	1963	Moneda		(none)	Argentina	quartzite	?
alleghaniensis-like	1998	Moreira	Borghi	Sil-Dev	Brazil	sandstone	?
alleghaniensis	1999	Moreira	Borghi	Sil	Brazil	sandstone	?
alleghaniensis	2003	Neto de Carvalho	Fernandes	Ordo	Portugal		A
alleghaniensis	1999	Nogueira	Truckenbrodt	Sil	Brazil	sandstone	A
alleghaniensis	1984	Pickerill	Romano	Ordo	Spain	sandstone	A
alleghaniensis	2003	Poire	Spalletti	Camb-Ordo	Argentina	arenite	A
alleghaniensis	1923	Prouty	Swartz	Sil	Maryland	sandstone	A
alleghaniensis	1991	Romano		Ordo	Spain, Portugal	quartzite	?
"alleghaniense"	1916	Schuchert		Sil	NY, PA, NJ	sandstone	?
alleghaniensis	1997	Seilacher		Sil?	Libya	sandstone	A
alleghaniensis	2000	Seilacher		Ordo-Sil	USA, Arg., N. Afr.		A
alleghaniensis	2003	Seilacher	Cingolani	Ordo-Sil	Argentina	quartzite	A
Harlania	1970	Selley		Ordo	Jordan	sandstone	A
Harlania	1972	Selley		Ordo	Jordan	siltstone	?
F. harlani, A. alleghaniensis	1944	Shimer	Shrock	Sil	E. North Amer.	sandstone	A
F. alleghaniensis	1834	Taylor		Sil	Pennsylvania	sandstone	A
F. alleghaniensis	1835	Taylor		Sil	Pennsylvania	sandstone	?

App. I, continued.

alleghaniensis	1983	Turner	Benton	Camb-Dev	Libya	sandstone	A
Harlania	2005	Turner	Makhlouf	Ordo	Jordan	sandstone	n
alleghaniensis	1961	Wolfart		Dev	Paraguay	sandstone	n?
alleghaniensis	1955	Young		Sil	Virginia	sandstone	A
annulatus	1977	Książkiewicz		Cret-Eo	Poland	sandstone	n
brongniartii	2006	Kumpulainen	Uchman	Ordo-Dev?	Eritrea	sandstone	A
brongniartii	1923	Prouty	Swartz	Sil	Maryland	sandstone	A
brongniartii	2003	Rindsberg	Martin	Sil	Alabama	sandstone	A
F. brongniartia	1837	Conrad		Sil	New York	sand/shale	?
F. brongniartii	1832	Harlan		Sil?	New York	sandstone	A
F. brongniartii	1835	Taylor		Sil	Pennsylvania	sandstone	A
R. corrugatus	1908	Fritsch		Sil	Czech Rep.?	quartzite	n
corrugatus	1992	Mikulas		Ordo	Czech Rep.	sandstone	n
dzulynskii	1977	Książkiewicz		Oligo	Poland	sandstone	n
elegans	1901	Herzer		Penn	Ohio	sandstone	A?
flabelliformis	1940	Hundt		Ordo	Germany	quartzite	n
hunanensis	1996	Zhang	Wang	Sil	China	sandstone	n?
isp	1935	Abel		Oligo	Austria		A
isp	2008	Acenolaza	Heredia	Ordo	Argentina	sandstone	?
isp	2003	Acenolaza	Acenolaza	Camb-Ordo	Argentina	quartzite	A
isp	1987	Akpan	Nyong	Cret	Nigeria	sandstone	n
isp	1975	Alpert		Camb	California		?
isp	1977	Alpert		Camb	California	variety	?
isp	1982	Banerjee		Cret	Nigeria	silty sands	n
isp	1952	Becker	Donn	Sil	Pennsylvania	sandstone	A
isp	1984	Bhargava	Bassi	Sil	India	arenite	n
isp	1988	Bhargava	Bassi	Sil	India	silts/shale	n
isp	1987	Bjerstedt		Dev-Miss	West Virginia	mudstone	A

App. I, continued.

isp	1975	Chiplonkar	Ghare	Cret?	India	sandstone	n
isp	1964	Correia Perdigao		Ordo	Portugal	quartzite	n
isp	1983	Cotter		Sil	Pennsylvania	sandstone	A
isp	1981	Crimes		Sil-Dev	N. Africa	sandstone	?
isp	1998	De Alvarenga	Guimaraes	Sil	Brazil	sand/silt	?
isp	1963	Duimovich		(none)	Argentina	clay sands	?
isp, likely *harlani*	1985	Durand		Ordo	France	sandstone	A
isp	2005	Dutta	Chaudhuri	Perm	India	sand/shale	n
isp	1985	Eagar	Baines	Carb	England	sandstone	A
isp	1970	Frey		Cret	Kansas	chalk/shale	n
isp	1972	Frey		Cret	Kansas	chalk	n
isp	1970	Frey	Howard	Cret	Utah, Kansas	chalk/sand	n
isp	1986	Ghare	Kulkarni	Jur	India?	limestone	n
isp	1999	Gong Yiming		Carb	China	variety	A
isp	1994	Greb	Chesnut	Penn	Kentucky	shale	n
isp	1966	Howard		Cret	Utah	sandstone	n
isp	1978	Kern		Cret	Austria		n
isp	1970	Książkiewicz		Cret	Poland	sandstone	n
isp + *Daedalus*	1981	Laird		Ordo?	Antarctica	quartzite	?
isp	1985	Legg		Camb	Spain	sandstone	n?
isp A and B	1993	Li		Ordo	China		n
isp	1986	Lin	Zhang	Late PreC	China		n
isp	2002	Lopez	Roy	Sil	Maine	silt/limestone	?
isp	1971	Maberry		Cret	Utah	sand/silt	n
isp	1986	Manca		Camb	Argentina	sandstone	n
isp	2000	Mergl	Massa	Sil	Libya/Niger	sandstone	?
isp	1933	Moore		Sil	Appalachia	sandstone	A
isp	1987	Mukherjee	Sen	Protero	India	quartzite	n

App. I, continued.

isp	1997	Peeples	Isaacson	Ordo	Idaho	sandstone	?
isp	1982	Pemberton	Risk	Sil	Ont., New York	sandstone	A
isp	1978	Perez	Salazar	Cret	Colombia	sand/silt	n
isp	1964	Pettijohn	Potter	Sil	Pennsylvania	quartzite	n?
isp (likely *alleghaniensis*)	1999	Pflueger		Sil	Libya	sandstone	A
isp	1991	Pickerill	Fillion	Camb-Ordo	Newfoundland	sandstone	n
isp	2003	Poire	Spalletti	Camb-Ordo	Argentina	arenite	A
isp	1991	Romano		Ordo	Spain, Portugal	quartzite	?
isp	1977	Roniewicz	Pienkowski	Eoc/Oligo	Poland	sandstone	?
isp + *Daedalus*	1906	Sarle		Sil	New York	sandstone	A
isp	1930	Schiller		Camb?	Argentina	quartzite	XX
isp	1988	Seilacher	Alidou	Ordo-Sil	Benin	sandstone	A
isp of "*Arthrophicus*"	1951	Silva		Sil	Brazil	sand/shale	?
isp	1998	Stanley	Feldmann	Ordo	South Dakota!	sand/silt	n
isp	1972	Terrell		Perm	Utah	sandstone	?
isp	1978	Wagner		Sil	Tenn, Penn	sandstone	?
isp	1977	Webby		Camb-Ordo	NSW (Australia)	clastic	?
isp	1981	Wolfart		Sil	Jordan	sandstone	?
isp	1996	Yang (F)	Wang	Triassic	China	siltstone	n
krebsi	1941	Hundt		Ordo	Germany	quartzite	n
lateralis	2002	Fernandes	Borghi	Ordo-Dev?	Brazil	sandstone	A
lateralis	2000	Seilacher		Ordo-Sil	Libya		A
linearis	2003	Acenolaza	Acenolaza	Camb-Ordo	Argentina	quartzite	A
linearis	2003	Neto de Carvalho	Fernandes	Ordo	Portugal		A
linearis	1997	Seilacher		Sil?	Libya	sandstone	A
linearis	2000	Seilacher		Ordo-Sil	many		A
linearis	2002	Seilacher	*et al.*	Ordo	Libya	sandstone	A

App. I, continued.

linearis	2003	Seilacher	Cingolani	Ordo-Sil	Argentina	quartzite	A
linearis mention	2002	Fernandes	Borghi	Ordo-Dev?	Brazil	sandstone	A
minimus	2005	Mangano	Carmona	Camb	Argentina	sandstone	A
minimus	2005	Mangano	Buatois	Camb	Argentina	sand/muds	A
minoricensis	1973	Bourrouilh	Wieczorek				XX
minoricensis	1995	Llompart	Wieczorek	Carb	Minorca Island	siltstone	n
minoricensis	1994	Orr		Carb	Menorca Island	sand/muds	n
montalto	1889	Lesley		Camb	Pennsylvania	sandstone	n
parallelus	2010	Brandt	*et al.*	Penn	Michigan	sandstone	A
qiongzhusiensis	1994	Luo	Tao	Camb	China	sand/sh/silt	n
siluricus	1879/1890	Schimper		Camb	Sardinia (Italy)	shale	n
simplex or *Harlania*	2003	Konate	Guiraud	Ordo-Sil	Niger-Benin	sand/silt	A
simplex	2002	Seilacher	*et al.*	Ordo	Libya	sandstone	A
strictus	1977	Książkiewicz		Cret	Poland	sandstone	n
strictus	1996	Paczesna		Camb	Poland		n
tarimensis	1994	Yang		Ordo	China		n
S. tenuis	1984	Alexandrescu	Brustur	Oligo-Mio	Romania	sandstone	n
S. tenuis	1977	Książkiewicz		Oligo	Poland	sandstone	n
tenuis	1999	Uchman		Cret	Germany	sandstone	n
cf. tenuis	1999	Uchman	Demircan	Miocene	Turkey	sandstone	n
unilateralis	1997	Seilacher		Sil?	Libya	sandstone	A

Appendix II: Character States for Quantitative Analyses

Ichnospecies	Groove	Annulations	Closeness	Wrinkles	Width (mm)	X-section	Shape
alleghaniensis	yes	biconvex	close	yes	2.5-30	subquad	curving
brongniartii	yes	biconvex	close	yes	9.3-14.1	subquad?	intermed.
montalto	yes	rings	some	not spec.	not spec.	not spec.	intermed.
siluricus	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.
elegans	no	rings	close	not spec.	1.6-4.8	not spec.	straight
corrugatus	no	rings	singleton	not spec.	10-12.	not spec.	straight
flabelliformis	not spec.	not spec.	close	not spec.	not spec.	not spec.	curving
krebsi	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.	straight
minor(i)censis	not spec.	rings	close	not spec.	10	elliptical	curving
annulatus	yes	concavo-vex	few	not spec.	10	cylindrical	straight
strictus	no	rings	few	not spec.	1.5-4	cylindrical	straight
dzulynskii	no	concavo-vex	singleton	not spec.	10-11.	cylindrical	straight
tenuis	no	rings	close	not spec.	0.5-1.0	hemicylind.	straight
qiongzhusiensis	no	concavo-vex	few	not spec.	1-2.	cylindrical	intermed.
tarimensis	no	rings	close	not spec.	3-4.	cylindrical	curving
hunanensis	no??	rings	few	not spec.	8-10.	cylindrical	intermed.
linearis	yes	biconvex	close	yes	8-27.	subquad	intermed.
lateralis	yes	yes	close	not spec.	7-11.	subquad	intermed.
simplex	no	rings	few	not spec.	5-10.	not spec.	intermed.
minimus	yes	chevrons	close	not spec.	1.8-4.8	subquad	straight
parallelus	yes	chevrons	close	not spec.	3.5-4.5	subquad	straight

App. II, continued.

Ichnospecies	Palmate	Radial	Branching	Parallel	Plane	Internal	Ends	Diameter	Smooth
alleghaniensis	palmate	no	no	no	multiplanar	backfill?	blunt	consistent	smooth
brongniartii	no	no	some	no	multiplanar	retrusive	blunt	consistent	smooth
montalto	no	no	some	no	coplanar	not spec.	blunt	consistent	smooth
siluricus	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.	not spec.
elegans	no	no	no	parallel	coplanar?	not spec.	blunt	consistent	smooth
corrugatus	no	no	no	no	N/A	not spec.	blunt	inconsistent	smooth
flabelliformis	palmate?	no	no	no	coplanar	not spec.	not spec.	consistent?	not spec.
krebsi	not spec.	no	not spec.	not spec.	coplanar?	not spec.	not spec.	not spec.	not spec.
minor(i)censis	no	radial	no	no	coplanar	no structure	blunt	consistent	smooth
annulatus	no	no	some	no	coplanar	not spec.	blunt	consistent	smooth
strictus	no	some	some	no	coplanar	not spec.	both	consistent	smooth
dzulynskii	no	no	no	no	N/A	not spec.	blunt	consistent	smooth
tenuis	no	no	no	no	coplanar	not spec.	pointed	consistent?	smooth
qiongzhusiensis	no	no	extensive	no	coplanar	not spec.	blunt	consistent	smooth
tarimensis	no	no	extensive	no	coplanar?	not spec.	blunt	consistent	smooth
hunanensis	no	no	no	no	coplanar?	not spec.	blunt	inconsistent?	rough
linearis	no	no	some	no	multiplanar	backfill	blunt	consistent	smooth
lateralis	asymm.	no	no	no	multiplanar	backfill	blunt	consistent	smooth
simplex	no	no	no	no	coplanar	not spec.	blunt	consistent	smooth
minimus	no	no	some	no	multiplanar	retrusive	blunt	consistent	smooth
parallelus	no	no	some	parallel	coplanar	no structure	pointed	consistent	smooth

Appendix III: Coded Characters

Isp	Gro	Close	Ann	X-sec	Shape	Palm	Radial	Bran	Para	Plane	Int.	Wrink	Width	Ends	Diam	Sm
alleghaniensis	1	3	3	0	0	2	0	0	0	1	1	1	2	0	1	0
brongniartii	1	3	3	0	1	0	0	0	0	1	1	1	2	0	1	0
montalto	1	2	0	1	1	0	0	1	0	0	0	0	1	0	1	0
elegans	0	3	0	1	2	0	0	0	1	0	0	0	0	0	1	0
corrugatus	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0
minor(i)censis	0	3	0	2	0	0	1	0	0	0	0	0	2	0	1	0
annulatus	1	1	1	1	2	0	0	1	0	0	0	0	2	0	1	0
strictus(K1)	0	1	0	1	2	0	0	1	0	0	0	0	0	0	1	0
strictus(K2)	0	1	0	1	2	0	1	0	0	0	0	0	0	1	1	0
dzulynskii	0	0	1	1	2	0	0	0	0	0	0	0	2	2	1	0
tenuis	0	3	0	2	1	0	0	0	0	0	0	0	0	1	1	0
qiongzhusiensis	0	1	1	1	1	0	0	2	0	0	0	0	0	0	1	0
tarimensis	0	3	0	1	0	0	0	2	0	0	0	0	0	0	1	0
hunanensis	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	1
strictus(P)	1	1	0	0	2	0	0	1	0	0	0	0	0	1	1	0
linearis	1	3	3	0	1	0	0	1	0	1	1	1	2	0	1	0
lateralis	1	3	3	0	1	1	0	0	0	1	1	0	1	0	1	0
simplex	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0
minimus	1	3	3	0	2	0	0	1	0	1	1	0	0	0	1	0
parallelus	1	3	2	0	2	0	0	1	1	0	0	0	0	1	1	0

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