Tubular shell infestations in some Mississippian spirilophous brachiopods

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Evidence of brachiopod shell infestation by tube dwelling parasitic–commensal organisms is very rare in the fossil record. The oldest record of this kind of biotic interaction is known as *Eodiorygma acrotretophilia* from the Early Cambrian phosphatic acrotretoid *Linnarsonia*. The youngest evidence of parasitic infestation was documented in the Early Cretaceous rhynchonellide *Peregrinella multicarinata*. Two other records of vermiform tubes inside brachiopod shells come from the Devonian. These are *Diorygma atrypophilia*, infesting Givetian atrypide shells, and *Burrinjuckia spiriferidophilia*, found in some Emsian spiriferides. Here we describe the fifth record of this kind of infestation for which a name *Haplorygma dorsalis* ichnogen. et ichnosp. nov. is proposed. The tubular infestation structure was revealed in two silicified dorsal valves of spirolophous brachiopods found in the Mississippian Muhua Formation of the Southern China. The affinity of the tube-dwelling organism is rather enigmatic, but its annelid relationship and kleptoparasitic nature seems highly probable. In addition, the phoronid affinity of *Diorygma* is here questioned.

Key words: Brachiopoda, Spiriferida, Spiriferinida, biotic interaction, endosymbionts, Mississippian, Muhua Formation, Southern China.

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Introduction

Infestations inside brachiopod shells in the form of tubular vermiform outgrowths (bioclaustrations of Palmer and Wilson 1988; see also Tapanila 2005) are very scarce in the fossil record. One of the most remarkable skeletal responses of this kind is *Diorygma atrypophilia* Biernat, 1961. This endosymbiont was revealed in the interior of the ventral valves of the Middle Devonian atrypoid *Atrypa zonata* Schnur, 1851 (subsequently re-assigned to *Desquamatia subzonata* Biernat, 1964) from Poland (Biernat 1961). The second record of tubular trace fossil inside brachiopod shells was described as *Burrinjuckia spiriferidophilia* Chatterton, 1975. It was described in three different Emsian spiriferides from Australia by Chatterton (1975). Recently, two other cases of biotic interaction between the brachiopod host and tube-dwelling infester were recorded. One of them has been described as *Eodiorygma acrotretophilia* Bassett, Popov, and Holmer, 2004 from a Lower Cambrian organophosphatic lingulate brachiopod (Bassett et al. 2004). Lately, the worm-infested specimens of the Early Cretaceous hydrocarbon seep-restricted brachiopod *Peregrinella multicarinata* Lamarck, 1819 from southeastern Crimea, Ukraine were documented by Kiel (2008).

This paper describes a fifth and the youngest in the Palaeozoic phenomenon of such biotic interaction revealed in the Mississippian (Tournaisian) spiriferide and spiriferinide brachiopods that were equipped with the spirolophe lophophore. Thus, entire extent of time in which this particular kind of relation has been documented spans from the Early Cambrian to the early Cretaceous.

Material and methods

In studies of the Tournaisian silicified brachiopod fauna from Muhua (Guizhou Province, Southern China) conducted by the authors (e.g., Baliński 1995; Sun and Baliński 2008), two dorsal valves among several thousands of specimens preserve evidence of endosymbiotic infestation. The infested specimens include the spiriferide *Tylothyris laminosa* (M'Coy, 1841) and the spiriferinide *Spiriferellina* cf. *insculpta* Phillips, 1836.

A single juvenile dorsal valve of *Tylothyris laminosa* measuring 3.7 mm in width and 2.4 mm in length and collected from sample MH1 has a very small, simple tube growing from its inner surface (Fig. 1B). The tube is about 600 μm long and 160–190 μm thick. It has an apical, presumably single (there is some siliceous deposit obscuring the aperture), subcircular opening 90 μm in diameter. This tubular outgrowth is located on the inner right flank of the valve not far from the median fold. It is posteromedianly directed, somewhat sinuous, with its tip turning ventrally. Although the ultrastructure of the tube cannot be assessed due to silicification, it is clear that it was originally secreted by the brachiopod outer mantle lobe.

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A structure similar to that in *T. laminosa* has been found also in one dorsal valve of *Spiriferellina* cf. *insculpta* Phillips, 1836 from the sample GB (Fig. 1A). The dorsal valve, although imperfectly preserved, is about 7.8 mm wide and 5.1 mm long. The tube is located on the left internal flank of the valve in its posterior region and is posteromedianly inclined with its distal part upturned ventrally. The tube is about 750 μm long, 190–240 μm thick, with a single subcircular aperture 90 μm in diameter.

The two aforementioned specimens indicate a very low frequency of endosymbiotic infestation among brachiopods from the Muhua Formation. In the case of *Tylothyris laminosa* it is one out of 90 specimens whereas in *Spiriferellina* cf. *insculpta* a single infested dorsal valve was found among 6 specimens.

The tubular outgrowths described above were presumably inhabited by an unknown vermiform filter-feeding organism whose larva infested the dorsal valve of the brachiopod host either by entering its mantle cavity or by attaching directly to the anterior margin of the valve. In either case the growing body of a vermiform intruder was isolated by brachiopod mantle secreting the secondary shell material continuous with rest of the shell. The valve of *Tylothyris* attained at the moment of infestation probably about 1.5 mm in length and that of *Spiriferellina* attained about 2 mm length. In both cases the distal end of the fully grown tube extended into the mantle cavity close to the first or second turn of the spiral lophophore of the host (Fig. 2).

The general morphology of the protuberance on the inner surface of the dorsal valve of *Tylothyris laminosa* and *Spiriferellina* cf. *insculpta* indicates that the endosymbiotic intruder was probably an elongated, worm-like, filter-feeding small-sized organism living in the mantle cavity of the brachiopod host. The location of the tube on one side of the valve indicates that infesting organism did not intercept its food from the main inhalant feeding current of the brachiopod. Instead, it is more probable that it derived nutrition from the currents which passed through the lophophore of the host (Fig. 2).

The fossil record of parasitic–commensal infestations in brachiopod shells

The findings of tubular vermiform outgrowths inside brachiopod shells are very scarce in the fossil record. The first record of the parasitic–commensal relationship of this kind was described by Biernat (1961). She found characteristic tube-like protuberances (one or two per valve) inside as many as 15% of all ventral valves of *Desquamatia subzonata* Biernat, 1964 from Givetian shales in the Holy Cross Mountains, Poland (illustrated here for comparison on Fig. 1C). Each of these protuberances, named *Diorygma atrypophilia* Biernat, 1961, encloses two long contiguous tubes which open into the brachiopod interior by two round or slightly elliptical apertures (Biernat 1961). The outgrowths reach up to 12.2 mm in length and 2.5 mm in thickness and are anterodorsally directed. At first Biernat (1961) interpreted these structures as associated with an annelid-like parasitic organism. Later, however, McKinnon and Biernat (1970) suggested a probable phoronid relationship, pointing out that U-shaped tubes of *Diorygma* reflect the similarly shaped digestive tract of phoronids. This seems unlikely as phoronids are elongated worm-shaped animals having just U-shaped digestive tract, not their body (see also Emig http://paleopolis.rediris.es/Phoronida/SYST/PHORONIDA/Pho-FOSSIL/Diorygma-Eodiorygma.html). Two separate openings of *Diorygma* suggest that its digestive tract was straight and that its mouth and anus were located on opposite ends of a long U-turned vermiform body. This condition is unlike that in phoronids in which the gut ends close to the mouth (a result of the U-turned digestive tract) at one end of a more or less straight elongated body. It seems that the original interpretation of Biernat (1961) concerning the affinity of *Diorygma* is more plausible. It is not unusual to find some polychaetes housed in U-shaped galleries which have limbs running more or less straight and closely together (see, e.g., Rodrigues 2007; Rodrigues et al. 2008).

The second record of vermiform tubes inside brachiopod shells was that of Chatterton (1975). He found these structures on the inner surface of dorsal valves of three different Emsian spiriferide species from Australia and named those trace fossils as *Burrinjuckia spiriferidophilia* Chatterton, 1975. The tubes reach up to about 1.5 mm in diameter and are located invariably in the anteromedian part of the valve projecting sub-ventrally or anteroventrally between the bases of the spiralia. The location of the tubular protuberances indicates that they were inhabited by filter-feeding organisms that took advantage of the median inhalant feeding current of the host brachiopod (Chatterton 1975; see also Manceñido and Gourvennec 2008). According to Chatterton (1975), this is evidence of a commensal relationship between the brachiopods and *Burrinjuckia spiriferidophilia* (which is of uncertain taxonomic affinities).

The third recorded case of a parasitic–commensal relationship between brachiopods and tube-dwelling organisms

Fig. 1. Endobionts inside brachiopod shells. **A**. Dorsal valve of spiriferinide *Spiriferellina* cf. *insculpta* Phillips, 1836 showing infestation by *Haplorygma dorsalis* ichnogen. et sp. nov., PKUM02-0388; external view (A_1), stereopair of the interior (A_2) with the tube arrowed, SEM micrographs showing enlargement of the tube in lateral (A_3) and oblique ventral (A_4) views; note the corroded wall of the tube and partially exposed central canal; Muhua Formation, sample GB, Muhua, Guizhou Province, China. **B**. SEM micrographs of dorsal valve of spiriferide *Tylothyris laminosa* (M'Coy, 1841) showing infestation by *Haplorygma dorsalis* ichnogen. et sp. nov. (holotype, PKUM02-0389); stereopair of general internal view (B_1), stereopair of enlarged view (B_2), and oblique lateral view (B_3); Muhua Formation, sample MH1, Muhua, Guizhou Province, China. **C**. Stereopair of ventral valve of atrypide *Desquamatia subzonata* Biernat, 1964 showing two sub-symmetrically disposed tubular outgrowths of *Diorygma atrypophilia* Biernat, 1961; holotype ZPAL A 1/6; Middle Devonian (late Eifelian), Holy Cross Mountains, Skały (Poland); same as Biernat (1961: pl. 1: 6); new photographs.

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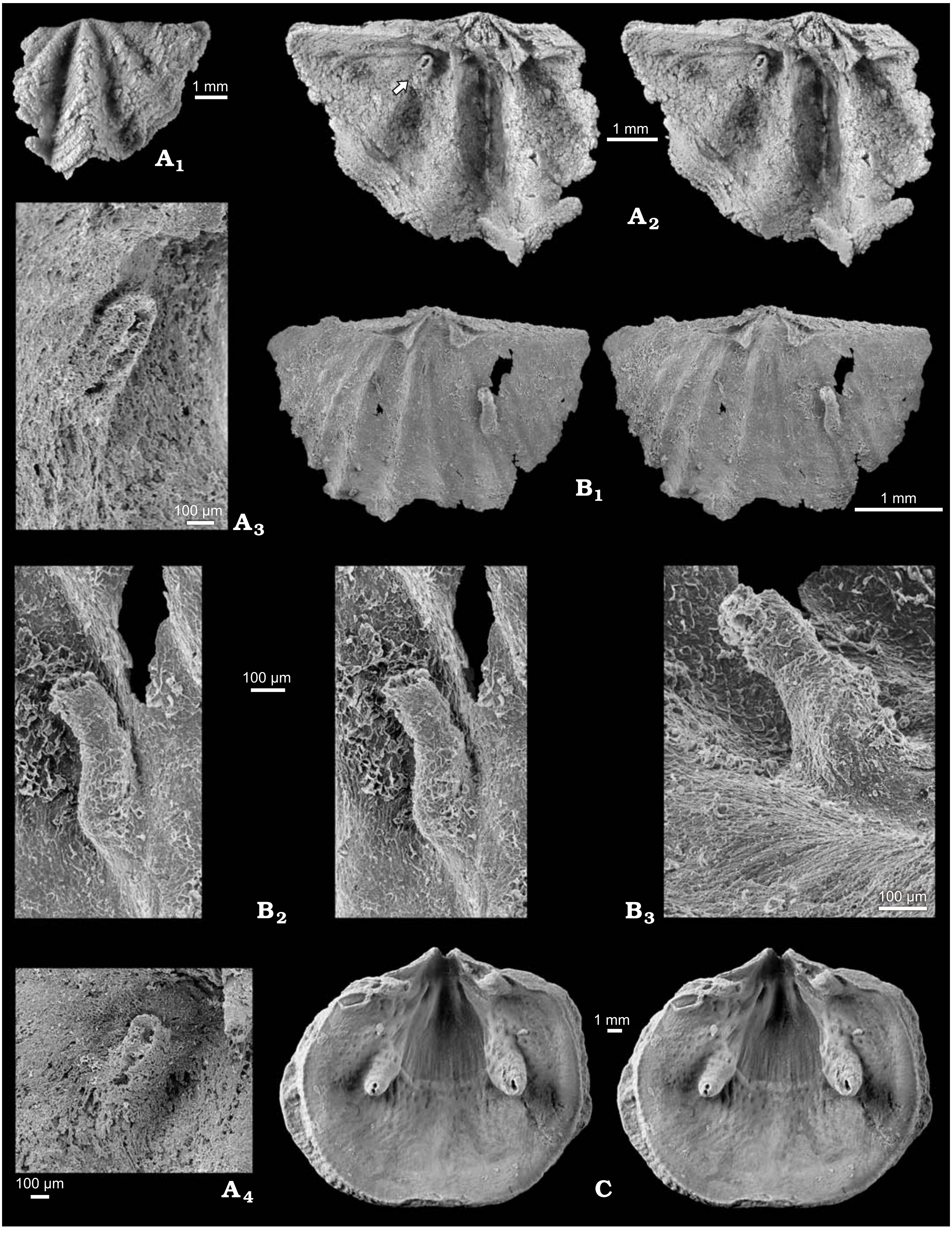

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is a unique specimen of the trace fossil *Eodiorygma acrotretophilia* Bassett, Popov, and Holmer, 2004 found recently in the phosphatic acrotretoid *Linnarsonia constans* Koneva, 1983 from the late Early Cambrian of Kazakhstan (Bassett et al. 2004). The brachiopod host is up to 3 mm in size while the tube itself is about 0.4 mm long and 0.1 mm wide with a single circular aperture 45 μm in diameter. The tube is laterally inclined indicating that the endosymbiont inhabited the brachiopod mantle cavity and exploited the host's filter-feeding system for its own respiratory and feeding needs (Bassett et al. 2004).

The fourth recorded case of a tubular infestation inside brachiopod shells was described in the Early Cretaceous hydrocarbon seep-restricted rhynchonellide *Peregrinella multicarinata* Lamarck, 1819 from southeastern Crimea, Ukraine (Kiel 2008). The tubes attain up to 75 mm in length and about 3.5 mm in diameter distally. They are often curved, undulating, sometimes U-turned, and always grow towards the anterior margin (= ventral margin of Kiel 2008). According to Kiel (2008) the tubes were built by polychaete worms within only the large shells of living brachiopods attaining at least 55 mm in width. A parasitic mode of life was suggested for this polychaete infester (Kiel 2008).

These four records discussed above of tubular vermiform structures inside brachiopod shells, as well as *Haplorygma dorsalis* ichnogen. et ichnosp. nov. reported here in the early Mississippian *Tylothyris* and *Spiriferellina*, indicate a similar phenomenon of a biotic inter-relationship (impedichnia of Tapanila 2005) between a brachiopod host and a filter-feeding organism invading its mantle cavity. However, each of these structures shows sufficient morphologic differences to distinguish them taxonomically.

Discussion

The taxonomic affinity of the tube-dwelling organism inside the shell of *Tylothyris laminosa* (M'Coy, 1841) and *Spiriferellina* cf. *insculpta* Phillips, 1836 is very difficult to assess. Bassett et al. (2004) discussed the possible relationship of *Eodiorygma* with some filter-feeding organisms and their remarks may be fully applied to *Haplorygma* described here. They sought the probable affinity of *Eodiorygma* within cycliphorids (a recently described new phylum) or entoprocts. For *Haplorygma* an annelid affinity possibility should not be discarded as well. There are numerous reports in the literature documenting trace fossils on invertebrate skeletons which are interpreted as a result of a biotic interaction with polychaetes (e.g., Kiel 2008; Martinell and Domènech 2009). Anatomical and ecological characteristics of *Haplorygma* suggest that while living in the mantle cavity of a brachiopod, it nourished on stolen undigested nutrients from the host and thus probably was kleptoparasitic. While living in the shell interior of a brachiopod host an infester gained a well protected place to live and a reliable supply of nourishment.

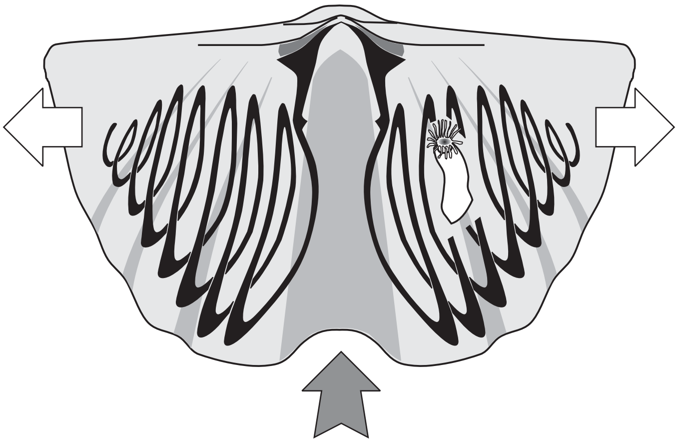

Fig. 2. Diagrammatical reconstruction of the dorsal valve of spiriferide brachiopod *Tylothyris laminosa* with part of the right spiralium removed to show hypothetical life position of the infester *Haplorygma dorsalis* ichnogen. et sp. nov. Grey arrow indicates presumable inhalant, open arrows exhalant currents.

All five records of endosymbionts in brachiopod shell have their own distinctive features and each appears isolated in space and time. Thus most probably they are not closely related to each other. On the contrary, it seems more probable that this kind of a biotic interaction between brachiopods and infesters appeared independently several times during the Palaeozoic and Mesosoic. Two of these records, namely the Cambrian *Eodiorygma* and Mississippian *Haplorygma* ichnogen. nov. are rare findings represented by one and two specimens, respectively. This suggests that relations of brachiopod host–infester in these two cases were quite unusual in those brachiopod populations, and that those infesters might have been more common in other benthic invertebrates although no evidence in the fossil record so far supports this idea. On the other hand, *Burrinjuckia* was found in three different species of spiriferide brachiopods and although "...only a small percentage of the total number of specimens" (Chatterton 1975: 371) were involved, several infested dorsal valves have been found. Noteworthy, *Burrinjuckia* shows some degree of specialisation, being invariably associated with the interior of spiriferide dorsal valves only. The case of *Diorygma* is distinguished by a comparatively high percentage of infested specimens. Moreover, some of the infested shells of *Desquamatia subzonata* show double infestation with two sub-symmetrically disposed tubular outgrowths (Biernat 1961; Fig. 1C). *Diorygma* is also distinguished by its apparent specialisation because it was found only in one of several other co-occurring atrypide species. What is more, in this case the infestation is associated exclusively with the ventral valves, and the tubes of *Diorygma* protrude into the conical spiral cavity of the infested atrypide. Thus, all five described cases of endosymbionts inside brachiopod shells have their own characteristics and peculiarities. They document what may be a wide and complex spectrum of biotic interactions that developed between brachiopods and infesters in the geological past.

Systematic palaeontology

Ichnogenus *Haplorygma* nov.

Ichnospecies type: *Haplorygma dorsalis* ichnosp. nov., by monotypy.

Etymology: Greek *haplóos*, simple, onefold, single; *orygma*, tunnel; from the simple tubular structure of the trace fossil.

Diagnosis.—Simple, posteromedianly inclined with distal part upturned ventrally, microscopic tubular outgrowth of the inner surface of the secondary organocalcitic shell layer of the dorsal valve of spiriferide and spiriferinide brachiopods.

Remarks.—The name of the trace fossil here described is treated in the meaning of Articles 10.3 and 42.2. of the International Code of Zoological Nomenclature (1999; see also Dzik 2005) and thus refers to the animals that are responsible for formation of the named structure. Because homeomorphy of the Cambrian *Eodiorygma* and Carboniferous *Haplorygma* is very probable (in contrary to their monophyly), we prefer to distinguish these trace fossils as separate genera.

This new genus of the trace fossils attains about 20 times smaller size of the tube than that in *Diorygma* Biernat, 1961 found inside shells of *Desquamatia subzonata* Biernat, 1964. What is more, the tube of *Haplorygma* is simple, inclined posteromedianly and sub-ventrally, and has only one distal aperture whereas that in *Diorygma* encloses two long U-turned contiguous tunnels which open distally by two round or slightly elliptical apertures and is anterodorsally inclined. The tube of the latter occurs exclusively in ventral valves of the atrypide host while the former was found in dorsal valve of *Tylothyris laminosa* and *Spiriferellina* cf. *insculpta*.

Haplorygma ichnogen. nov. reveals similar preference for dorsal valves of spiriferide (and spiriferinide) hosts as *Burrinjuckia* Chatterton, 1975 described from the Early Devonian of southern New South Wales (Chatterton 1975). The tube of the latter, however, is several times larger, shows somewhat irregular morphology, and is always located in the anteromedian part of the valve projecting sub-ventrally or anteroventrally whereas *Haplorygma* was found on the side of the valve and is clearly posteromedianly and sub-ventrally inclined. The polychaete tubes (not formally named) inside shells of the Cretaceous *Peregrinella multicarinata* Lamarck, 1819 from southeastern Crimea (Kiel 2008) are also large-sized attaining up to 75 mm in length.

In terms of size range and general appearance of the tubular outgrowth, the new genus is very similar to *Eodiorygma* Bassett, Popov, and Holmer, 2004 described from the late Early Cambrian of Kazakhstan (Bassett et al. 2004). Both structures do not exceed 1 mm in length. The main and obvious difference is that the structure of *Eodiorygma* occurs in a phosphatic-shelled brachiopod while *Haplorygma* is built in calcitic-shelled hosts. They differ also in the location and inclination of the tube within the dorsal valve: the Chinese form is positioned closer to the median sector of the valve whereas *Eodiorygma* seems more laterally located and has lateral inclination.

Stratigraphic and geographic range.—As for the type species.

Haplorygma dorsalis ichnosp. nov.

Fig. 1A, B.

Etymology: After the occurrence of the trace fossil in the dorsal valve of a brachiopod host.

Holotype: Trace fossil in the dorsal valve of spiriferide *Tylothyris laminosa* PKUM02-0389 figured in Fig. 1B.

Type locality: Muhua section, between villages of Muhua and Gedoungguan (Guizhou province, South China).

Type horizon: Muhua Formation, correlated with the middle Tournaisian *Siphonodella crenulata* Zone.

Diagnosis.—Microscopic tubular outgrowth of the dorsal valve of spiriferide and spiriferinide brachiopods, attaining 600–750 μm in length and 160–240 μm in thickness, with a single subcircular to elliptical aperture measuring about 90 μm in diameter.

Material.—One specimen of this trace fossil was found in dorsal valve of *Tylothyris laminosa* collected from sample MH1, the other specimen was revealed in dorsal valve of *Spiriferellina* cf. *insculpta* from sample GB.

Description.—The tubular outgrowth simple, small (see Diagnosis for detailed dimensions), posteromedianly inclined, with its distal tip upturned sub-ventrally; subcircular to elliptical in cross section.

Remarks.—As for genus.

Stratigraphic and geographic range.—Known only from the type locality, i.e., Muhua village (Guizhou Province, Southern China), Muhua Formation, Tournaisian, early Mississippian. For details on location, geology, and stratigraphy of the occurrence, see Sun and Baliński (2008).

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