

Bivalve borings in Lower Jurassic *Lithiotis* fauna from northeastern Italy and its palaeoecological interpretation

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ABSTRACT

Random shell sections of the Pliensbachian (Early Jurassic) larger bivalve *Opisoma* from columns within the Main Post Office building of Ferrara, northern Italy, have been discovered to bear neat clavate-shaped boreholes. These boreholes belong to the ichnogenus *Gastrochaenolites* Leymerie and represent bivalve borings. *Opisoma* is a subordinate component of the *Lithiotis* fauna characterised by aberrant shells thriving in tropical lagoonal settings which were widespread throughout the Tethyan and Panthalassa coasts. Although the *Lithiotis* fauna is well known in the palaeontological literature, no bivalve boring has been so far formally described. The uniqueness of the morphology, size and substrate of these borings merits the designation of the new species *Gastrochaenolites messisbugi* ichnosp. nov. which thereby represents the first ichnospecies described from this fauna. The morphology of the boreholes and the included bivalves allows the boring activity to be ascribed to a mytilid bivalve. Palaeoecological and taphonomic analyses allowed the presence of the boreholes to be correlated to the *Opisoma* mode of life (epifaunal, free-living form) as well as to generally low sedimentation rates and seasonal mesotrophic conditions during an overall oligotrophic regime.

KEYWORDS

Bivalve borings; ichnology; *Lithiotis* fauna; palaeoecology; Lower Jurassic; Italy

Introduction

The rapid increase of infaunal boring activity in the Mesozoic led to the rapid degradation of hard substrates especially in tropical and subtropical environments (Behrensmeier et al. 2000; Taylor & Wilson 2003). The infaunalisation of hard substrates may be a response to the rise of predators known as the Mesozoic Marine Revolution (Vermeij 1977, 2011; Aberhan et al. 2006). Mesozoic sclerobionts (*sensu* Taylor & Wilson 2003) which have encrusting, nestling and boring behaviour on or within biogenic hard substrates (e.g. shells) were particularly important during the Jurassic when they increased significantly with respect to diversity and abundance (Stanley & Hardie 1998; Taylor & Wilson 2003). Thus far, most data concerning Jurassic bioerosion originates from the Middle and Late Jurassic (e.g. Olóriz et al. 2004; Wilson et al. 2008; Hara & Taylor 2009; Zatoń, Machocka et al. 2011, Zatoń et al. 2011; Reolid & Benito 2012; Nieto et al. 2014; Reolid et al. 2015). There is much less known with respect to Lower Jurassic boring communities within biogenic substrates such as shells (e.g. Seilacher 1982).

The Early Jurassic represents a key period in the evolution of boring bivalves (Carter 1978; Carter et al. 2008) which are represented by three subfamilies: the Permophoridae (Carboniferous–Late Cretaceous), Gastrochaenidae (later-most Early Jurassic–Recent) and Hiattellidae (Late Triassic–Recent; Carter 1978). It is thus far uncertain whether or not the Gastrochaenidae and the Hiattellidae can be regarded as derivatives of the Permophoridae (subclass Heteroconchia; Carter et al. 2008). Two gastrochaenid genera, however, have been reported from the Jurassic: *Gastrochaena* Spengler, 1783 and *Spengleria* Tryon, 1872 (e.g. Pisera 1987). *Gastrochaena* has been reported from the Triassic and Early Jurassic (e.g. *G. infra-lisina* Terquem, 1855). *Spengleria* is represented in the Middle Jurassic by '*Gastrochaena*' sp. (Palmer & Fürsich 1974) and in the Late Jurassic by *S. recondita* (Phillips), 1829 and *S. corallensis* (Buvignier), 1843. All bore into calcareous substrates including both limestone rock and skeletons of corals and molluscs (Morton 1983, 1990; Pisera 1987).

The clavate (flask-shaped) bivalve borings in hard substrates including both cemented carbonate sediments and shell substrates are ascribed to the ichnogenus *Gastrochaenolites* Leymerie, 1842 (Kelly & Bromely 1984). *Gastrochaenolites* ranges from the Early Ordovician (Kelly & Bromely 1984; Benner et al. 2004) to the Recent (e.g. Ekdale & Bromley 2001; Vallon 2007). Although this ichnogenus is very common in Cretaceous and Cenozoic shallow-water marine shells (e.g. Taylor & Wilson 2003), Jurassic records are rather rare. Reliable occurrences of *Gastrochaenolites* are from Middle Jurassic ostreoliths (i.e. circumrotatory accumulations of oysters), corals and sponges (Wilson et al. 1998, 2008) as well as from Upper Jurassic crinoids (Feldman & Brett 1998). To date, the Jurassic *Gastrochaenolites* bivalve tracemaker remains unknown.

Abundant and diverse large, thick shelled bivalves suddenly appeared in the Early Jurassic along the southern Tethyan and Panthalassa margins giving rise to widespread assemblages such as the Pliensbachian *Lithiotis* fauna (Broglia Loriga & Neri 1976). Despite numerous investigations regarding this fauna, no information concerning ichnotaxa in these bivalve shells has been published. The fauna potentially offers an ideal study object to explore the evolutionary trends which gave rise to increasing biodiversity of the boring bivalves and to their ichnological products, the domichnia, i.e. borings. The rare examples of

boreholes found within Lower Jurassic marine shallow-water lagoonal bivalves from northern Italy thus represent important data points for the study of sclerozoan evolution. The aim of this study is to illustrate for the first time bivalve borings in larger bivalve shells, accessory taxon of the Pliensbachian *Lithiotis* fauna.

The studied ichnospecimens, which are rare throughout the *Lithiotis* fauna, are preserved in a column of Pliensbachian grey limestone used as ornamental stones in the Main Post Office (Palazzo delle Poste) in Ferrara (northern Italy). Studying the palaeoecology and taphonomy of the borings and their hosts allow for various ecological parameters such as trophic regimes and sedimentation rates to be assessed. The bivalve borings occurring in the Pliensbachian larger bivalves represent a new ichnospecies, which is described herein.

The *Lithiotis* fauna and its palaeoecological setting

The *Lithiotis* fauna represents a Lower Jurassic larger bivalve fauna distributed along the southern coasts of the Tethys and Panthalassa (e.g. Chinzei 1982; Posenato & Masetti 2012). Its distribution ranges from Southern Spain and Morocco, through Italy and Turkey/Iran/Iraq, to Tibet and Timor (e.g. Broglio Loriga & Neri 1976; Geyer 1977; Yin & Wan 1998; Leinfelder et al. 2002) and even reached Oregon (Nauss & Smith 1988; Fraser et al. 2004).

The *Lithiotis* fauna is dominated by the aberrant bivalves *Cochlearites* Reis, 1903, *Lithioperna* Benini 1979; and *Lithiotis* Gümbel, 1871. They were gregarious semi-infaunal and sessile suspension-feeders adapted to muddy substrate with high sedimentation rates (Chinzei 1982; Seilacher 1984, 1990; Broglio Loriga & Posenato 1996; Savazzi 1996). Subordinate bivalves of the *Lithiotis* fauna are represented by *Gervilleioperna* Krumbeck, 1923 and *Mytiloperna* Ihering, 1903, with similar life habits to the dominating aberrant bivalves (Broglio Loriga & Neri 1976; Seilacher 1984; Fraser et al. 2004; Posenato & Masetti 2012) as well as *Opisoma* Stoliczka, 1871, the subject of this study. *Opisoma* is an alatoform, opisthogyrate bivalve adapted to photosymbiosis and characterized by an epifaunal, sedentary habitat (see Posenato, Bassi and Nebelsick 2013).

The *Lithiotis* fauna usually occurs in hard cemented lime-stone in which only random sections of the bivalve shells are available. Detailed shell analysis has thus been largely based on isolated specimens serially sectioned along their lengths. These analyses allowed some genera to be identified even in random sections from hard cemented limestone using diagnostic shell characters (e.g. Accorsi Benini & Broglio Loriga 1977; Chinzei 1982; Seilacher 1984; Debeljak & Buser 1998; Posenato, Bassi and Nebelsick 2013).

In northern Italy, the fauna occurs in the Pliensbachian Formazione di Rotzo, a shallow-water sedimentary succession of the Trento Platform, a palaeogeographic unit of the Southern Alps (Venetian area; e.g. Bosellini & Broglio Loriga 1971; Clari 1975). The *Lithiotis* fauna, known from northeast Italy since 1871 (Gümbel 1871), thrived in shallow-water tropical lagoonal settings contributing to various sized mounds (Posenato & Masetti 2012) as well as bivalve carpets (Bassi et al. 2015). Associated benthic organisms are testate amoebae, dasycladaleans algae, larger foraminifera, brachiopods, gastropods, ostracods, and echinoderms (e.g. Boomer et al. 2001; Fugagnoli 2004; Bassi et al. 2008; Posenato, Bassi and Avanzini 2013; Posenato, Bassi and Nebelsick 2013, and references therein; Fugagnoli & Bassi 2015).

The Jurassic *Lithiotis* limestones of the Venetian area have been mined since the Roman times due to the attractive polished fossiliferous carbonates. They are characterized by the bright white larger lithiotid shells which contrast starkly to the dark grey or nearly black colour of the matrix. This building stone was used to decorate numerous palaces and churches in northeast Italy in, among others, Verona, Venice, Vicenza, Padua, Trento and Ferrara. Limestone from both the Formazione di Rotzo and the overlying Rosso Ammonitico Veronese (e.g. Martire et al. 2006) have been commonly used as building stones, decorative elements and statues in Ferrara as can be seen in many churches (e.g. Ferrara Cathedral), Renaissance buildings (Palazzo dei Diamanti) and in the later buildings including the Main Post Office which bears the columns analysed in the present study (Figure 2).

The Main Post Office of Ferrara: historical and architectural setting

The Main Post Office, designed by Angiolo Mazzoni was built in 1927 to 1929 and inaugurated on the 1st of June 1930. This monumental building is characterized by a marble facade with the main entrance punctuated by three large portals supported by tall twin columns. Details of the building allude to the rich architectural history of Ferrara including: (1) phytomorphic patterns of antiquity, (2) the Renaissance inspired faceted diamond motif, a clear reference to the Este banner which is repeated in the pilasters of the two upper floors, and (3) geometric brick patterns, a reference to the metaphysical art movement of the early twentieth century. In fact, one side of the Main Post Office is located next to the former Cavour barracks, where the modern metaphysicist painter Giorgio de Chirico, who often included the Este Castle in his iconic paintings, was once stationed.

Lithiotis limestones are included in various architectural elements of the building including panelling and columns. The studied ichnospecimens occur in the right column (one of two) about 3 m high and 0.50 m in diameter in the main entrance of the Main Post Office of Ferrara (Figures 1 and 2). Research carried out in the historical archives of the city of Ferrara did not provide any information concerning the suppliers of the materials used for the construction of the Main Post Office. The quarries of the Province of Vicenza have generally been the source of limestone rocks used in the monumental buildings of Ferrara. Furthermore, since the outcrops of the Formazione di Rotzo nearest to Ferrara are near Vicenza, it seems reasonable to attribute the origin of the studied columns to this area.

Bivalve hosts and their sedimentary matrix

The limestone of the columns consist of rudstone and float-stone with a wackestone to packstone matrix showing the characteristics microfacies of the *Lithiotis* facies as described in detail by Fugagnoli (2004), Posenato and Masetti (2012), and Posenato, Bassi and Nebelsick (2013).

Dominant components are the very rarely articulated shells with flattened and symmetrical valves ascribed to *Cochlearites* or *Lithioperma*. Thick, abraded and disarticulated shell fragments showing large teeth belong to *Opisoma* Stoliczka, 1871 (Figure 3(b) and (g)). The studied ichnospecimens occur only in these thick *Opisoma* shells. Subordinate components are represented by entire and fragmented thin-shelled bivalves (entire and frag-mented), and rare small brachiopods.

Many of the studied shells show high rates of surface abrasion thus only preserving the lower part of the burrows. Nevertheless, distinct morphological features of the *Opisoma* shells can be identified (Figures 3 and 4). The two burrows as shown in Figure 3(a) (including the holotype on the left hand side) show apertures in close proximity to one another suggesting that these at least are close to the original surface of the shell thus preserving the original morphology of the burrow. The burrows can be found on both the external and internal surfaces of the *Opisoma* shells. Besides the described borings there are also highly micritized shell surfaces.

Systematic palaeoichnology

Remarks. All the specimens studied and illustrated here are found in the column at the right-hand side of the main entrance of the Main Post Office of Ferrara, Italy (Figure 2). The age of the *Gastrochaenolites*-bearing limestone is referred as to Pliensbachian (Early Jurassic) by mean of the occurrence of large aberrant bivalves of the *Lithiotis* fauna (e.g. Posenato & Masetti 2012). The term 'specimen' is used as defined in Art. 72.1.2, International Code of Zoological Nomenclature (ICZN 1999). Morphological terminology follows Kelly and Bromely (1984). Guidelines proposed by Bertling et al. (2006) regarding the naming of trace fossils (ichnotaxobases) were followed.

Features relevant for the ichnotaxobase of the ichnogenus are:

(1) type of substrate, (2) clavate shape of the main chamber (e.g. Kelly & Bromely 1984). Features relevant for the ichnotaxobases of the ichnospecies are: (1) shape, and (2) ornamentation in the main chamber, (3) elongation of the boring, (4) details of the neck region, and (5) base of the boring.

(2)

Ichnogenus *Gastrochaenolites* Leymerie, 1842

Type ichnospecies *Gastrochaenolites lapidicus* Kelly and Bromley, 1984

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Figures 3 and 4

Diagnosis. Diagnosis. Clavate, smooth borings of circular section throughout; with a smooth shaft gently widening towards the main chamber.

Holotype. the holotype specimen, designated here, comprises a single individual, with preserved boring shell, embedded in an *Opisoma* shell fragment (Figure 3(a)), conserved in the column at the right-hand side of the main entrance of the Main Post Office of Ferrara, Italy

Paratypes. the specimens illustrated in Figures 3 and 4 occur-ring in the column at the right-hand side of the main entrance of the Main Post Office of Ferrara, Italy.

Derivation of name. The specific epithet honours Cristophorus Messisbugus (end of the fifteenth century–1548) who was a renowned Italian cook of the Renaissance in the service of the House of Este in Ferrara. His book 'Banchetti, composizioni di vivande e apparecchio generale' (Recipes and general utensils of banquets), published posthumously in 1549, is addressed to those preparing royal feasts and provides detailed descriptions of the menus for his official banquets at the Este court (Capatti & Montanari 2003).

Description: Borings clavate, smooth, ovate in longitudinal profile (Figures 1(a), 3(a), (c), (e) and 4(e)) and circular in section throughout (Figures 3(c), 4(h), and 5). Case of boring smooth, bluntly parabolic. Largest specimen 9 mm long (Figure 3(a); minimum 5 mm, s.d. 1.6) and 7 mm width (minimum 3 mm, s.d. 1.4). The average burrow volume is 0.15 cm³. Interior walls of the chamber are smooth, with no ornamentation present. The smooth circular aperture, which neither bear a tube nor a lining, gently widens towards the main chamber (Figures 3(c), and 5). The borings, nearly perpendicular to the outer surface of the host's shell, are infilled by dark micrite. Some borings preserve the shell of the producer, a bivalve mollusc (Figures 3(c), (e), and 4(e)). The bivalves preserved into the holes are up to ca. 8 mm long.

Remarks. The studied ichnospecimens are ascribed to the ichnogenus *Gastrochaenolites* Leymerie, 1842, which is produced by boring bivalves (e.g. Kelly & Bromely 1984). Kelly and Bromely (1984) re-assessed the ichnogenus *Gastrochaenolites* and morphologically circumscribed it as clavate boring in lithic substrates. The main chamber of this ichnotaxon ranges in shape

from sub-spherical to elongate with an aperture that can be separated from the main chamber by a neck region. The diagnostic characters used to distinguish the species are the shape of the main chamber, the occurrence of one or two tubes in the neck region, and the shape (bilobate, smooth, parabolic) of the base of the boring (e.g. Kelly 1980; Kelly & Bromely 1984; Edinger & Risk 1994; Wilson & Palmer 1998; Ekdale & Bromley 2001; Donovan 2002; Kleemann 2009; Rahman et al. 2015). The species identification needs, therefore, well preserved ichnospecimens or representative sections showing these diagnostic characters (Bertling et al. 2006), as with the investigated specimens.

At least ten specific ichnotaxa have been assigned to *Gastrochaenolites* (e.g. Kelly & Bromely 1984; Donovan 2002; Donovan & Hensley 2006; Santos et al. 2011; Donovan et al. 2014). Diagnostic morphological features of species are summarized in Table 1. *Gastrochaenolites messisbugi* ichnosp. nov., with the characteristics of *Gastrochaenolites sensu* Kelly and Bromely (1984), differs from other species in having the following combination of features: (1) a main chamber ovate in longitudinal profile and circular in section throughout, and (2) a circular aperture (neck absent; Table 1). *G. messisbugi* ichnosp. nov. shows affinities with the chamber shape of *G. lapidicus* Kelly and Bromley, 1984 but differs from it in having a circular aperture (no neck) in cross section. In circumscribing *G. lapidicus* Kelly and Bromley (1984) state that ‘there is a clear neck region which is a distinguishing feature separating it from *G. turbinatus*’ and Donovan (2013) found that the ‘neck may have been slightly elliptical in section’. *G. turbinatus* Kelly and Bromley, 1984 has in fact a completely different chamber with an evenly tapered chamber and neck (Table 1). Furthermore, *G. lapidicus* and *G. turbinatus* show larger dimensions (nearly twice the size) than *G. messisbugi* ichnosp. nov. and have been found boring lithic substrates, *G. turbinatus* is rarely present in bivalve shells (e.g. Cachão et al. 2011; Santos et al. 2011; Donovan 2013; Pineda-Salgado et al. 2015; Table 1).

Gastrochaenolites messisbugi ichnosp. nov. is presently known only from the studied Pliensbachian limestone making up the column occurring in the Main Post Office di Ferrara. *G. messisbugi* ichnosp. nov. is, as far as known, the only ichnospecies made by bivalves (preserved into the borings) occurring in Lower Jurassic larger bivalves. There also do not seem to be any published records of Jurassic *Gastrochaenolites* with preserved boring bivalves in larger bivalve host.

In hard carbonate substrate such as shells boring bivalves inhabiting holes are sedentary and boring is accomplished by secretion of low pH chemicals and/or mechanical rasping (Kleemann 1996; Taylor & Wilson 2003). Most boring mytilids are chemical borers and prefer hard carbonate substrates, while all pholadids are mechanical borers preferring firmgrounds such as hardened mud and wooden substrates (Savazzi 1999; Owada 2007, 2009, 2015). Considering that the base of the studied chambers is smooth, it can be argued that the boring bivalves acted as chemical borers. Mechanical action produces ornamented interior walls and the chamber bases (Savazzi 1999), which is not the case in the present study (Figures 3 and 4). The producer of *Gastrochaenolites messisbugi* ichnosp. nov. is, therefore, interpreted to be a mytilid bivalve. Since boring mytilid bivalves do not have a siphon (e.g. Carter 1978), they always keep up their position at the chamber entrance in order to respire and feed. Consequently, there is no neck of the chamber as in the case study. Boring mytilids differ from pholadids in having a space between the shell and the borehole wall since the specimen needs to move back and forth (Carter 1978; Owada 2007). The preserved bivalve specimens inside the studied holes are thus smaller in size than the chamber which they produce and occupy (e.g. Figure 3(a), (c), and (e)). Gastrochaenids, which are also chemical borers, also produce a tube and a calcareous lining in the borehole. These two characters are not present in the studied boring bivalves preserved in the holes. An ascription to gastrochaenids as the producer of *Gastrochaenolites messisbugi* ichnosp. nov. is therefore ruled out. This reinforces the taxonomic ascription of the boring bivalve to the mytilid group and the introduction of a new ichnospecies of *Gastrochaenolites*. In fact, *G. lapidicus*, as above discussed in the systematic remarks, is most likely produced by the bivalves *Gastrochaena* and *Barnea*, which are respectively gastrochaenid and myoid taxa (e.g. Donovan 2013; Donovan & Jagt 2013).

Pisera (1987) described boring bivalve species in Upper Jurassic coral colonies from northern Poland. Although these bivalve species show comparable shell sizes to the holes represented by *G. messisbugi* ichnosp. nov., chamber shapes and apertures differ from the Pliensbachian studied ichnospecimens. The recorded boring mytilid bivalves represent thus far the first record of this group in the Lower Jurassic *Lithiotis* fauna.

Palaeoecology of bivalve borings and the bivalve host

Jurassic *Gastrochaenolites* have been found occurring in corals, sponges, and crinoids (Feldman & Brett 1998; Wilson et al. 1998, 2008), but no examples are reported from bivalve shells including the larger bivalves of the widely distributed Lower Jurassic *Lithiotis* fauna. The paucity of macroborings in the *Lithiotis* fauna is enigmatic given the numerous and diverse number of thick bivalve shells present in this facies. This scarcity is not due to sampling bias as a very large number of these shells have been examined. The scarcity of macroborings may thus reflect a complex palaeoecology and taphonomic history.

Gastrochaenolites messisbugi ichnosp. nov. only occurs in *Opisoma* shells and not in the other larger bivalves of the *Lithiotis* fauna. *Opisoma* was an alatoform, opisthogyrate bivalve adapted to photosymbiosis and characterized by an epifaunal sedentary life. This bivalve lived on soft substrates, under low sedimentary rates, with the flattened surface facing the bottom. The *Opisoma* shell consists of two parts. The rarely preserved anterior part was very fragile and thin and was exposed outside the sediment permitting the transmission of light into the internal tissues harbouring photosymbionts in the chambered wings and main body cavity (Posenato, Bassi and Nebelsick 2013; Figure 6(a)). The posterior part of the shell was massive and heavy for the substrate stabilization and is generally the only part preserved (Seilacher 1990; Aberhan & von Hillebrandt 1999; Posenato, Bassi and Nebelsick 2013).

The studied ichnospecimens were formed necessarily on post-mortem disarticulated, abraded and fragmented *Opisoma* shells. The photosymbiotic *Opisoma* was highly specialised and sensible to environmental changes (Posenato, Bassi and Nebelsick 2013). Colonization by borers in living *Opisoma* shells is thus ruled out. The shells experienced a prolonged surface residence time before burial (Figure 6(b)) allowing for surface micritization and abrasion to occur. The texture of the pack-stone sediment matrix, characterized by chaotically arranged, fragmented biogenics suggests that the final burial was caused by a high energy event (i.e. storm; see also Posenato, Bassi and Nebelsick 2013).

Present-day species of boring bivalves (such as *Gastrochaena hians*, *G. (Rocellaria) ovata*, *Lithophaga patagonica*, *Lithophaga lithophaga*, *Spengleria rostrata*) show ages from 10 to 54 years old (Carter 1978; Bagur et al. 2013; Peharda et al. 2015). Comparing the length of the studied *Gastrochaenolites*, presumably corresponding to the length of the mytilid boring bivalve, with the length/growth-rate ratio of Recent mytilid boring bivalves, the studied specimens are likely to only be up to a few years in age. Bioerosion rates as such are obviously difficult to calculate for fossil bioeroders. Given the small size of the specimens described here, however, lower bioerosion rates are assumed than for example those of ca. $0.20 \text{ cm}^3 \text{ yr}^{-1}$ calculated for intertidal *Lithophaga patagonica* from Southwestern Atlantic (Bagur et al. 2013). The high amount of bioerosion shown in *Opisoma* shells is in accordance with the interpreted low sedimentation rates of the original sedimentary environment. Substrates such as recent dead corals (e.g. Bertling 1997; Buatois & Mángano 2011) also show intense bioerosion rates in areas of reduced sedimentation.

In addition, bioerosion by macroborers is higher in macroalgal-dominated habitats that are close to sources of terrestrial runoff and experience increased nutrient loading (Holmes et al. 2000; Chazottes et al. 2002; Smith 2011). Increased nutrient supply and substrate exposure time are factors facilitating bio-erosion among heterotrophs (Tapanilla & Hutchings 2012). During its formation, the Formazione di Rotzo recorded distinct changes from eutrophic to oligotrophic conditions (Fugagnoli 2004). Within these sediments, *Opisoma* occurs within the upper *Orbitopsella* Zone toward the top of the formation in an interpreted oligotrophic setting (Figure 2; Posenato, Bassi and Nebelsick 2013). The occurrence of high rates of bivalve borings on these mollusc shells may thus point to a seasonal or temporal change from oligotrophic to at least mesotrophic conditions (e.g. Fugagnoli 2004) favourable to the occurrence of the filter feeders bioeroding bivalves.

Boring organisms in the bivalves of the Pliensbachian *Lithiotis* fauna seem to be restricted to *Opisoma* and are lacking in *Cochlearites*, *Lithioperla* and *Lithiotis*. *Opisoma* was an epifaunal, free-living bivalve, while the other three bivalves are considered mud-sticking, semi-infaunal forms (Benini 1979; Seilacher 1984). Rare bioerosion traces (e.g. *Trypanites*, *Entobia*) have been identified in *Lithiotis* faunas (Lee 1983; Fraser et al. 2004), but never illustrated. Furthermore, in a detailed study of bivalves carpets within the Formazione di Rotzo, Bassi et al. (2015) reported only very rare examples of narrow, tunnel-like borings with in thin-shelled Isognomonidae-like bivalves. This paucity of bioerosion is accompanied by a general lack of encrustation on these large, hard substrates both during life and after death. This general lack of evidence for Lower Jurassic bioerosion has been attributed to taphonomy (i.e. low preservation potential; Harper et al. 1998) and to the Triassic–Jurassic mass extinction which eliminated a larger part of the bioeroding organisms (Fraser et al. 2004). The examples described in this study show, however, that under certain conditions including the availability of suitable carbonate substrates and trophic regimes as well as low sedimentation rates, bioerosion did in fact occur.

Concluding remarks

- (1) Boreholes occurring in Pliensbachian larger bivalve *Opisoma* of the *Lithiotis* fauna are ascribed to the ichnogenus *Gastrochaenolites*, which is produced by boring bivalves. These borings are preserved in a limestone column present within the Main Post Office in Ferrara, northern Italy.
- (2) *Gastrochaenolites messisbugi* ichnosp. nov. is described. It is distinguished by a main chamber circular in section throughout, a smooth, ovate main chamber with a circular aperture.
- (3) This is the first record of boreholes and their producers (mytilid bivalves) in one of the larger bivalves of the globally occurring *Lithiotis* fauna which is a unique facies in the Lower Jurassic Tethys and Panthalassa.
- (4) The presence of mytilid boring bivalves was positively influenced by the presence of thick bivalve shell substrates of epifaunal, free-living forms, low sedimentation rates, and seasonal or temporal mesotrophic conditions within an overall oligotrophic regime.

Acknowledgements

The paper greatly benefited from thoughtful reviews of M. Reolid and an anonymous reviewer.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by local research funds at the University of Ferrara (FAR 2012–2015, Bando FIR 2016).

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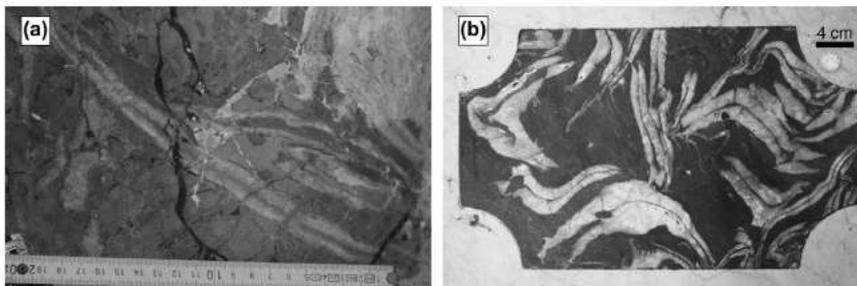


Figure 1. Lower Jurassic (Pliensbachian) limestones of the Trento Platform have often been used in the Renaissance Italian palaces. (a) Detail from the column occurring in main entrance of the Main Post Office of Ferrara, northern Italy, with a large bivalve (*Lithioperna?*) of the *Lithiotis* fauna. (b) Detail of the floor in the Duke Ercole's chapel (1587–1590) in the Este Castle, Ferrara.



Figure 2. Panoramic view of the Main Post Office of Ferrara, built in 1927–1929, showing the main entrance with the column (arrow) bearing the studied ichnospecimens (with location of the holotype) consisting Pliensbachian shallow-water limestone originated from the Trento Platform, southern Alps, Italy.
 Notes: The probable stratigraphic setting of the studied *Opisoma*-bearing limestones (arrows) on the Trento Platform (Southern Alps, northern Italy); modified from Posenato, Bassi and Nebelsick 2013. Mid Jur, Middle Jurassic; Sinemur, Sinemurian; Toar, Toarclan; Lool, Lopplo Oolite; Oz, *Orbitopsella* Zone; Lcz, *Lituosepta compressa* Zone; MOL, Massone Oolite Limestone; TF, Tenno Formation; SVO, San Vigilio Oolite; RAV, Rosso Ammonitico Veronese.

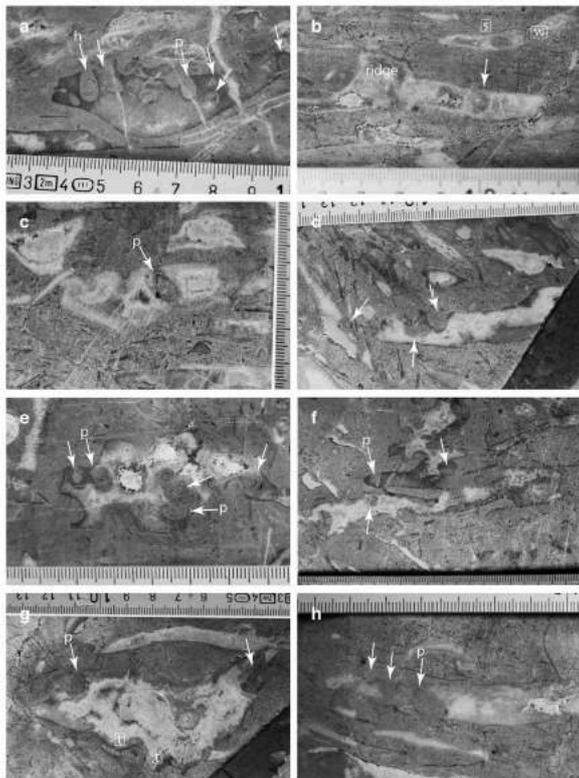


Figure 3. *Gastrochaenolites messibugi* ichnospp. nov., Pliensbachian, southern Alps, Italy. (a) Holotype (h), showing the characteristic clavate, smooth shape and the typical smooth shaft generally widening towards the main chamber. (b–h) *Gastrochaenolites messibugi* ichnospp. nov., (arrows; p, paratypes); some borings preserve the shell of the producer, a bivalve mollusc: (c, e, g).
 Note: The bivalve borings occur in the *Stalofium* *Opisoma* shells which are characterized by wings (w) with septa (s), a thick apical ridge and a strong hinge (h, tooth).

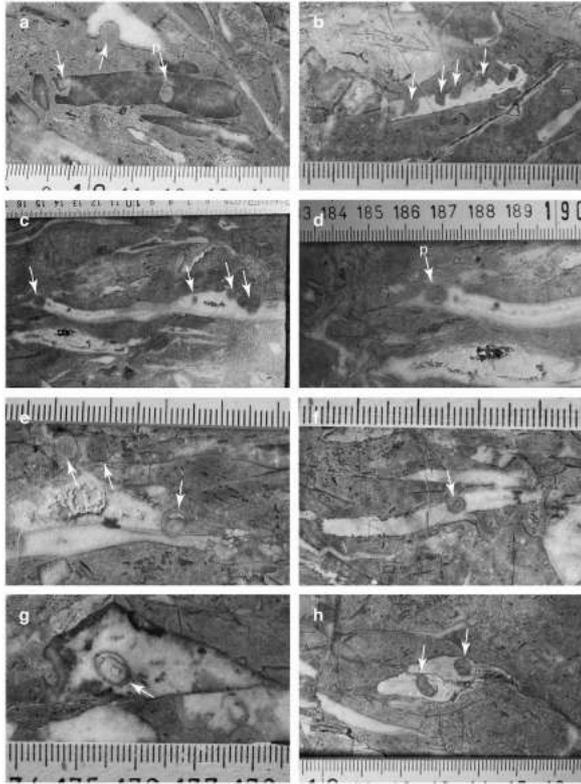


Figure 4. *Gastrochaenolites messisbugi* ichnosp. nov., Pliensbachian, southern Alps, Italy. (a-h) ichnospecimens (arrows; p, paratypes), nearly perpendicular to the outer surface of the host shell, are infilled by dark micrite and can preserve the shell of the producer (e-h). Note the bivalve hosts are never encrusted.

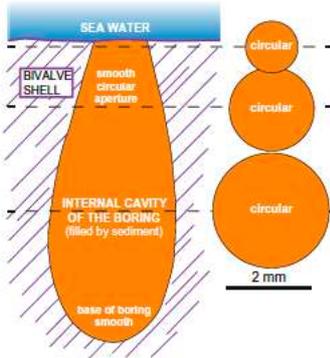


Figure 5. Sketch of the longitudinal section through *Gastrochaenolites messisbugi* ichnosp. nov., Pliensbachian of northeast Italy, without the boring bivalve fossil, showing cross-sectional shapes at various levels within the boring.

Table 1. Comparison of ichnotaxobases characteristics of *G. messisbugi* ichnosp. nov. with *Gastrochaenolites lapidicus* Kelly and Bromley, 1984 and *G. turbinatus* Kelly and Bromley, 1984.

	<i>G. lapidicus</i>	<i>G. turbinatus</i>	<i>G. messisbugi</i> ichnosp. nov.
Morphology			
Overall shape	Smooth clavate, elongate ovate, circular cross-section throughout length, neck slightly narrower than the main chamber	Acutely conical, evenly tapered body and neck, circular cross-section throughout length	Smooth ovate, circular cross-section throughout length, circular aperture, neck absent
Orientation	Sub-perpendicular, undetermined	Sub-perpendicular, undetermined	Perpendicular to the outer shell surface
Ornamentation	Absent	Absent	Absent
Internal structure	Absent	Absent	Absent
Substrate	Lithic (clasts, cobbles)	Lithic (clasts, cobbles), bivalves ^a , oysters ^b	Bivalve shells

^aDonovan and Hershey (2006).

^bDonovan et al. (2014).

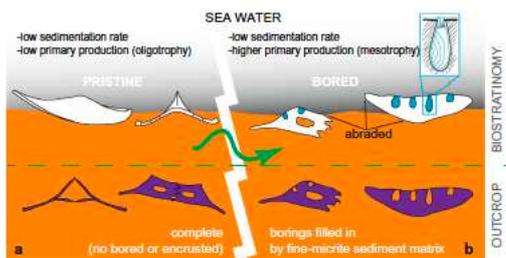


Figure 6. Schematic summary of development and preservation of the Pliensbachian bivalve borings in disarticulated larger *Opisoma* shells. Not to scale. (a) *Opisoma* thrived as epifaunal, free-living on soft substrate under low sedimentation rates (Posenato, Rasi and Nebelick 2013). After the death of the bivalve, if little or no disarticulation occurred, the shells were preserved without bioerosion or encrustation. (b) The subsequent high energy events such as storms lead to the disarticulation and fragmentation of the *Opisoma* valves. These served as hard substrates for the infesting boring bivalves during a seasonal or temporary periods with mesotrophic conditions. Ichnospecimens within their bivalve host are filled in by very fine micritic matrix which marks the burial of the bioeroded bivalves.