

# *Arachnostega* Bertling, 1992 in the Drumian (Cambrian) sediments of the Teplá-Barrandian region (Czech Republic)

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## ABSTRACT:

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The presence of the ichnospecies *Arachnostega gastrochaenae* Bertling, 1992 is documented from the Cambrian for the first time. It occurs in several stratigraphical levels of the “middle” Cambrian sediments in the Příbram-Jince and Skryje-Týřovice basins of the Teplá-Barrandian region in the Czech Republic. Simple tunnels as well as the complicated morphologies of *Arachnostega* were observed on internal moulds of trilobite exoskeletons and hyolith conchs and represent the oldest record of this ichnogenus. The Cambrian occurrences of *Arachnostega* on skeletal body fossils evoke the connection between the *Arachnostega*-type feeding strategy and the sudden appearance of numerous skeletal animals. The development of the *Arachnostega*-type behaviour can be considered a feature of the “Cambrian substrate revolution.”

**Key words:** Cambrian; Teplá-Barrandian region; Czech Republic; Ichnofossils; Jince Formation; Buchava Formation; *Arachnostega*.

## INTRODUCTION

The ichnogenus *Arachnostega* Bertling, 1992 shows, in contrast to numerous and equally common Phanerozoic trace fossils, certain very specific features, especially its association with concave parts of skeletal body fossils. Though relatively common in the fossil record (see below), it was first systematically treated and named by Bertling as late as 1992. The explanation for

this is probably the fact that *Arachnostega* is by definition associated with body fossils (usually components of well-preserved shelly faunas) and hence it was often mentioned and figured in papers dealing with trilobites, molluscs and other groups of skeletal fossils (see below for references), being thus effectively ‘isolated’ from the attention of ichnologists.

This investigation shows both the wide occurrence of *Arachnostega* in post-Cambrian rocks, especially in

the Ordovician and Cretaceous, as well as demonstrating its potential for solving palaeobiological questions, such as deciphering the environment of infaunal elements and the cohesiveness of the substrate. In considering studies of the substrates of Cambrian and Ordovician marine settings (e.g., Bottjer *et al.* 2000; Dronov *et al.* 2002), the question of the appearance of the behaviour responsible for the origin of *Arachnostega* may prove useful. It is noteworthy that this ichnogenus was not recorded in sediments older than the Early Ordovician before the discovery of the presently described material from the Teplá-Barrandian region. The aim of the paper is therefore to document the ichnogenus *Arachnostega* from Cambrian sediments for the first time and to outline the possible palaeobiological and palaeoenvironmental implications.

#### PREVIOUS REPORTS OF THE ICHNOGENUS *ARACHNOSTEGA*

For the reasons mentioned above, it is difficult to present a complete review of literature data on *Arachnostega*. Many authors figured body fossils with adjacent *Arachnostega* but provided no comment on the traces themselves. Such reports can be used in reconstructing the stratigraphic and palaeogeographic range of the ichnogenus; they can be included to the synonymy of the ichnogenus/ichnospecies but they have no impact on nomenclature.

In the synopsis below, records of *Arachnostega* are listed by stratigraphical range and region. It should be noted that the traces have in some cases been recognized from photographs in which they appeared ‘inadvertently’, i.e., without the intention of the author. Only a selection of the ‘inadvertent’ reports of *Arachnostega* is presented herein; the list compiled so far exceeds the scope and extent of the paper. Numerous data have been provided by Juan Carlos Gutiérrez Marco (*personal communications*, 1992–2007).

#### Cambrian

The only Cambrian specimen of *Arachnostega* was published by Marek (1975, pl. 2, fig. 3), who figured, but did not name, a short tunnel preserved on the dorsal side of an incomplete hyolith from the Buchava Formation.

#### Ordovician

Ordovician records of *Arachnostega* are by far the most numerous compared to those from other systems.

It is known in African and South American Gondwana but is especially widespread in European peri-Gondwana; it has also been recognized, albeit rarely, in Baltica and Kazachstania.

#### *Gondwana*

From the Upper Ordovician of Libya, Becq-Giraudon and Massa (1997) figured common *Arachnostega* on trilobite cranidia and pygidia. The Upper Ordovician of Morocco yielded *Arachnostega* on trilobites (Destombes 1972) and gastropods (Horný 1997a).

From the “Arenigian” of Argentina (Suri Formation, Famatina range), Aceñolaza and Aceñolaza (2002) depicted moulds of bivalves, brachiopods and asaphid trilobites with the trace.

#### *European peri-Gondwana*

**Sardinia.** From the lower “Kralodvorian” (equal to Katian, upper Ordovician) of southwest Sardinia (upper Portixeddu Formation), *Arachnostega* was reported from cranidia and pygidia of trilobite-like arthropods and trilobites by Hammann *et al.* (1990) and Hammann and Leone (1997) respectively. Villas (1985) reported the trace on brachiopod shells from the same strata.

#### *Armorican Terrane Assemblage*

**Armorica s.s.** From the Montagne Noire of France, Horný and Vizcaïno (1995) figured the ichnogenus from gastropod shells of the upper Tremadocian and basal middle “Arenigian” (equal to Floian). Babin (in Babin *et al.* 1982) documented *Arachnostega* from the rostroconch *Ribeiria* and from the bivalve *Ekaterodonta*, both earliest “Arenigian” in age (equal to Floian). In the Armorican Massif of France, Henry (1980) figured several specimens of *Arachnostega* on pygidia and cranidia of trilobites of “Dobrotivian” age (equal to late Darriwilian to early Sandbian); from the same strata Babin (1966) figured *Arachnostega* from bivalve moulds; Pillet (1993) reported *Arachnostega* from one trilobite pygidium of the uppermost Armorican Quartzite Formation (Floian to Dapingian); while Mélou (1990) figured the trace from an articulated specimen of a brachiopod from the Upper Ordovician “Kralodvorian” Stage (equal to early Katian). Ubaghs (1969) figured *Arachnostega* on stylophoran echinoderms.

**Iberia.** Young (1988) figured *Arachnostega* from the cephalon of the trilobite *Dalmanitina* from the Middle to Upper Ordovician of the Buçaco Syncline

in Portugal. Numerous reports of *Arachnostega* come from the Spanish Ordovician. Arbizu *et al.* (1999) and Gutiérrez-Marco *et al.* (1999) noted the trace fossil from the Upper “Dobrotivian” (equal to early Sandbian) of the Cantabrian Zone. From the low Middle Ordovician “Tristani Beds” of central Spain, Gutiérrez-Marco and Rábano (1999) and Laurent (1974) figured or noted *Arachnostega* on mollusc and trilobite shells. Rábano (1989) and Hammann and Rábano (1987) mentioned and figured it on trilobite cephalons from the Oretanian (Darriwilian) strata of central Spain. Other Oretanian occurrences of *Arachnostega* in Spain (on molluscs and trilobites) were recorded by Gutiérrez-Marco (1997), Born (1918) and Babin and Gutiérrez-Marco (1985, 1991). The records from the “Dobrotivian” Stage also derive from papers by Babin and Gutiérrez-Marco (1991) and Gil Cid and Domínguez-Alonso (2001). Gutiérrez-Marco and Sá (2006) documented the presence of *A. gastrochaenae* on internal moulds of gastropods and asaphid trilobites from the Middle Ordovician Valongo Formation (Oretanian Regional Stage = Darriwilian) of Portugal.

**Saxothuringia.** The expected presence of *Arachnostega* has been recently confirmed in the Grifelschiefer (“Arenigian” Regional Stage, equal to Dapingian to early Darriwilian) of Thuringia by Budil and Fatka (unpublished observation).

**Perunica.** From the Ordovician of the Teplá-Barrandian region (Czech Republic), numerous albeit brief to inadvertent references to *Arachnostega* have been given. The oldest one comes from the “Arenigian” Klabava Formation (equal to Floian to Dapingian), where it was observed on a pygidium of an agnostid (Pek and Smola 1989). From the Šárka Formation (Oretanian Regional Stage, Darriwilian), Horný (1991, 1992, 1997b) figured specimens on gastropod moulds; Kříž (1995) depicted the trace from the same formation on a rostroconch; Slavičková (1999), Bruthansová and Kraft (2003) on a trilobite and Lefebvre (2007) on cystoids. The overlying Dobrotivá Formation (upper Darriwilian) yielded the trace on a trilobite (Šnajdr 1990), as has the succeeding Libeň Formation (Havlíček and Vaněk 1996). From the Zahofany Formation (Middle “Berounian” Regional Stage = late Sandbian–early Katian), *Arachnostega* was figured by Horný (1996, 1997a), Příbyl and Vaněk (1976), and Pojeta and Runnegar (1976). The trace was also described by Shaw (1995, 2000) from trilobites of the Upper Ordovician Králův Dvůr Formation (“Kralodvorian” Regional Stage = Katian). The first

ichnological description of the trace comes from the Šárka Formation (Mikuláš 1990).

*Kazachstania and Baltica*

Outside peri-Gondwana, Popov *et al.* (2002) described a brachiopod with *Arachnostega* from the Upper Ordovician of Kazakhstan and Mikuláš and Dronov (2005) briefly described the ichnogenus from the Middle Ordovician of the St. Petersburg Region, Russia (Baltica).

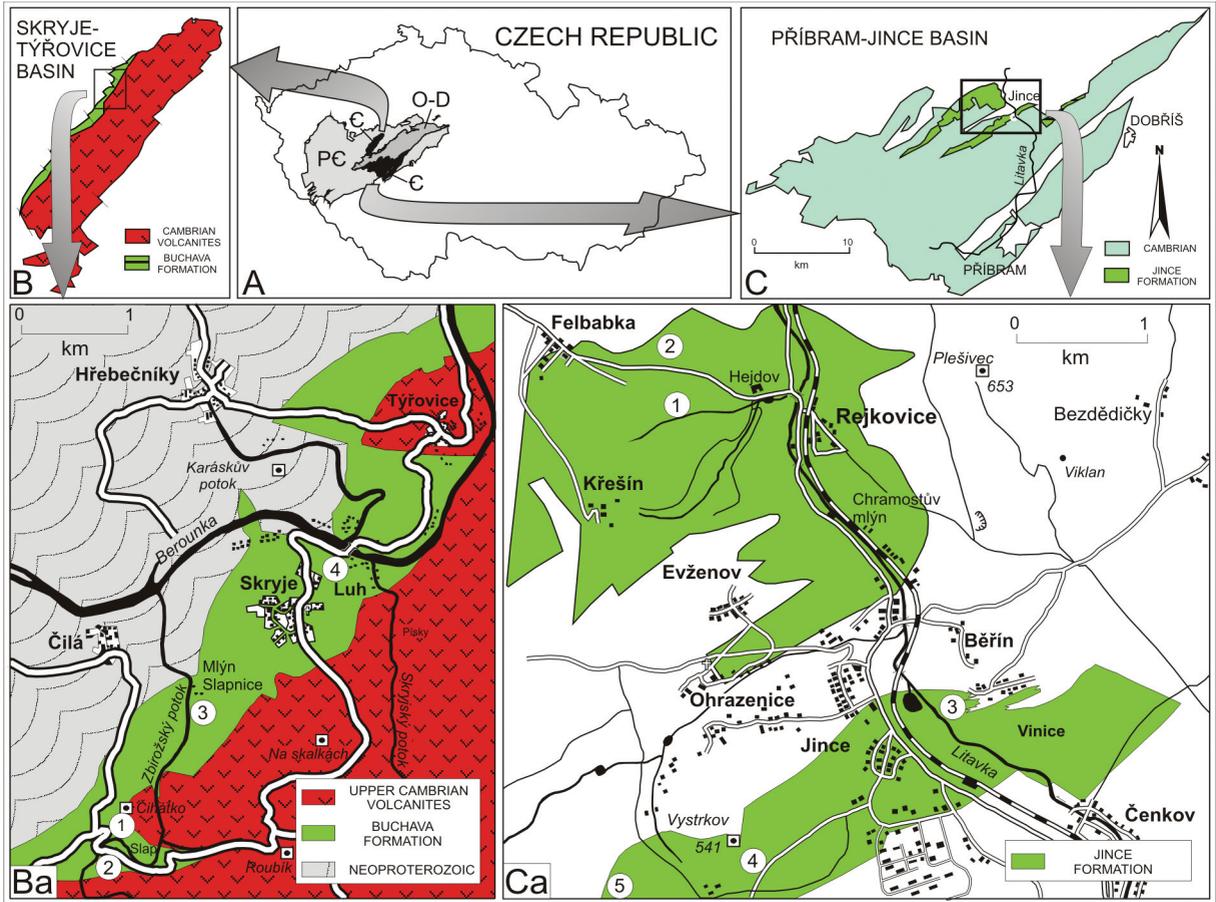
Younger occurrences of *Arachnostega* are not listed herein, being necessarily a subject of future research including a comprehensive ichnotaxonomical treatment. As a preliminary statement, most post-Ordovician occurrences of *Arachnostega* appear to be linked to clastic sediments, with probable peaks in the Devonian, Jurassic, Neogene and Quaternary. Future research should avoid the tendency to determine all bioturbation inside shells as *Arachnostega*.

PALAEOENVIRONMENT

*Arachnostega*-like tubes were reported in the echinoderms *Balanocystites primus* and *Anatifopsis barrandei* from the Middle Ordovician Šárka Formation of the Prague Basin (Teplá-Barrandian region) by Lefebvre (2007, p. 161, fig. 1 B, C), who documented the occurrence of this ichnogenus from his taphofacies D–E (D – well oxygenated middle shelf, quiet environmental conditions at or below the average storm wave base; E – deep, low-energy, distal shelf or slope environments far below average storm wave base).

GEOLOGICAL SETTING OF THE CAMBRIAN OF THE TEPLÁ-BARRANDIAN REGION

In the Teplá-Barrandian region, Cambrian fossils are known in two separate areas: in the larger Příbram-Jince Basin and in the smaller Skryje-Týřovice Basin (Text-fig. 1). Nine formations have been distinguished by Havlíček (1971, 1998) and Fatka and Mergl (2009) in both Cambrian basins. The only richly fossiliferous rocks (greywackes and shales with local intercalations of sandstones to fine conglomerates) have been assigned to the Jince and Buchava formations (Geyer *et al.* 2008; Fatka *et al.* 2011). The age of the fossiliferous units corresponds to the middle levels of the third unnamed series of the Cambrian System, namely the Drumian Stage, and partly also to the immediately underlying fifth unnamed stage (Alvaro *et al.* 2004).



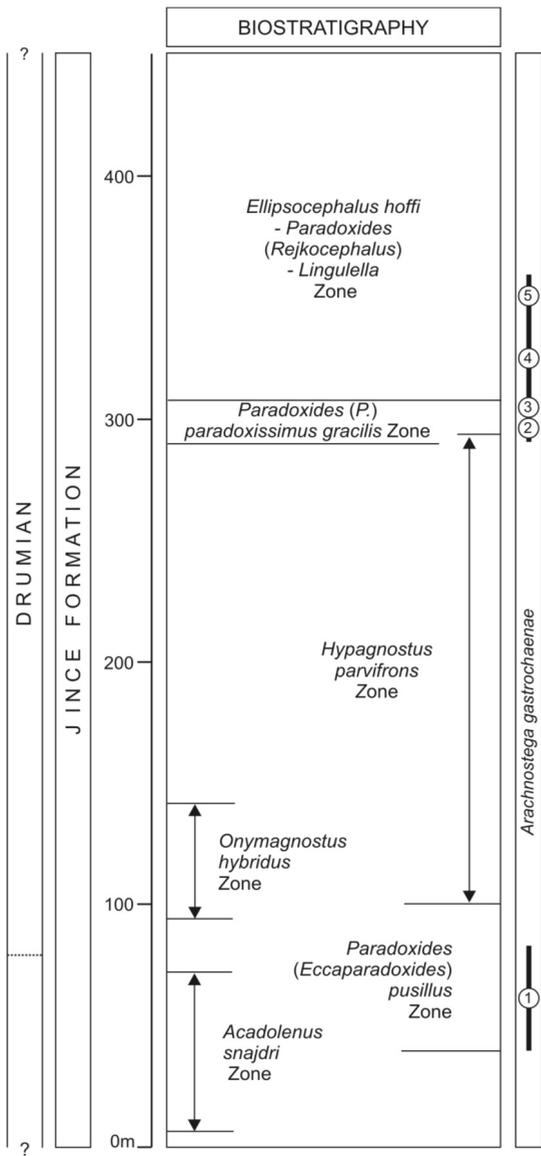
Text-fig. 1. **A** – Simplified map of the Teplá-Barrandian region within the Czech Republic, black are the areas of unmetamorphosed Cambrian rocks. PC – Precambrian, C – Cambrian, O-D – Ordovician to Devonian. **B** – Sketch map of the Skryje-Týřovice Basin. **Ba** – Fossil localities in the Skryje-Týřovice Basin: 1 – Čihátko–Milíř, 2 – Buchava, 3 – Dubinky Hill, 4 – Luh near Skryje. **C** – Sketch map of the Příbram-Jince Basin. **Ca** – Fossil localities in the Příbram-Jince Basin: 1 – Rejkovice–Potůček, 2 – Felbabka–Ostrý vrch Hill, 3 – Vinice Hill near Jince, 4 – Vystrkov Hill, 5 – Koniček Hill. Geology in B, Ba, C and Ca modified from Havlíček (1971)

## Příbram–Jince Basin

Skeletal macrofossils of the Jince Formation in the Příbram-Jince Basin have been used to define three bathymetrically dependent assemblages (Fatka 2000; Fatka and Mergl 2009; Text-fig. 2). The oldest and the youngest levels of the Jince Formation are represented by fine sandstones and greywackes and are characterized by a shallow-water *Lingulella*-dominated assemblage containing rare ellipsocephalid and conocoryphid trilobites associated with rare paradoxidids. A comparatively deeper assemblage is dominated by polymeroid trilobites (ellipsocephalids, paradoxidids, ptychoparioids, and solenopleurids), usually associated with common agnostids (*Peronopsis* and *Phalagnostus*), locally common edrioasteroid, eocrinoid and ctenocystoid echinoderms, rare acrotretacean, linguliformean and rhynchonelliformean brachiopods, bradoriids and other bivalved

arthropods and hyoliths. This type of assemblage is represented in greywackes to shales. Shales representing the deepest-water environment are dominated by agnostids (e.g., *Onymagnostus* and *Hypagnostus*) associated with rare polymeroid trilobites (paradoxidids and conocoryphids), foraminifera and paragas-tropod molluscs. The stratigraphic ranges of all taxa recognized in the “middle” Cambrian Jince Formation of the Příbram-Jince Basin have been recently summarized by Fatka *et al.* (2004). The generally common fossils provide a very good basis for biostratigraphical zonation. All the published zonal schemes for the formation have been recently summarized by Fatka (2006) and Fatka and Szabad (in press).

The stratigraphic range and geographic distribution of *Arachnostega* is restricted to successions representing the deeper environments of the assemblages dominated by polymeroid trilobites.



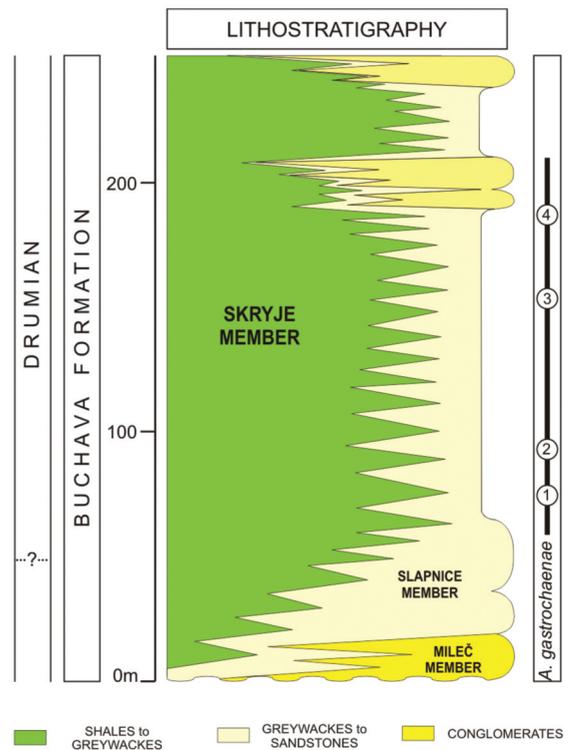
Text-fig. 2. Biostratigraphic subdivision of the Jince Formation in the Přibram-Jince Basin (left) with stratigraphic range of *Arachnostega gastrochaenae* Bertling, 1992 and stratigraphic location of fossil localities in the substitute for the Přibram-Jince Basin: 1 – Rejkovice–Potůček, 2 – Felbabka–Ostrý vrch hill, 3 – Vinice hill near Jince, 4 – Vystrkov hill, 5 – koniček hill (right).

Biostratigraphy modified after Fatka and Szabad (in press)

**Skryje–Týřovice Basin**

In this basin, three separate lithostratigraphical units, the Mileč, Slapnice and Skryje members were recently distinguished within the “middle” Cambrian Buchava Formation by Fatka *et al.* (2011; Text-fig. 3). The basal sediments of the monomictic white to grey Mileč Member (conglomerates and sandstones) are restricted to the area of Týřovice and Skryje. Kukal

(1971) considered that most of these sediments originated on beaches, coastal barriers and bars. In the northeastern part of the basin such light-coloured lithotypes are usually overlain by a succession of darker polymictic conglomerates, greyish-green shales and greywackes of the Slapnice Member, interpreted by Kukal (1971) as fluxoturbidites deposited on the steep slopes of the sedimentary basin. The fragmentary fauna comprises common brachiopods, locally common helcionelloid molluscs and polymeroid trilobites (Mergl and Kordule 2008), associated with rare graptoloids (Maletz *et al.* 2005) and the enigmatic genus *Wiwaxia* (see Fatka *et al.* 2011). The most widespread lithofacies of the Skryje Member is represented by an up to 200 m thick sequence of greenish clayey shales and greywackes with silty and sandy intercalations. The high diversity fauna locally comprises abundant brachiopods (*Bohemiella*), diverse polymeroid trilobites (e.g., *Paradoxides (Eccaparadoxides)*, *Conocoryphe*, *Ptychoparia*, *Sao*, *Agraulos*, *Skreiaspis*), also agnostids (e.g., *Condylopyge*, *Pleuroctenium*) in the higher levels, locally also common cinctan and stylophoran



Text-fig. 3. Lithostratigraphic subdivision of Cambrian rocks in the Skryje-Týřovice Basin (left) with stratigraphic range of *Arachnostega gastrochaenae* Bertling, 1992 and stratigraphic location of fossil localities in the Skryje-Týřovice Basin: 1 – Čihátko–milř, 2 – Buchava, 3 – Dubinky hill, 4 – luh near Skryje (right). Lithostratigraphy modified after Havlíček (1971) and Fatka *et al.* (2011)

echinoderms (*Trochocystites*, *Ceratocystis*), edrioasteroids (*Stromatocystites*), rare molluscs and hyoliths. Kukul (1971) interpreted all lithotypes as fluxoturbidites deposited on the steep slopes of the basin. Taxa recognized in the Buchava Formation of the Skryje-Týřovice Basin have been recently summarized by Fatka (1990).

Like in the Příbram-Jince Basin, *Arachnostega* occurs in sediments representing the deeper environments of the assemblages dominated by polymeroid trilobites.

## TRACE FOSSILS

Cambrian trace fossils of the Teplá-Barrandian region were mentioned for the first time more than one hundred years ago by Vlček (1902). More recently, they were studied by Mikuláš (1994, 1996, 2000, 2001), Chlupáč and Mikuláš (1995), Mikuláš and Kordule (1998), Mikuláš *et al.* (1996, 2002) and Fatka and Szabad (2011). Stratigraphic ranges of all described ichnotaxa were summarized by Fatka *et al.* (2004) for the Příbram-Jince Basin. The ichnofacies characteristics of the locality 'Buchava', published by Chlupáč (1993), i.e. "the rather shallow-water *Cruziana* ichnofacies: frequent epi- and intrastratal, planar or oblique burrows mostly ranged with fodichnia (feeding structures) and pascichnia (grazing traces) made by deposit feeders" generally apply to most of the Cambrian localities of the Teplá-Barrandian region. An ichnofacies evaluation using the concepts published, e.g., by Frey and Pemberton (1984), Frey *et al.* (1990) and Bromley and Asgaard (1991) was used in a preliminary report on the ichnological study of the area (Mikuláš 1994). These preliminary conclusions have been supplemented during the last phase of the fieldwork and laboratory studies (e.g., Mikuláš 2000, 2001).

### Character of the ichnoassemblages

The first phase of the marine transgression in the Příbram-Jince Basin is documented by finds of *Diplocraterion parallelum* Torell, 1870 in the lowermost layers of the Jince Formation (siltstones alternating with greywackes and subgreywacke layers of various thickness). *Diplocraterion* is a representative of the *Skolithos* Ichnofacies (e.g., Frey and Pemberton 1984) typical of shifting substrates in a high energy setting. The *Skolithos* ichnofacies usually reflects a low diversity (but in places a high density) of the original benthic assemblage. The localities of the middle part of the Jince Formation, and the Skryje Member, commonly

yielded the following ichnofossils: *Planolites* isp., *Teichichnus rectus*, *Daedalus* isp., *Thalassinoides* div. isp., *Palaeophycus* isp., coprolites; taxonomically indeterminate bioturbation structures are also locally significant. Specific forms such as *Amanitichnus omitus* Chlupáč and Mikuláš, 1995 (Buchava locality) or *Rejkovicichnus necrofilus* Mikuláš *et al.*, 1996 (Rejkovice-Potůček locality) are also locally common. These ichnoassemblages may be placed in the *Cruziana* ichnofacies (e.g., Frey and Pemberton 1984), which most often represents a shallow sublittoral setting below the fairweather wave base and above the storm wave base. This setting provided the space for the development of the highest diversity benthic assemblages in siliciclastic substrates in the Early Palaeozoic, comprising many K-selected forms (e.g., Pemberton 1992).

In the upper part of the Jince Formation, finds of *Skolithos rotundus* Mikuláš, 2000, *Daedalus* isp., "*Thalassinoides*" isp. and *Skolithos* isp. are common. This assemblage is comparable with the *Skolithos* Ichnofacies in the low diversity, high abundance and numerous vertical components of the burrows.

## SYSTEMATIC ICHNOLOGY

### Ichnogenus *Arachnostega* Bertling, 1992

1990. Fodinichnion ichnogen. indet. (ichnogen. nov.); R. Mikuláš (MS), p. 41, pl. 16, fig. 1.

1992. *Arachnostega* n. ichnog.; M. Bertling, p. 179.

TYPE ICHNOSPECIES: *Arachnostega gastrochaenae* Bertling, 1992.

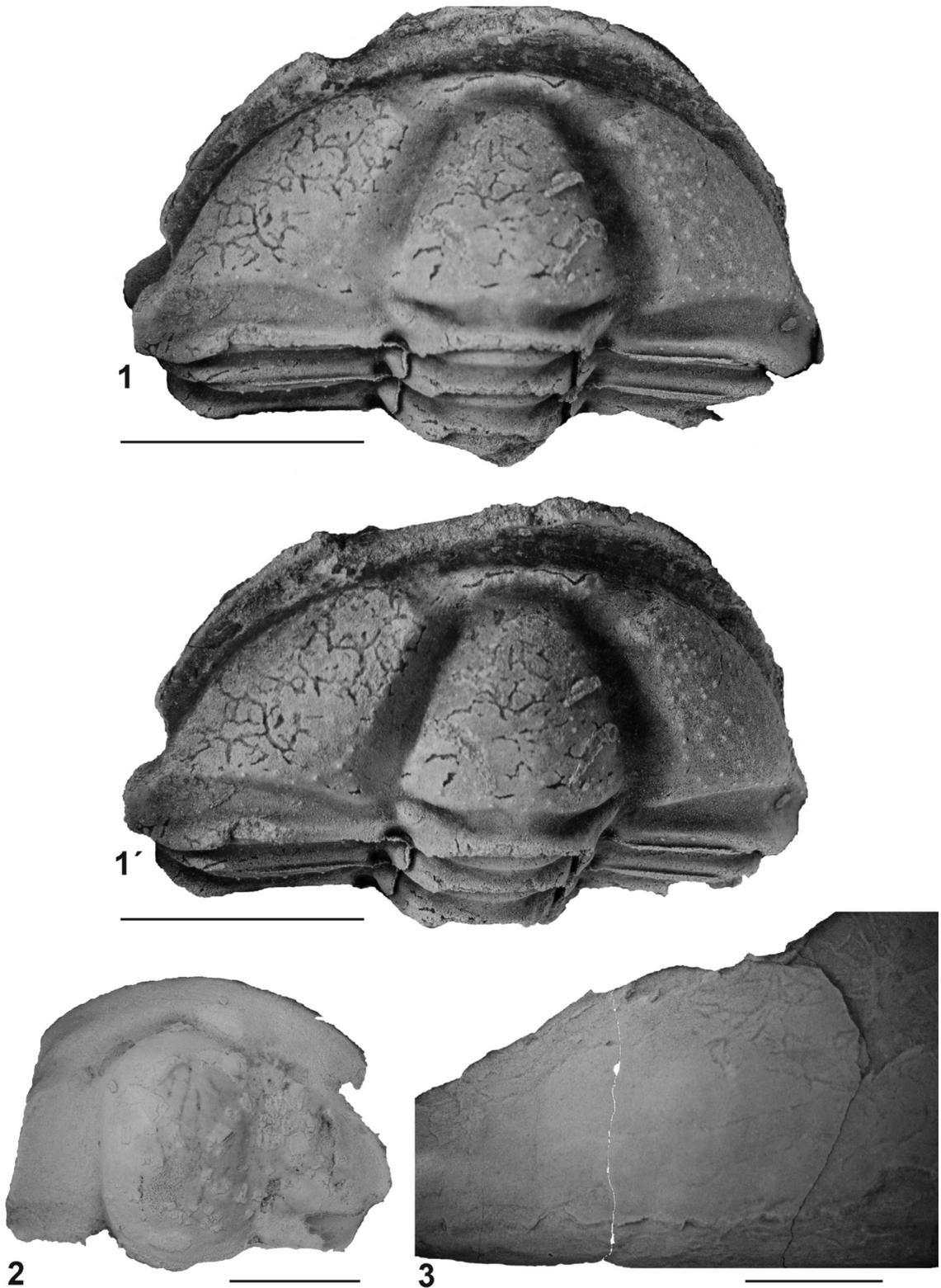
EMENDED DIAGNOSIS: Irregular, basically net-like burrows in sediment fill of shells, visible on the surface of internal moulds. The size of the whole structure may vary from microns to centimetres. The networks may continue laterally as ramifying, simply branching and, less commonly, also looping burrows (emended after Bertling 1992).

### *Arachnostega gastrochaenae* Bertling, 1992 (Text-figs 4, 5)

1974. marques de prédateurs; J.-M. Lauret, pp. 29, 31, pl. 3, figs 4–6, pl. 4, fig. 3.

1985. *Talpina* sp.; R.A. Henderson and K.J. McNamara, p. 312, fig. 5D.

1990. Fodinichnion ichnogen. indet. (ichnogen. nov.); R. Mikuláš (MS), p. 41, pl. 16, fig. 1.



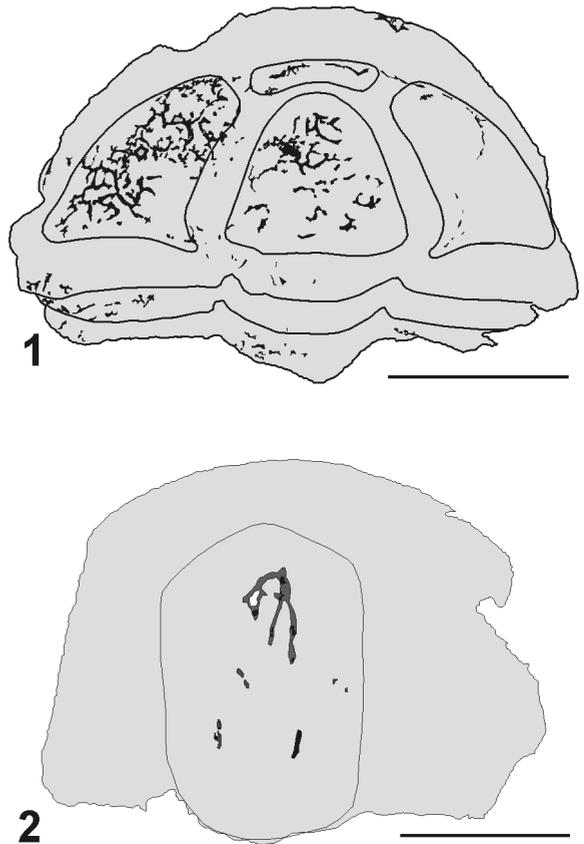
Text-fig. 4. *Arachnostega gastrochaenae* Bertling, 1992 preserved in trilobites (1, 2) and a hyolithid (3). 1 and 1' – *Conocoryphe sulzeri* (Schlotheim, 1823), Příbram-Jince Basin, Jince Formation, *Paradoxides (P.) paradoxissimus gracilis* Zone, Felbabka-Ostrý vrch Hill (MV – 015); 2 – *Ellipsocephalus hoffi* (Schlotheim, 1823), Skryje-Týřovice Basin, Buchava Formation, Skryje Shale, *Paradoxides (Eccaparadoxides) pusillus* Zone (NML – )1607); 3 – *Maxilites maximus* (Barrande, 1867), Skryje-Týřovice Basin, Buchava Formation, Skryje Shale, *Paradoxides (Eccaparadoxides) pusillus* Zone (MV – 003). Scale bars = 1 cm

- cf. 1990. Branched tunnels of burrowing organisms; W. Hammann *et al.*, p. 172, pl. 3, fig. 3.
1992. *Arachnostega gastrochaenae* n. ichnosp.; M. Bertling, p. 180, figs 2 a–f.
1994. *Arachnostega gastrochaenae* Bertling; F.T. Fürsich *et al.*, p. 161, pl. 3, figs 1, 2 and 4.
1996. *Arachnostega* isp. aff. *gastrochaenae* Bertling; S.E. Damborenea and M.O. Manceñido, p. 113, figs 1a–1b, pl. 1, figs 1, 3 and 5.
1999. *Arachnostega* isp.; J.-C. Gutiérrez-Marco *et al.*, p. 39.
1999. *Arachnostega* isp.; M. Arbizu *et al.*, p. 530.
1999. *Arachnostega gastrochaenae* Bertling; F.T. Fürsich and D.K. Pandey, p. 126, fig. 7g.
1999. *Arachnostega*; J.-C. Gutiérrez-Marco and I. Rábano, p. 38.
2002. *Arachnostega gastrochaenae* Bertling; G. Aceñolaza and F.G. Aceñolaza, p. 182, fig. 6D.

**MATERIAL:** More than twenty finds (individual networks or incipient networks adjacent to skeletal body fossils) are known from the Cambrian of the Teplá-Barandian region. They come from the nine localities listed below.

Figured material is deposited in the collection of the Czech Geological Survey in Prague (MV-003, MV-015) and the National Museum in Prague (NML-01607).

**DESCRIPTION:** Burrow systems formed of straight, curved or angular tunnels on the surface (or, less commonly, slightly below the surface) of internal moulds of skeletal fossils (trilobites, hyolithids). Forms considered to represent initial phases show a simple branching, mostly at an angle of 45–50° or they may contain loop-like components. In the final phase, the burrows form irregular polygonal meshes. The tunnels are oval to circular in cross-section (or semi-oval to semi-circular, when fully pressed to the wall of subsequently dissolved skeletons). Each system shows a roughly constant diameter of tunnels, usually 0.2 to 0.5 mm. However, two systems, varying in the diameter of tunnels (e.g., 0.3 and 0.5 mm), and showing individual patterns of branching, may be present on one mould. The largest systems occupy an area of several square centimetres (derived from the area of the moulds). However, not all the systems found cover the whole mould surface – this concerns both the initial stages, and the top network systems. Intervals of ramifying of initial forms usually are 0.5–5 mm long. Diameter of meshes in the network forms depends on the diameter of the tunnels; the diameter of meshes is mostly three- to ten times larger than that of the tunnels. Most of the systems (both ini-



Text-fig. 5. Schematic drawings of *Arachnostega gastrochaenae* Bertling, 1992 on trilobite moulds. 1 – *Conocoryphe sulzeri* (Schlotheim, 1823), Přibram-Jince Basin, Jince Formation, *Paradoxides* (*P. paradoxissimus gracilis*) Zone, Felbabka-Ostrý vrch Hill (MV-015), the same specimen as in Text-fig. 4.1; 2 – *Ellipsocephalus hoffi* (Schlotheim, 1823), Skryje-Týřovice Basin, Buchava Formation, Skryje Shale, *Paradoxides* (*Eccaparadoxides*) *pusillus* Zone (NML-1607), the same specimen as in Text-fig. 4.2. Scale bars = 1 cm

tial and top forms) are fully joined to the inner wall of a shell and, therefore, they are fully visible on the surface, only a very small portion of the tunnels is developed below the mould surface.

**STUDIED SPECIMENS:** Five specimens with *Arachnostega*, two associated with polymeroid trilobites and three associated with hyolithids, were selected as typical examples illustrating the type of preservation of this ichnogenus in moulds of Cambrian trilobites and hyolithids.

#### TRILOBITES

*Conocoryphe sulzeri* (Schlotheim, 1823)  
(Text-figs 4.1, 4.1', 5.1)

DESCRIPTION: Internal mould of cephalon with two thoracic segments preserved in fine-grained greywacke. A dense network of fine diverticulate tunnels is visible on the glabella as well as on the right fixigena; the preglabellar and right pleura bear simple tunnels.

*Ellipsocephalus hoffi* (Schlotheim, 1823)  
(Text-figs 4.2, 5.2)

DESCRIPTION: Internal mould of cephalon preserved in greywacke. Several simple tunnels are developed in the glabella. The tunnels are ca 0.2 mm in diameter; branching is relatively rare and irregular.

HYOLITHIDS

The first and, up to now, the only Cambrian finds of *Arachnostega* were published in a short report by Marek, who figured a short tunnel preserved on the dorsal side of an incomplete internal mould of *Buchavalites primus* (Barrande, 1867) (see Marek 1975, pl. 2 fig. 3) and simple divergent tunnels developed on both dorsal and ventral sides of *Buchavalites pompeckji* Marek, 1975, all collected at the Buchava locality.

At the Čihátko-Milíř locality, the trace was found on internal moulds of the hyolithid *Maxilites maximus* (Barrande, 1867).

*Maxilites maximus* (Barrande, 1867)  
(Text-fig. 4.3)

DESCRIPTION: External and internal moulds of incomplete conch preserved in an originally calcareous sandy to greywacke concretion. The preserved part of the hyolith conch is 77 mm long and up to 32 mm wide. Fine tunnels measuring from 0.15 to 0.4 mm in width are preserved in the central portion of the venter of both the internal and external moulds. In the right anterior sector the tunnels extend to the apical part of the conch.

REMARKS

The specimens of *Arachnostega* from the Teplá-Barrandian Cambrian show, despite the limited amount of material, a morphologically continuous spectrum. Irregular networks are the most common form of the trace. Bertling (1992), on the basis of Upper Jurassic material (not as numerous as specimens from the Spanish Ordovician, Mikuláš and Gutiérrez-Marco,

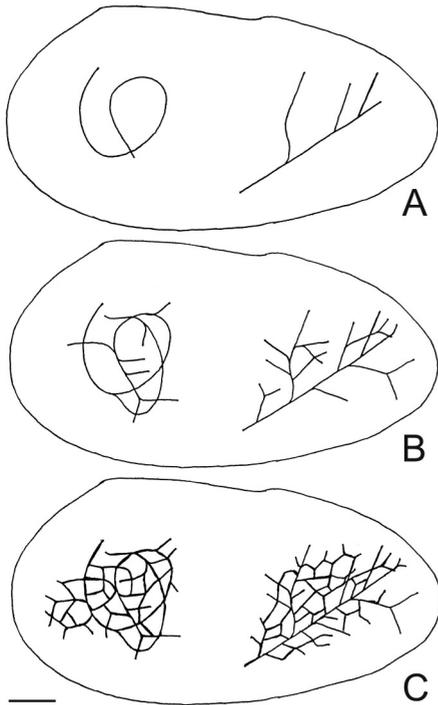
unpublished), stated in his original diagnosis of the ichnogenus: “Irregular elongate and net-like burrows...”. However, some specimens show burrow systems that do not form nets, but instead ramify in an analogous manner to *Chondrites* von Sternberg, 1833 or even show winding features. These burrows therefore do not agree with Bertling’s diagnosis even at ichnogenetic level. However, because they are connected to typical *Arachnostega* networks by morphologically transitional forms; the original diagnosis is emended herein.

A similar situation is found, for example, in the ichnogenus *Entobia* Bronn, 1837 (sponge borings in carbonate substrates). Individual representatives of *Entobia* were described in detail by Bromley and D’Alessandro (1984, 1989). Boring systems of *Entobia* are typical domichnia bounding the living space of their tracemakers. Their unusual morphological variability is reflected in the existence of several (five at maximum) considerably differing growth phases. The first of them is represented by “exploratory threads”; later the system thickens and usually forms chambers. The individual growth phases are not considered to be different ichnotaxa (though they represent distinguishable types of the animal’s activity – “exploratory phase”, “growth phase”, etc.). Besides this case of morphological variability, there exist also transitional forms among numerous individual entobian ichnospecies that are readily distinguishable in their typical forms (Bromley and D’Alessandro 1990).

In our opinion, the “*Chondrites*-like” or winding forms of *Arachnostega* are analogous to the growth phases of entobians (compare Text-fig. 6), and consequently their ichnotaxonomical separation would not be useful.

OCCURRENCE IN THE CAMBRIAN OF THE TEPLÁ-BARRANDIAN REGION

In the Příbram-Jince Basin, *Arachnostega* has been noted from numerous localities (e.g., Rejkovice-Potůček, Felbabka-Ostrý vrch Hill, Vinice Hill near Jince, Vystrkov Hill, Koniček Hill) which are assigned to the *Paradoxides* (*Eccaparadoxides*) *pusillus*, *Paradoxides* (*P.*) *paradoxissimus gracilis* and *Ellipsocephalus hoffi* – *Paradoxides* (*Rejkocephalus*) – *Lingulella* biozones of the Jince Formation (Text-figs 1, 2). In the Skryje-Týřovice Basin, *Arachnostega* is known from four localities: Buchava, Čihátko-Milíř, Dubinky Hill and Skryje-Plazy, which are assigned to the *Paradoxides* (*Eccaparadoxides*) *pusillus* Biozone of the Buchava Formation (Text-figs 1, 3).



Text-fig. 6. Presumed "growth stages" of the *Arachnostega* meshwork. Drawn from numerous specimens (including Ordovician specimens). From left to right, from top to bottom: Simply looping or ramifying systems represent an initial "growth stage" (more exactly, a "burrowing stage"). Found as such, they cannot be classified with certainty as *Arachnostega*. The system is subsequently completed by further tunnel "junctions" to form a network; new ramifying or looping parts may appear on marginal parts

## DISCUSSION AND CONCLUSIONS

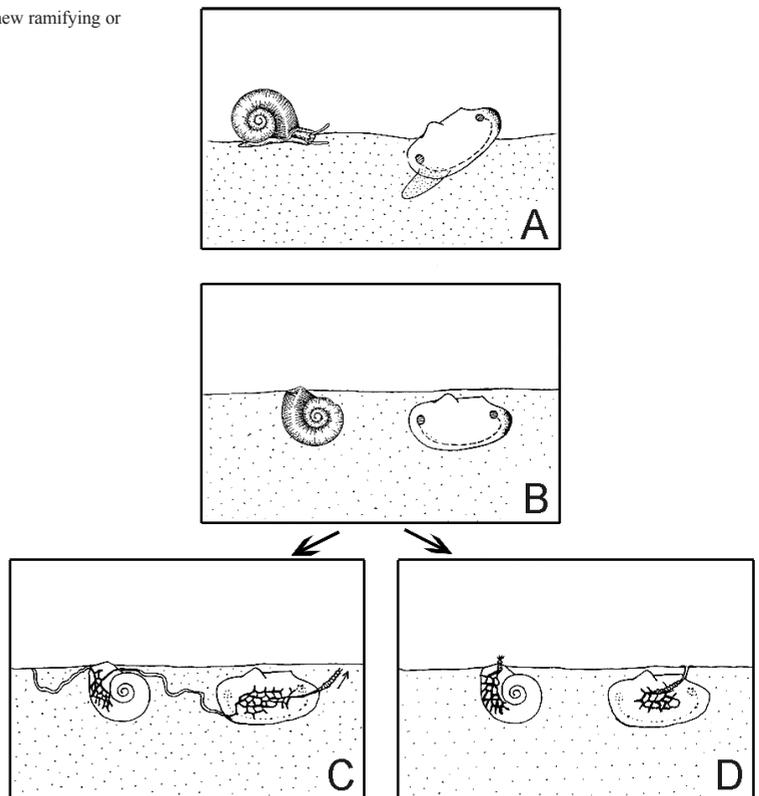
In contrast to the Jurassic material from internal carbonate reef sediments described by Bertling (1992), the specimens of *Arachnostega* studied herein come from clastic rocks, mainly greywackes, locally with a carbonate admixture. We agree with Bertling (1992) that the burrows were made in a relatively coherent substrate (consolidated soft-ground to firmground), as otherwise the tunnels would have collapsed.

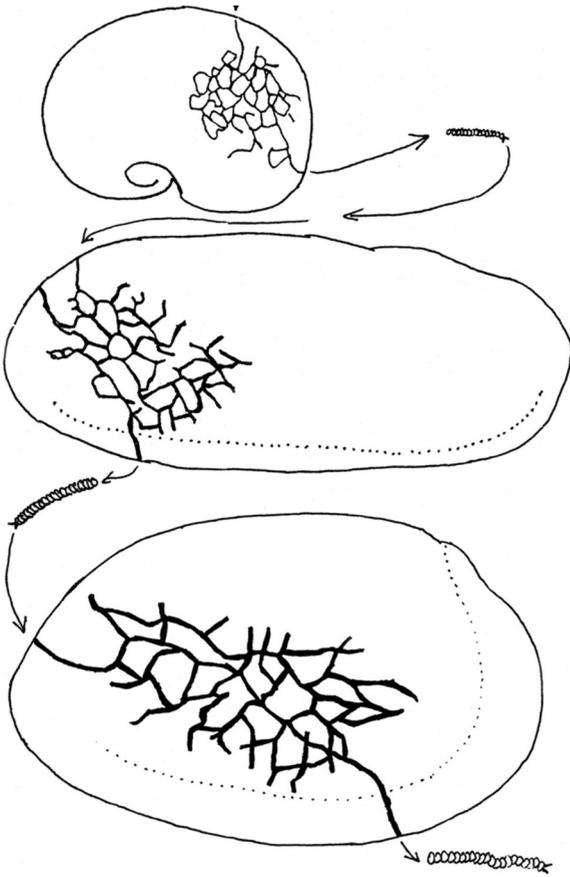
The ethology and biology of the burrowers can be interpreted from the specific taphonomy of the traces. The skeletal parts were attacked by the tracemakers after being covered and filled with the sediment.

Text-fig. 7. Two possible ethological explanations of *Arachnostega*. Two possible ethological explanations of *Arachnostega*. A, B and C: *Arachnostega* as fodinichnion; A, B and D: *Arachnostega* as domicnion.

Reineck (1980), in a study of Recent *Arachnostega*-like traces from the North Sea, stated that only specimens of molluscs that had been exhumed after filling with mud were infested with tracemakers; unexhumed specimens were not colonized. As we cannot expect any deep bioturbation in the dark siltstones and shales in the Cambrian (cf. Bottjer and Droser 1994), we can presume that most of the bioturbated shells were in contact with the sediment surface.

Concerning *Arachnostega*, the shape of the burrows and knowledge of morphologically similar traces provide two possible interpretations of the ethology represented (Text-fig. 6). First, we can consider *Arachnostega* to be analogous to 'open substrate' burrows such as *Chondrites*, *Gordia* or *Protopaleodictyon*. These can be classified as chemichnia, fodinichnia or agrichnia (cf. Bromley 1996). The analogy is supported by the uniform size of tunnels in the framework of each *Arachnostega* network, which suggests that the network was a feeding trace (fodinichnion) constructed during a relatively short period (e.g., a single feeding event; Text-fig. 6C), because there is no evidence of the growth of the tracemaker. However, the possibility that *Arachnostega* represents a dwelling burrow (domicnion) cannot be excluded with certainty since the net-like form is also characteristic of some domicnion, such as *Ophiomorpha*. Bromley (1996) regards *Tha-*





Text-fig. 8. Constant diameter of the tunnels of *Arachnostega* proves that individual networks do not preserve the tracemaker's growth

*lassinoides* as a fodichnion and *Arachnostega* could be an analogue of this type of trace fossil (see Text-fig. 6C). In this case, it is more probable that the tracemaker always formed a new burrow system when an existing one became too small, rather than re-burrowing the old network (Text-fig. 7). In our material, there is no evidence of such re-burrowing. These conclusions are in accordance with those of Bertling (1992), which were based on Jurassic material in the very special conditions of carbonate 'inner substrates' in a coral patch reef.

Bertling (1992) considered that *Arachnostega* represented a feeding trace; in his opinion, the internal sediments may have been richer in nutritional particles because of the decay of the mollusc. In the Spanish Ordovician material, there is no evidence of growth of the tracemaker (e.g. tunnels of various diameters, remains of smaller networks, presence of spreite-structures). However, Bertling (1992) considered the tracemakers to be r-strategists that did not actively search for the correct substrate. In our opinion, the tracemaker probably changed the 'host shell' several, or even many times (Text-fig. 7), and hence we presume its active searching for food.

The presence of *Arachnostega* on skeletons lying on and/or partly embedded in the clastic sea bottom presented in this paper evokes a possible connection between the *Arachnostega*-type behaviour (strategy) and the appearance of numerous large animals with skeletons as early as the Cambrian.

The sudden appearance and worldwide distribution of shallow-burrowing animals is one of the typical features of the 'Cambrian substrate revolution' (Bottjer *et al.* 2000) and the strategy of animals producing *Arachnostega*-like traces was obviously a very successful behaviour pattern. The 'explosion' of this behaviour culminated in the Ordovician, and was probably connected with the general increase in the bioturbation of muddy substrates in the Ordovician (e.g., Ekdale *et al.* 1984).

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