Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 122(1): 53-62. **March 2016**

BULLDOZING AND RESTING TRACES OF FRESHWATER MUSSEL *ANODONTA WOODIANA* AND SUBSTRATE CHARACTERISTICS IN LAKE-MARGIN AND RIVER SETTINGS OF UMBRIA, ITALY

PAOLO MONACO[1*], FEDERICO FAMIANI[2] & FABIO LA IACONA[3]

[1]Dipartimento di Fisica e Geologia, via Pascoli snc, 06123 Perugia, Italy. E-mail: paolo.monaco@unipg.it. *Corresponding author.
[2]School of Advanced Studies-Geology Division, University of Camerino, Via Gentile III da Varano, I-62032 Camerino, Italy. E-mail: federico.famiani@unicam.it
[3]Via Masaniello 50, 93016 Riesi, Caltanisetta, Italy. E-mail: laiaconaf@gmail.com

To cite this article: Monaco P., Famiani F. & La Iacona F. (2016) - Bulldozing and resting traces of freshwater mussel *Anodonta woodiana* and substrate characteristics in lake-margin and river settings of Umbria, Italy. *Riv. It. Paleont. Strat.,* 122(1): 53-62.

Key words: Ichnology, freshwater, *Anodonta* mussel, substrate, Umbria, Italy.

Abstract. The neoichnology of the freshwater mussel *Anodonta* (*Sinanodonta*) *woodiana* (Lea, 1834) is examined herein in some continental environments of Umbria (central Italy), such as lake-margin and river dam-margin settings. This study, based on analysis of about 200 traces, reveals that this mussel burrows employing two types of behaviours: bulldozing which produces horizontal meanders to straight bilobate traces, often filled with peloidal faecal pellets (pseudofaeces and backfill), and resting (vertical stationary into substrate) while filter feeding. A new type of very soft substrate, the 'cloudground' is proposed. It is placed at the water-sediment interface, above the soupground. After four years of observation, the cloudground was buried with shells and traces, preserving through the fossilization barrier about 20% of the *Anodonta* traces. This bivalve activity is a useful tool to recognize preservation of mud in quiet environments and parallels ichnological evidence of unknown epichnial trace fossils in the continental realm. Cloudground with resting traces must be investigated also in modern marine basin floor environments where cloud of mud dominates and considered also in geological record.

INTRODUCTION

Some substrate characteristics, such as firmness and water content, may influence the formation of traces (modern and fossils) and their preservation is fundamental to trespass the fossilization barrier in many types of marine and freshwater environments (Bromley 1990, 1996; Ekdale 1985; Goldring 1995; Hasiotis 2002; La Croix et al. 2015; Melchor et al. 2012; Miller 2007; Monaco 2002; Seilacher 1964, 1982). Among burrowing bivalves, mussels and clams can represent a very important category of burrowers in different types of marine, transitional and freshwater substrates (Bromley 1996; Frey & Seilacher 1980; Frey & Pemberton 1985; Ekdale 1985; Goldring 1995; Ekdale & Bromley 2001; Gingras et al. 2001; Buatois & Mángano 2011; Melchor et al. 2012; Scott et a. 2012; Gosling 2015; Knaust 2015). The most known are endobenthic siphon-bearing bivalves such as tellinids and nuculids, some of which include tracemakers of the recently named ichnofamily Siphonichnidae (*Siphonichnus* ispp.), which includes equilibrichnia with a predominantly deposit-feeding behaviour (Dashtgard & Gingras 2012; Zonneveld & Gingras 2013; Knaust 2015). Less known are studies in the freshwater substrates, such as lake margin settings (Buatois & Mángano 2007; Scott et al. 2012) or fluvial environments (Buatois & Mángano 2007; Melchor et al. 2012). Different ethologic behaviours, e.g. pascichnia, fodinichnia and repichnia, are preserved in different types of grounds, usually softground, hardground or woodground (Clarke 1981; Crampton 1990; Evans 1999; Hasiotis 2002; Monaco et al. 2011; Buatois & Mángano 2011; Melchor et al. 2012; Knaust & Bromley 2012; Scott et al. 2012; Seilacher 1990; Stárková et al. 2015). La Croix et al. (2015) indicate that there is a marked diminution in the sizes of traces and a corresponding decrease in their distribution (reduced abundance of burrowed versus unburrowed beds) with decreasing salinity. The salinity influence has been discussed also in Buatois & Mángano (2011). The soupground and soupground/softground boundary, in contrast to the case of soft-firm-hard and wood substrates, has been poorly exploited in the littoral zone of the freshwater realm (Hasiotis 2002; Buatois & Mángano 2011; Melchor et al. 2012; Scott et al. 2012).

Received: November 03, 2015; accepted: February 12, 2016

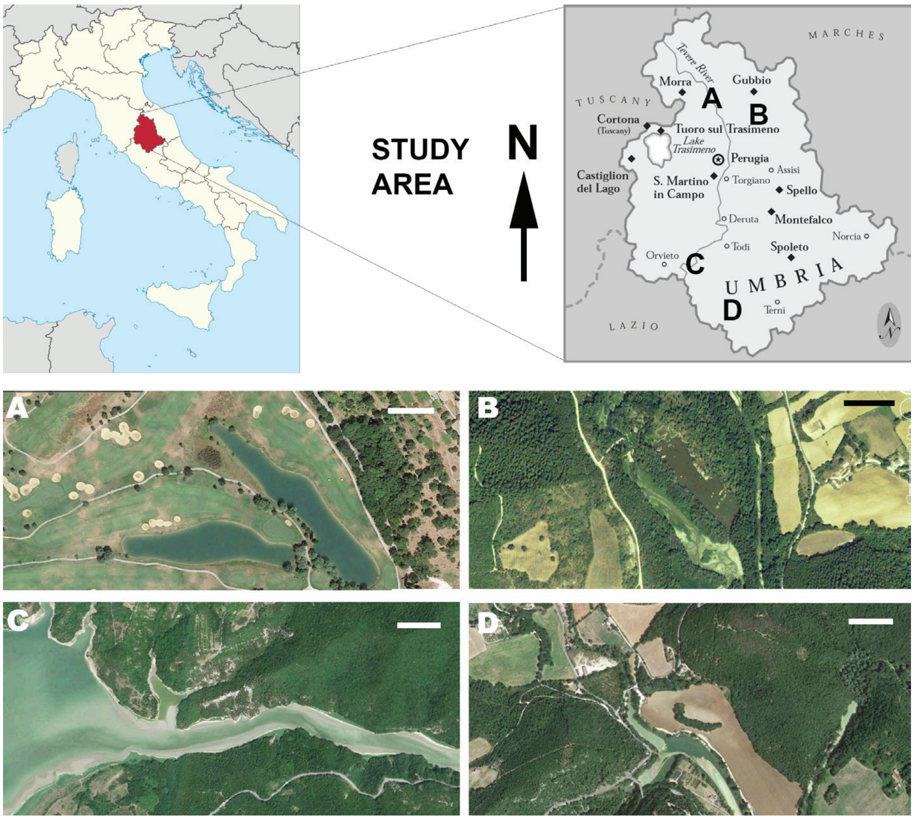

Fig. 1 - Study area with localization of *Anodonta* sites. A) Antognolla lakes. B) Chiascio river. C) Corbara dam - Tevere river; D) Rio Grande - Amelia dam. Umbria map is redrawn from IGM map 1:100.000. Bar = 500 m.

Anodonta is a genus of freshwater mussels in the family Unionidae, the river mussels, and can be found in many freshwater environments as lakes, rivers and continental ephemeral pounds but little is known about their burrowing activity (Taylor 1981). In North America, since the important studies of the great American conchologist Isaac Lea (1792 -1886), many species have been described (Clarke 1981; Taylor 1981; Yen 1947), indicating that further phylogenetic analysis of the Anodontinae is required including both North American and Eurasian species (Douda et al. 2011). Since the time of Lea there has been much confusion regarding the taxonomic status of this and other *Anodonta* of western North America (Williams et al. 1993).

The aim of this paper is to show how the freshwater mussel of the species *Anodonta woodiana* can produce burrows in littoral lakes and river margins of Umbria (central Italy), reaching a few centimeters in thickness over softground, producing locomotion and resting traces.

Study area and methods

In recent decades several species of freshwater mussels have a remarkable expansion, representing some of the most invasive species; they have considerably altered ecosystems worldwide (Kiss 1992; Paunovic et al. 2006; Douda et al. 2011). One of the most invasive aquatic species is the Chinese pond mussel *Anodonta* (*Sinanodonta*) *woodiana* (Lea 1834; Kiss 1992). *A. woodiana* is a species of East Asian unionid mussel that has a mandatory parasitic stage (*glochidium*) which encysts on fish. The high incidence of *A. woodiana* is due to introduction of allochthonous species of fishes at different sites in Europe (Kiss 1992; Douda et al. 2011). Their high invasion potential has been partially attributed to their free-living larvae, which have a high dispersal capability. The first documentation of *A. woodiana* in Italy was made in 1996 (Cianfanelli et al. 2007). The beginning of colonization in Umbria is not documented but in recent years a colonization by allochthonous aquatic species has increased among plants, vertebrates and invertebrates. *A. woodiana* is dispersed along lowland rivers, associated wetlands and manmade canals. Heavily modified and artificial aquatic habitats, with high silting rates, are especially suitable for population by *A. woodiana*. A mass occurrence of the Chinese pond mussel was observed among these habitats, particularly where bottom substrates were characterized by the domination of silt-clay where traces are preserved at the soupy/softground boundary.

A. woodiana lives almost entirely in mud and fine sand in lentic or weakly flowing waters (rivers, channels), filter feeding on suspended phytoplankton by filtering water through the oral siphon, which protrudes outside the shell in the back. Has a higher resistance to pollution than the native species, making it able to live in heavily populated areas.

The study sites are: A) the dam of Amelia, B) dams on the Tiber River (Valfabbrica and Corbara) and C) the Antognolla artificial lakes (two wide manmade basins in a golf course) (Fig. 1). The widespread distribution of *Anodonta* gives us reason to analyse the different sites where it was found or documented its presence.

A) Dam of Amelia. The basin of the Rio Grande is located northwest of Amelia. The reservoir 'Lago Vecchio' is an artificial lake with the Great Dam Bridge made at the bottleneck between Mount Cimino and the Colle of Amelia. The basin was used in the past for the operation of mills downstream from the dam. Today the Lake is used for tourist and recreational purposes, though it has undergone considerable silting. The fill consists of silty/clay that has bridged a large part of the reservoir. During the summer of 2012, the severe drought almost completely dried up the basin and revealed a significant population of *A. woodiana*. Most of the specimens were in life position.

B) Dams on the Tiber River (Valfabbrica and Corbara). Northwest of Valfabbrica, a dam of reservoir is under construction. The basin, of considerable size (up 5 km long), is sited where outcrops sandy to marly rocks belonging to the Marnoso-arenacea Formation, crumble easily, producing mostly clay-rich sediments. A rather significant population of *A. woodiana* was observed in deposits that have accumulated in the submerged area. The Corbara dam (a very large dam basin of the Tiber River valley up to 15 km long during rainy periods) was built on various deep-water carbonate Mesozoic to Cainozoic sediments of the Umbro-Marchean succession to generate electricity in the 1960s. Abundant *Anodonta* has been observed along sides of lake and in the seasonal variations of the water level. The alteration of the equilibrium profile of the Tiber River and the abundant supply of terrigenous material due to the frequent floods of recent years has led to a significant accumulation of deposit in the upper part of the basin. It varies from pebbles, sand and silt to clay that accumulated during the rainy periods and emerged periodically, highlighting a considerable population of *A. woodiana* (hundreds of specimens in the freshwater margins). There are numerous examples disarticulated by heron predation (Fig. 2A). Most of the specimens are in life position of (Fig. 3A, B, C).

C) Two lakes in the Golf course of Antognolla (Fig. 2A-F, 3D) are located close to Pierantonio close to Umbertide, where artificially produced excavations were made at the beginning of 1990 to produce the Golf Course; these lakes are now populated by hundreds of *A. woodiana* that feed along every sides of two lakes together with tens of carp (up one meter long) and many other invertebrates (annelids, snails and small crustaceans). Methods of analysis consist of observation and measurement of size, depth and taphonomy of traces and shells that show results summarized in Fig. 4. Traces of *Anodonta woodiana* mussels, distributed along the banks of rivers and lakes, are analysed focusing on the soupy/soft boundary; the main tool to analyze the differences in the consistency of silt-clay deposits is a manual penetrometer or a telescopic ball boy for golf balls (Fig. 2D), measuring the time of settling the cloud of mud in suspension. Variables are the quiet condition of water during seasons and the distance of traces from the coast. Consistency has been evaluated up to one meter in water depth during spring, summer and autumn over a period of four consecutively years (2012 to 2015) and during water level rise. About 200 traces of *A. woodiana* are considered in this study.

Anodonta life history

Anodonta (with several species largely studied in the USA and Canada) occur in lakes, slow rivers (Taylor 1981) and some reservoirs (Nedeau et al. 2009) in mud or sand substrates (Clarke 1981) and are typically found at low elevations (Frest & Johannes 1995). The distribution of freshwater mussels within a water body is probably dependent on the size and geology of the water body and on the distribution of host fish during the mussel's reproductive period (Watters 1992). *Anodonta* is a relatively sedentary filter feeder that consumes plankton and other particulate matter (e.g. organic material and polluting particles) that is suspended in the cloudy water column. As they feed, they filter large quantities of particulate matter and excrete those particles as 'pseudofaeces', which can be an important, nutrient-rich food source for benthic macro- and microinvertebrates (reviewed by Vaughn et al. 2008). In general, species of *Anodonta* grow quickly, reach sexual maturity in four to five years, and have a maximum life span probably of about 15 years (Dudgeon & Morton 1983; Heard 1975). Like other freshwater mussels, they rely on host fishes and other organisms to reproduce and disperse (Lefevre & Curtis 1910; Kiss 1992; Cianfanelli et al. 2007; Douda et al. 2011). Because freshwater mussels are usually unable to move far on their own, their association with fish allows them to colonize new areas, or repopulate areas from which mussels have been extirpated (Paunovic et al. 2006; Douda et al. 2011). Fertilization occurs when female mussels inhale sperm through their incurrent siphon during the appropriate reproductive period (Lefevre & Curtis 1910). Eggs incubate and hatch into larvae, or glochidia, which are released into the water, either individually or in packets (called conglutinates). Glochidia attach to fish, heron legs and encyst in host fish tissues from 2 to 36 hours after they attach. Once metamorphosed, juvenile mussels drop from their host fishes to the substrate (McMahon & Bogan 2001).

Results

Substrate characteristics and burrows of *Anodonta woodiana.*

A) Substrate characteristics. Before feeding, *Anodonta woodiana*, moves through shallow substrates producing different traces (Fig. 2A-F). In previous literature the soupground represents the least cohesive category of ground (Bromley 1996; Ekdale 1985; Goldring 1995, among others). As indicated by Bromley (1996) "the aquatic soupground has fluid consistency; the grains are hardly in contact or are separated by mucoid substances, and animal may 'swim' through the substrate. Neverthless, mucus- and other organic-walled tubes may be constructed by sedentary endobenthos" (Bromley 1996, p. 17). The upper part of the soupground is poorly

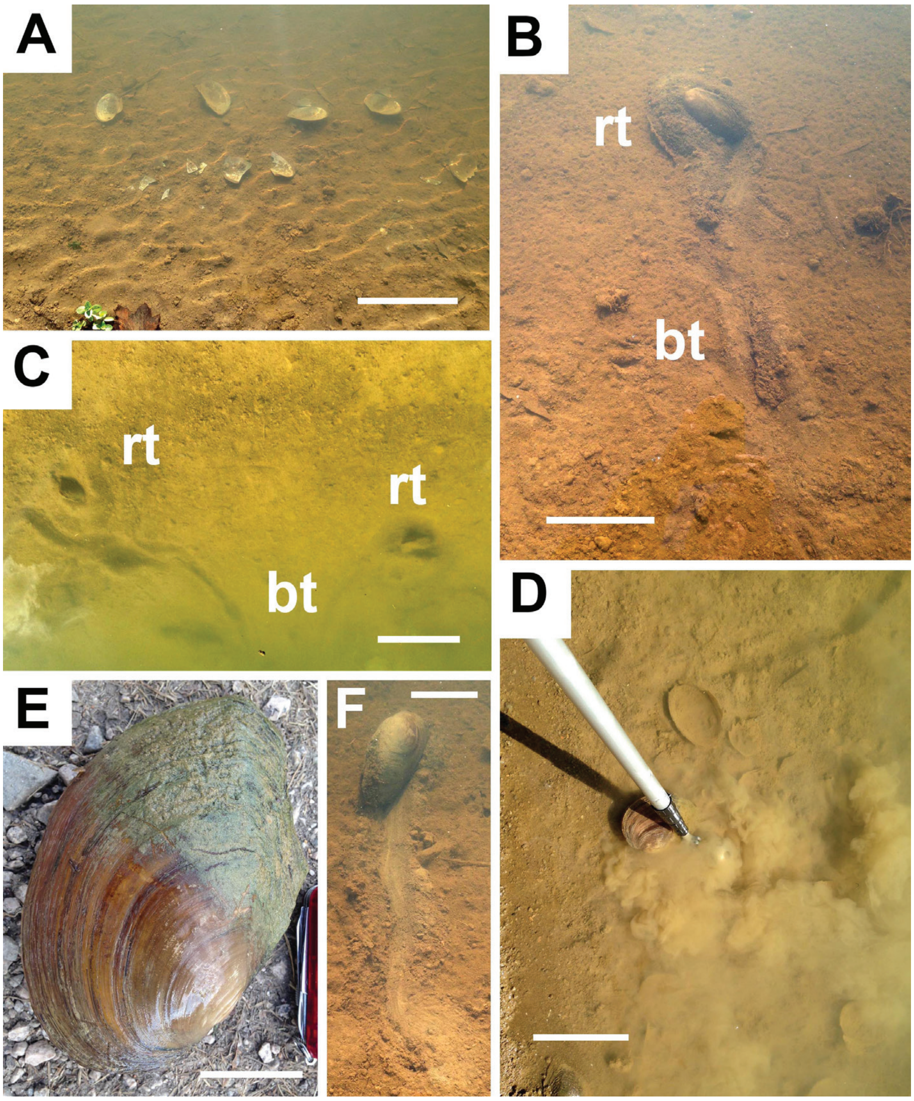

Fig. 2 - Burrows of *Anodonta* (*Sinanodonta*) *woodiana* (Lea, 1834) in Antognolla Golf course marginal lakes. A) Detached shells after the heron feeding activity (late summer), bar = 50 cm. B-C) Bulldozing trace (bt) and resting trace (rt) of *Anodonta woodiana*, bar = 20 cm. D) Cloudground disturbed by a telescopic ball boy for golf balls, depth 40 cm, bar = 25 cm. E) *Anodonta woodiana* complete shell (live specimen) with mud in resting trace, bar = 5 cm. F) Horizontal movement towards deepest part of lake, bar = 15 cm.

exploited by researchers because not preserved in the geological record (Lobza & Schieber 1999), although this substrate is the rule in modern aquatic realms (e.g. in continental lacustrine deposits, Hasiotis 2002; Buatois & Mángano 2011; Scott et al. 2012, or in abyssal basin plain, Rona 2004; Rona et al. 2003; see cloud of mud in the film 'Volcanoes of the Deep Sea'). Usually, in polluted marginal lakes and dams of Umbria the mere touch of the upper part of a soupground creates a wide cloud of mud that suspended for long time (up two hours) in water (Fig. 2D). Single particles of clay/silt dispersed in the water remain for long time in suspension due to the presence in the water of many pollution particles. Polluting particles, probably formed by nitrates or sulfates (dispersed in the waters by human activity) or other fats pollutants, tend to produce a proliferation of algal mucilaginous film that adhere to the particles of sediment causing them to remain in suspension for a long time, much greater than a sediment in unpolluted waters. Another type of clay/silt dispersion above the bottom are benthic nepheloid layers (BNL, Cindy Pilskaln, personal communication, 2010). Benthic nepheloid layers are permanent clays particle (2-5 µm) that form resuspension of mud, in which their behaviour is different close the sediment-water interface in marine (and freshwater) realm and more complicate due the presence of salinity-induced currents and energetic flows (Cindy Pilskaln, personal communication, 2010). Due to this characteristic this upper, up to 2 cm thick level, can be considered as a new type of substrate which is named here as 'cloudground'. Cloudground, if disturbed, produces a cloud of clay that can fluctuate within the water for a very long time, much greater that a soupground. Softground (mud or silty mud) and looseground (sand and gravels) conversely, include thixotropic sediment and soft dilatant sediments; Seilacher (2007) said: "the initial establishment of a permanent burrow in softground requires some wall-support mechanisms either through compression alone or together with mucus impregnation". Excavation and backfill burrowing techniques become practicable in looseground and towards the firmer end of the softground range (Bromley 1996, p. 17).

B) Anodonta (Sinanodonta) woodiana burrowing. In littoral grounds of lakes and rivers of Umbria, hundreds of *Anodonta* burrows reveal two different behaviours and traces of this mussel: the first consists of 'bulldozing' activity (Seilacher 2007, pp. 75 and 80); this occurs in the cloudground and soupground, where the mussel not only rolls over the ground, but forcefully accumulates quantities of green-yellow mud in front distributing laterally, producing two ridges separated by a central furrow (bt = bulldozing traces in Figs. 2B, C). This vagile locomotion produces unidirectional, meandering to straight traces, 4 to 8 cm wide and up to 250 cm long, with frequent loops and an irregular shape. The movement of the mussels using their foot is so slow as not to disturb the cloudground (if not in small part). Usually, each of outer marginal ridges are elevated, up to 3 cm high respect to central furrow (Fig. 2B, C). The base of the central furrow reaches the upper part of underlying softground and often is filled by pseudofaeces (see Fig. 2F). Locally, the central furrow appears more brown and with some backfill structures. The resting traces (rt = resting trace in Fig. 2B, C), conversely, are oval, round to elongate and are present when the mussel slips through the mud, reaching the softground (anchored to firmground) and placing their shell vertically or obliquely (see the grey half of the mud-filled test in Figs 2E, 3A-B), opening their valves in order to filter food. Abandoned resting traces leave circular structures at the end of the traces of movement, up to 20 cm wide (Fig. 2C).

Considerations

Some taphonomic characteristics, such as trail shape, ground type, ethology, articulated or disarticulated shells, destroyers of traces and their preservation are showed in Fig. 4. Other elements can be detected by observation of behaviours of *A. woodiana* in Umbrian dams and lakes.

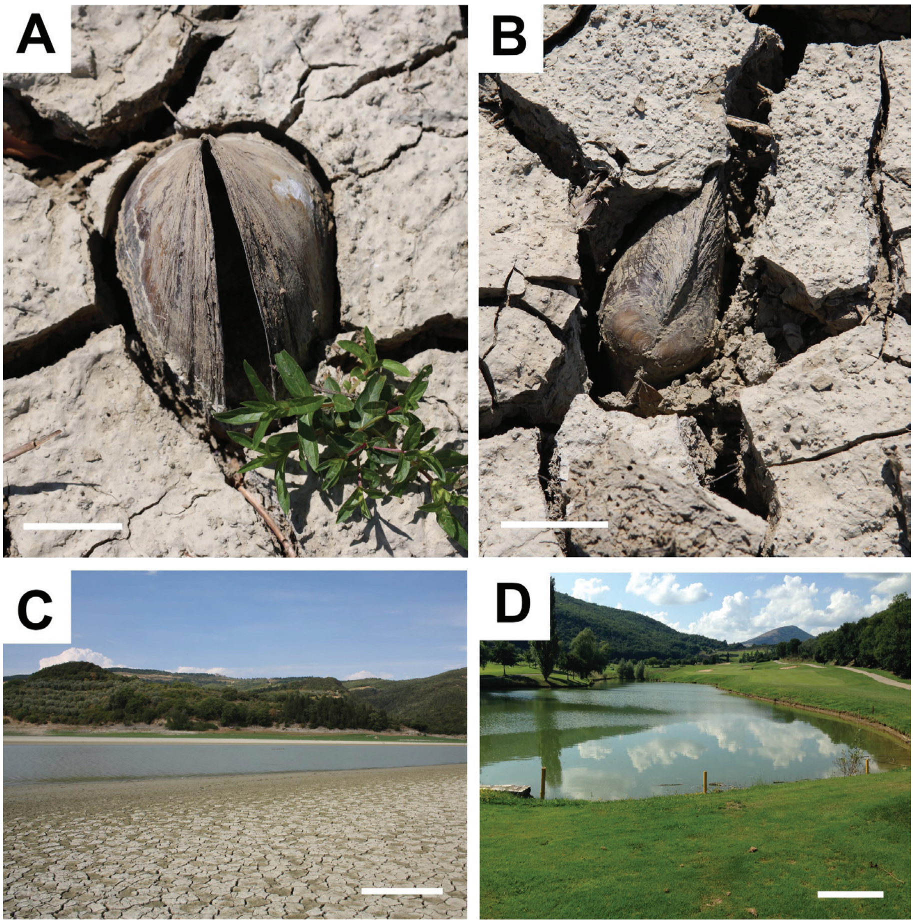

Fig. 3 - A-B) Two in situ specimens of *Anodonta* (*Sinanodonta*) *woodiana* (open and attached valves) buried within the desiccated bank mud, Corbara Dam, bar = 5 cm. C) The Corbara dam during falling water (summer), bar = 1 m. D) Lake of Antognolla Golf course, bar = 1 m.

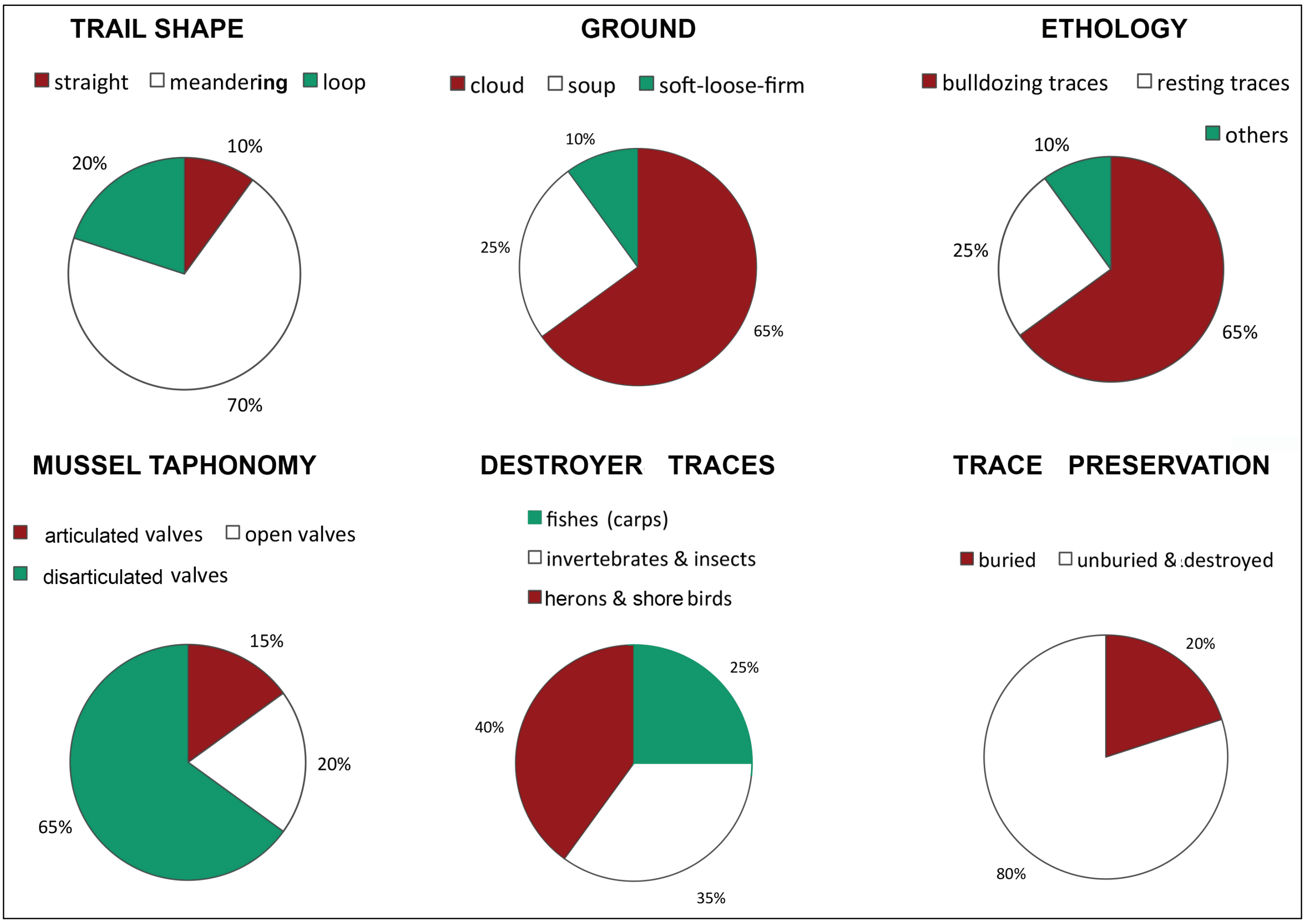

Fig. 4 - Taphonomic features of 200 traces of *Anodonta* (*Sinanodonta*) *woodiana* and substrate characteristics from Umbria dams, rivers and lakes.

a) Continental ichnofacies and substrate characteristics. The vertical organization of the substrate and their cohesiveness are fundamental to preserve traces of organisms (Ekdale 1985) in different ichnofacies (Hasiotis 2002; Buatois & Mángano 2011). In submerged continental sediments of the geological record bioturbation usually took place mainly in water-saturated sediments close below the water-sediment interface, in soft to firmer levels below, in which discrete trace fossils can be preserved as cubichnia and repichnia among many others (Ekdale et al. 1984; Uchman et al. 2013; Wetzel 2010; Buatois & Mángano 2011). In lacustrine deposits different types of structures can be observed, such as clastic dikes, ball and pillows, water escape structures, deformation by growth of carbonate and silica minerals and pervasive to surficial bioturbation (Buatois & Mángano 2011; Stárková et al. 2015). Many other structures are known in river environments and sub-environments (Buatois & Mángano 2011; Melchor et al. 2012). Continental ichnofacies thus are largely exploited and traces are largely differentiated (see among others Bromley 1996; Hasiotis 2002; Melchor et al. 2012; Miller 2007; Buatois & Mángano 2011; Scott et al. 2012). *Scoyenia, Mermia, Coprinisphaera* and continental *Skolithos* ichnofacies are the main known ichnofacies and occur with hundreds of ichnotaxa (Hasiotis 2002; Zonneveld et al. 2006; Buatois & Mángano 2011; Melchor et al. 2012; Scott et al. 2012).

Exploiting the fluvio-lacustrine substrates of Umbria we can demonstrate that is not true that freshwater *Anodonta woodiana* burrowed only in soft/firmgrounds, contrary to the current consensus among ichnologists (e.g. Buatois & Mángano 2011; Stárková et al. 2015), but can also originate (100%) in polluted cloudground and upper part of soupground.

b) Fossilization barrier. Usually, geologists and ichnologists make little use of information derived from modern environments in their analysis of biogenic structure because biological information cannot be applied directly to trace fossils and the geological record of bioturbation (Bromley 1996, chapter 6). A barrier separates the two realms, modern and fossil respectively, that Seilacher (1967) called 'the fossilization barrier' or 'modern to fossil transition'. This concept is valid not only for body fossils but also for trace fossils (see more explication and examples of ichnological fossilization in Bromley 1996; Buatois & Mángano 2011). Neoichnological study of *Anodonta woodiana* in Umbria can help to understand how modern traces can cross the fossilization barrier; in fact, only 20% of the bulldozing/resting traces of *A. woodiana* are completely covered after four years by soft mud, with a sedimentation rate of 2 cm every year. The destruction of the other 80% of tracks is due to the very rapid escape of carp, or caused by rapid movement or feeding by the fishes, which produce *Undichna* or *Piscichnus* of the *Mermia* ichnofacies (Buatois & Mángano 2011; Scott et al. 2012). In Umbria the disturbance is due to large carp (often longer than 1 m), which remove the surface of the very soft mud. The traces preserved in the littoral zone from the destructive action by organisms such as fishes, herons, annelids, aquatic and semi-aquatic insects (dipterans, coleopterans), crustaceans and molluscs show crossing and a slight flattening (Bromley 1996; Dashtgard & Gingras 2012). When the water levels of lakes and rivers rise (the falling produces a subaerial exposure that can forms polygonal essiccation cracks with destruction of traces, see Fig. 3A-B), they can be buried by sediment and cemented, crossing the fossilization barrier (Hasiotis 2002; Buatois & Mángano 2011; Melchor et al. 2012; Scott et al. 2012).

c) Mass mortality and burial. Hundreds of *Anodonta* are killed every year by herons and other shorebirds (Fig. 2A); their dead shells are found mostly disarticulated with valves scattered (Fig. 2A) or still attached but distant from their traces. A year later with rising water all open shells are covered with 2 cm of mud, and in four years are totally buried by mud or colonized by green algae.

d) Potential for preservation in fossil record. It is very difficult to calculate accurately the preservation potential of traces and shells of *Anodonta woodiana*; however, from observations made after four years, we have seen that the greatest potential for preservation occurs in buried traces far from shore, while those closer to the banks and shoreline tend to be fragmented or destroyed by birds and waves. It is estimated that a small percentage, about 20% of the deepest traces are buried by mud and thus preserved. We must also consider changes in the water levels of all areas due to rainy periods and seasonal waves affecting the preservation of traces (Hasiotis 2002; Buatois & Mángano 2011; Scott et al. 2012).

In many studies of the geological record, it seems that the food for bioturbating organisms was concentrated near the water-sediment interface (mixed tier, see Bromley & Ekdale 1986; Savrda 2007; Scott et al. 2012; Uchman 2007) or distributed in the water column; therefore, few organisms exploit the deeper, more cohesive sediments in which preservation of discrete trace fossils would be possible (Buatois & Mángano 2011; Monaco et al. 2012; Uchman et al. 2013, among others). This issue has produced a number of misleading models that must be revised taking into account new neoichnologic observations about cloudground-soupground horizons for repichnia, cubichnia, pascichnia and foodinichnia. Therefore, this question remains open for paleoichnologists and only fresh neoichnologic studies, as the case of *Anodonta woodiana*, can be utilized to provide new data on the preservation of burrows in the substrate according to environmental characteristics.

Final remarks

The analysis of about 200 traces of *Anodonta woodiana* in reservoirs and lake margins in Umbria (central Italy) show a diffuse activity of this mussel in the very soft substrate (see diffusion trend in Wetzel 2008). The new category of this substrate, the cloudground, is proposed herein; it develops when pollution is very high and moved particles of mud/silt that remain in suspension for a long period time over the trace due to the presence of pollutant fats surrounding the particle of clay/silt. These chemical and biological conditions of polluted fresh water induce the bloom of foreign pioneer and invasive species such as *Anodonta woodiana*. Cloudground can be preserved above the soupground and colonized. Remains unesplored if it can be recovered also in the geological record, crossing the fossilization barrier and be compacted. The activity of *Anodonta woodiana* consists of two traces, the first due to the meandering to straight locomotion producing bulldozing structures of the mud (bulldozing redistribution with two ridges and a central furrow filled with pseudofaeces and backfill), and the second due to burial when the mussels place their shell vertically with open valves to filter nutrients in suspension (oval to round resting traces). The first resembles bulldozing trace fossil (e.g. *Nereites missouriensis* or sand dollar echinoids) preserved as epichnia in shallow or deep water marine deposits (other traces of infaunal bivalves are not considered here, because far from the aim of this work), while the second, resting traces or cubichnia (Buatois & Mángano 2011), can be compared to some resting trace fossils (e.g. *Lockeia* or *Cardioichnus*, among others, see Seilacher 2007).

Anodonta woodiana is subject to periods of mass mortality that are testified by a sudden increase of dead concave-upwards specimens and coquinas pavements of disarticulated shells on the lake-river floors; mass mortality is balanced by rapid repopulation in short periods (months?) with larvae attached to legs of herons and encysted to fishes in each lake and river of Umbria. Mass mortality occurs also in underwater conditions whose reasons require further analysis over a long period of time. This little-studied mussel provides new useful information about the behaviour of invasive populations of freshwater mussels and the substrate characteristics.

Acknowledgements. We thank to two reviewers (A. Baucon and an anonymous reviewer) and the associate Editor F. Feletti to improve the manuscript. Thanks to Gabriele Bigini, Monica Alunni Bernardini, Linda Berardi and Gaia Giuliacci for providing acces for sampling and measurement of the cohesiveness of the substrate and sampling *Anodonta* (*Sinanodonta*) *woodiana* specimens in lakes of the Antognolla Golf course (Pierantonio, Umbertide). Funds Ric. Var. (2013-1014), University of Perugia, Physics and Geology Department (P. Monaco).

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