

Arthrodendron borberensis sp. nov., a large protist (Foraminifera) from the Pagliaro Formation (Paleocene), Northern Apennines, Italy

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Arthrodendron borberensis sp. nov. is described from the Pagliaro Formation (Paleocene) of the Northern Apennines. Specimens of the new species are preserved on the sole of a turbiditic sandstone bed. Arthrodendron borberensis sp. nov. is characterized by its long chambers (some exceeding 10 mm in length), its generally straight course, and rare branching at an acute angle. This large foraminifer lived infaunally within the sediment and possibly as epifauna after exhumation by erosion, prior to the deposition of the host turbiditic sandstone bed. Assemblages of smaller agglutinated foraminifera (a flysch-type fauna) and trace fossils (*Nereites* ichnofacies) point to a deep-sea environment for the discussed protist.

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INTRODUCTION

Arthrodendron is a large, rarely reported deep-sea protist, which is composed of a chain of agglutinated chambers. Because of its large size, morphology, and occurrence on the sole of turbidite sandstones, it escapes standard micropalaeontological observations and was in the past misidentified as a marine plant or as a trace fossil (Kaminski *et al.*, 2008; Kaminski *et al.*, 2010; Kaminski and Uchman, 2011). The taxonomy of the genus is still poorly known, as specimens recovered by normal micropalaeontological techniques are always fragmentary. The genus is currently ascribed to the foraminiferal superfamily Hormosinacea, but similarities to Komokiacea and the xenophyophores have been also noted (Kaminski *et al.*, 2010).

Species variation within the *Arthrodendron* group is still poorly known. The genus includes its type species: *A. diffusum* Ulrich, 1904; *A. maguricum* Kaminski, Uchman and Rindsberg, 2010; *A. carpathicum* (Neagu, 1964) and *A. moniliformis* (Neagu, 1964); *A. grandis* (Grzybowski, 1898) and *A. subnodosiformis* (Grzybowski, 1898). The validity of a 19th century species originally described as a fossil alga still needs to be evaluated, as it is possible that species described by

Unger (1847), Heer (1877) and by Fuchs (1894) may be senior synonyms of some of the foraminiferal species names in current usage (e.g., Brady, 1879).

The species of *Arthrodendron* are distinguished on the basis of the shape of the chambers and overall test architecture. Taking into account these morphological characteristics, we herein describe newly discovered, well-preserved specimens of *Arthrodendron* from the Pagliaro Formation (Paleocene) in the Northern Apennines. The species is characterized by its strongly elongated, elliptical chambers. The main aim of this paper is to provide a formal description of this new species based on a morphological comparison with previously described species.

GEOLOGICAL SETTING

The study area (Fig. 1) is located in the Northern Apennines north of Genova, in the Monte Antola Unit, which probably is an allochthonous slab within the Ligurid units. The Monte Antola Formation (middle to late Campanian) is 2000–3000 m thick and composed mostly of thick- and very thick-bedded



Fig. 1. Location of the study region (A), area (B) and section (C) of the Pagliaro Formation (Paleocene), Celio, Northern Apennines

mixed fine-grained carbonate-siliciclastic flysch (e.g., Scholle, 1971a, b; Abbate and Sagri, 1982; Argnani et al., 2004). The upper part is less calcareous, about 600 m thick, and is distinguished as the Bruggi Member or the Bruggi/Selvapiana Formation (late Campanian to late Maastrichtian; Abbate and Sagri, 1967). It contains alternating thick turbiditic marls with thin-bedded sandstones and shales. This unit is thinner and pinches out in the Borbera Valley (Levi et al., 2006). The Bruggi/Selvapiana Formation is overlain by the Pagliaro shale (Bellinzona et al., 1971; Marroni et al., 2001; Levi et al., 2006), which is also called the Pagliaro Formation (Marroni et al., 2002). It roughly corresponds to the Cabella Member of the Albirola Formation of Abbate and Sagri (1967) (Catanzariti et al., 2007). Calcareous nannoplankton dates the Pagliaro Formation as early Paleocene to early late Paleocene (Zones NP1-NP5; Marroni et al., 2001) or as late Maastrichtian to earliest late Paleocene (Zones CC25b-NP5; Levi et al., 2006; Catanzariti et al., 2007). It is overlain unconformably by lower Oligocene conglomerates of the Savignone Formation and locally by other Oligocene sediments, mainly the Ranzano Formation (e.g., Gelati and Gnaccolini, 1978; Gnaccolini, 1988).

The Pagliaro Formation is about 300-400 m thick (Abbate and Sagri, 1967). It passes gradually from the Bruggi/Selvapiana Formation (Antola Formation *s.l.*) and in the lower part contains mixed carbonate-siliciclastic, thin- to

thick-bedded turbidites alternating with thick shales partly representing turbiditic and background sedimentation. Massive grey turbiditic marls are also present here. Some of the marlstones are reddish in colour. Shales containing thin- to medium-bedded turbiditic sandstones alternating with thick beds of grey, partly turbiditic mudstones prevail in the middle to upper part of the formation. The sandstones display Ta-d Bouma intervals and are rich in plant detritus. In some sections, the sandstone beds display thickening upward trends in packages about 10 m thick. Isolated, thick beds of sandstones and marlstones are also present. The entire formation is gently deformed tectonically, with faults, internal detachments, especially in the upper part of the formation. In some areas beds are overturned. Tectonic deformations of the Antola Formation were characterized by Marroni et al. (2002) and Levi et al. (2006). Trace fossils of the Pagliaro Formation are typical of the deep-sea Nereites ichnofacies (Uchman, 2007).

The studied section (Fig. 2) occurs in the lower part of the Pagliaro Formation in the Borbera Valley near Celio (Fig. 1), in a bank of an unnamed stream, which is a left tributary of the Borbera River. There is an isolated outcrop (GPS co-ordinates: N 44°40.700'; E 009°05.042'; ± 6 m), in which alternating sandstone and shale beds are exposed. *Arthrodendron* occurs only on the lower surface of a single, ripple laminated, very fine-grained, calcareous, muscovitic sandstone bed (Fig. 2),



Fig. 2. The studied section of the Pagliaro Formation (Paleocene), Celio, Northern Apennines, with indication of the bed with *Arthrodendron borberensis*, trace fossil occurrences and location of samples C11 and Cl2 collected for smaller foraminifers

Grain size: $m-mud,\,s-silt,\,vf-very$ fine sand, f-fine sand, m-medium sand, c-coarse sand

that is 15–17 mm thick. A second, isolated find (specimen 6808) comes from a locality (Celio village; an escarpment of an abandoned forest road; GPS co-ordinates: N 44°40.662'; E 009°04.695') located ~400 m from the main locality at a stratigraphically higher position within the Pagliaro Formation.

SYSTEMATIC TAXONOMY

Class Foraminiferea d'Orbigny, 1826 Subclass Textulariia Mikhalevich, 1980 Order Lituolida Lankester, 1885 Suborder Hormosinina Mikhalevich, 1980 Superfamily Hormosinacea Haeckel, 1894 Family Aschemocellidae Vialov, 1966 Genus *Arthrodendron* Ulrich, 1904

D i a g n o s i s. – Branched chains of large chambers with an imperforate agglutinated wall that lacks biogenic barite crystals (Kaminski *et al.*, 2008).

R e m a r k s. – *Arthrodendron* (= *Aschemocella* Vialov, 1966) differs from other hormosinaceans in its large dimensions and in having a branching septate test. The test consists of many chambers in a meandering series that may branch from a central area. These chains of chambers may branch further. The species of *Arthrodendron* are distinguished by their predominant chamber shape and mode of branching. The genus differs from *Aschemonella* (type species *A. scabra* Brady, 1879) in possessing well-developed chambers and in lacking intracellular barite crystals. Gooday and Nott (1982) found that *Aschemonella ramuliformis* Brady possesses cytoplasmic strands (termed granellare) containing intracellular barite, and transferred the genus to the xenophyophores. This assignment has recently been confirmed by Gooday *et al.* (2011) based on a comparison of small sub-unit rDNA sequences.

Arthrodendron borberensis sp. nov. (Figs. 3–6)

Derivation of name. – From the Borbera Valley near Celio, Italy.

T y p e s a n d m a t e r i a l. – In the Geological Museum of the Jagiellonian University, Kraków. The holotype is on slab INGUJ175P24 as indicate in Figure 3A; all other specimens on the slab are paratypes. Slab INGUJ175P25 contains paratypes (Fig. 3B), slabs INGUJ175P27, 28, two pieces for SEM analysis (INGUJ175P29a, b), one thin section (INGUJ175P30). In the Museo Crocefieschi near Genova: 15 slabs (catalogue numbers 6800, 6808, 7003, 7154, 7164–7167, 7192–7198); slabs 7003 and 7164 contain paratypes.

D i a g n o s i s. – *Arthrodendron* with strongly elongated, mostly ovoid chambers, of which at least some exceed 10 mm in length, with sparse low-angle, dichotomous branching and linear, straight, or gently curved chains of chambers.

D e s c r i p t i o n. – Test free, consisting of a chain-like series of chambers. The course of chamber chains is linear, straight or slightly curved, or slightly winding. The longest specimen attains a total length of 22 cm. Most of the chains are oriented subparallel to one another on the bedding plane (Fig. 4A), but without any relationship to current structures. The chains can overlap one another (Fig. 3B, F). The chamber that is overlapped is deformed by the overlapping one (Fig. 3F). The proloculus was observed in only one specimen (Fig. 3B); it consists of a single round chamber, and is immediately followed by an ovoid or elongated second chamber. Successive chambers are long, ranging from 1.8 to 16.3 mm (m = 7.3,



Fig. 3. Type specimens of *Arthrodendron borberensis* sp. nov. on the lower surface of a turbiditic sandstone bed, Pagliaro Formation (Paleocene), Celio, Northern Apennines

A – holotype and paratypes; the quadrangle shows the branching area illustrated in Figure 3D (INGUJP175P24); B – paratypes; one of the specimens shows proloculus (pr), detail in quadrangle shown in Figure 3F (INGUJP175P25); C – other paratypes in the slab 7154; D – detail of A showing the a branching chamber; E – specimen INGUJP175P27; one chamber deformed by a trace fossil (tf); F – detail of B showing the crossing (cr) of two chains of chambers



Fig. 4. Other specimens of *Arthrodendron borberensis* sp. nov. from the Pagliaro Formation (Paleocene), Celio, Northern Apennines

 \mathbf{A} – slab 7164 with other paratypes showing subparallel orientation, a detail in quadrangle shown in Figure 4C; \mathbf{B} — meshes of the trace fossil *Paleodictyon* (Pa) covered by a chamber of *A. borberensis* (slab 7194); \mathbf{C} – detail of A showing a branched chamber; \mathbf{D} – slab 7192 showing a branched chain at the top and curved chain in the middle; \mathbf{E} – polished slab of shale just below the *A. borberensis* bearing bed showing articulated and disarticulated chains (Ab); \mathbf{F} – slab 7003 with other paratypes showing typical chains of chambers



Fig. 5. Arthrodendron borberensis sp. nov. in vertical cross-section along chambers; thin section INGUJ175P30, Pagliaro Formation (Paleocene), Celio, Northern Apennines

A – general view of two adjacent chambers with the septum area; **B** – details of the septum area: middle (md) and outer (ot) layer of the wall, inner layer of the wall and infilling of the chambers (in) and septum tunnel (sp); **C** – fragment of chamber showing the inner layer and filling of the chamber, and the middle layer of the wall; the latter, in the upper part of the test, is subdivided into two layers (md 1 and md 2) separated by a thin fine-grained layer; protrusions (pr) run up from the chamber

n = 96). Usually, every specimen contains chambers longer than 10 mm. Chambers vary in width between 1.1 and 3.2 mm (m = 1.9, n = 96). In outline, chambers are generally tubular, ovoid or slightly pyriform in shape. Pyriform chambers taper in the direction of growth. Chambers are constricted at the septa. Successive chambers have only a small amount of overlap with the previous chamber. Flattened edges of the chambers form a raised rim in respect to the bedding surface owing to compaction of the host bed. The surface of the chambers is undulating or wrinkled, flat, locally swollen, but commonly depressed along the axial zone. Some of the chambers are plastically deformed by trace fossils (Fig. 3E). Branching is very sparse, starting from an occasional V- or Y-shaped chamber (Figs. 3B, D and 4A, C), with branches diverging at an angle of between 20 and 34° , mostly about 25° .

The final chamber tapers toward the aperture. Aperture is single and terminal in position, with a produced neck. The final chamber may be kummerform: shorter, and hence more rounded than previous chambers.

According to thin section (Fig. 5) and SEM (Fig. 6) analyses, the test wall of A. borberensis is thin (50-100 µm) and comprises three layers (Figs. 5B, C and 6C, D, G) that are distinguished by differences in colour, grain size and composition. The fine-grained outer layer contains mostly silica, which is most likely a post-depositional feature. The middle layer (25-80 µm thick) consists of silt-sized mineral grains composed mainly of quartz with some feldspar. In places, this middle agglutinated layer is itself subdivided by an internal dark layer (Fig. 5C), which might correspond to the original primary organic membrane. In this case, the inner part of the middle layer is thinner (10–15 μ m thick) than the outer one (~35 μ m thick). In places on the upper side of the chamber, the dark inner layer and chamber fill protrude into the host sediment (Fig. 5C). The inner layer is composed of silica and clay minerals and is welded with the fill in some chambers (Fig. 5), while in other chambers the fill is similar to the host rock. The septa constitute thin tunnels surrounded by agglutinated grains like those in the middle layer (Fig. 5A, B).

DISCUSSION

TAXONOMIC PROBLEMS

The holotype specimen (Fig. 3A) is incomplete (the proloculus is missing), but the specimen was selected because of its typical chamber shape and low-angle branching that involves a Y-shaped chamber. In the holotype the successive branches then run parallel to one other, but this is not always the case.

Arthrodendron borberensis sp. nov. is similar to A. diffusum Ulrich, 1904 and A. carpathicum (Neagu, 1964) because of the generally ovate shape of chambers. However, analyses of chamber size (Fig. 7), angle of branching, and course of chamber chains show significant differences between these species.

The length of chambers of *A. carpathicum* never exceeds 10 mm (1.6–8.6 mm; m = 4.6, n = 111). Its chamber width is broader, ranging from 1.2 to 4.6 mm (m = 2.3, n = 111). The angle of branches in *A. carpathicum* is more variable, including cases of branching at right angles, and the course of the chamber chain is commonly winding (see Neagu, 1964). Chambers of *A. diffusum* (see Kaminski *et al.*, 2008) are even shorter (0.9–4.4 mm; m = 2.9, n = 55) and narrower (0.6–3.4 mm; m = 1.7, n = 55), and similarly to *A. carpathicum*, are smaller and the angle of the branches is more variable. The course of the chamber chain is slightly winding. Therefore, the long chambers (with some over 10 mm long), generally straight course, and low angle of rare branching are considered to be the main diagnostic features of *A. borberensis*. Only the proloculus is round in outline and if found in isolation could be confused with the species



Fig. 6. SEM images of Arthrodendron borberensis

A – general view of two incomplete chambers and the connecting septum; B – cross-section of the upper part of the test embedded in the sediment; C – chamber with oblique cross-section in the left; D – detail of C, layers of the wall: ot – outer layer, md – middle layer, in – inner layer, mdu – surface of the middle layer (upper part of the test); E – detail of D showing the outer layer of the wall, which is built of silica; F – detail of C, surface of the inner layer of the wall, which is built mostly of quartz and feldspar grains; G – detail of D showing the outer, middle and inner layers if the wall; grains of quartz (Qtz) and plagioclase (Pl) in the middle layer determined by the EDS analysis; H – detail of D and party H showing the inner wall, which is built of silica and clay minerals; B – INGUJ17P29b; others INGUJ17P29a



Fig. 7. Chart showing width versus length of chambers in Arthrodendron diffusum Ulrich, 1904, A. carpathicum (Neagu, 1964) and A. borberensis sp. nov.

Arthrodendron grandis (Grzybowski, 1898). The straight course of *A. borberensis*, without any evidence of relation to current structures, seems to be a species characteristic feature.

Kaminski *et al.* (2008) regarded the Carpathian species *A. carpathicus* (originally *Aschemonella carpathica* Neagu, 1964) as a junior synonym of *A. diffusum* Ulrich, 1904. Measurements of chamber dimensions between the two species show considerable overlap, but the generally smaller chamber length (Fig. 7) in the latter and its less winding course, can be considered as features allowing their separation.

A separate problem is the comparison of these fossil taxa to recent taxa, for example with the xenophyophore Occultammina profunda Tendal, Swinbanks and Shirayama, 1982. The genus Occultammina was originally described from a box core collected at 8.260 m depth in the Ogasawara Trench off the Bonin Islands in the Pacific. Its test may be tubular, unbranched, or bifurcating and anastomosing at a low angle, forming a polygonal network. It has a layered test wall, and the cytoplasm contains branched and anastomosing strings of dark stercomare. The organism is infaunal, found as deep as 6 cm (but mostly between 2 and 3 cm) below the sediment surface (Tendal et al., 1982). Aside from the fact that Occultammina has an undivided tubular test, the overall similarities with Arthrodendron borberensis sp. nov. in terms of both morphology and habitat are striking. Our specimens of A. borberensis are infilled with a dark substance, which could have been derived from original masses of stercomata, but this interpretation is speculative and cannot be confirmed in fossil material. Comparisons with species of Aschemonella preserved in the collections of the HMS Challenger Expedition at the NHM in London are more distant ones. The genus Aschemonella Brady, 1879 has a branching test and consists of tubular pseudochambers connected by short stolons, with rare short side branches. The several species of Aschemonella are differentiated on the basis of the shape of the pseudochambers. and Nott (1982) found that Aschemonella Gooday ramuliformis Brady is a xenophyophore based on its internal organization that includes anastomosing stercomare strings, and granellare strands with intracellular barite crystals. The syntypes preserved in the HMS Challenger Collection are from Station 244 (2900 fathoms depth in the North Pacific) and are preserved in Slides BMHN-ZF 1111, 1112 and 1113. The syntypes display a wide range of chamber form, from tubular to gently curved, Y-shaped, or tubular with multiple side branches. The chamber form is mostly tubular and fragments preserved in the slides are as long as 11.5 mm, but the collection mainly consists of broken fragments. The pseudochambers of Aschemonella ramuliformis are more irregular than those of our new species and possess constrictions and swellings, irregularly spaced lateral protuberances, or side branches that may diverge at right angles. Brady cut some specimens open, revealing a dark inner organic lining, The test wall is thin, composed of mineral grains several grains thick, but is not visibly layered. Aschemonella ramuliformis clearly differs from our new species based on its more irregular chamber shape, the fact that it possesses pseudochambers instead of true overlapping chambers, and in its thin, unlayered wall. Additionally, the modern species A. ramuliformis is known to have an erect epifaunal habitat, growing individually or in bush-like clusters on the sea floor (Gooday et al., 2011).

MORPHOLOGY, BEHAVIOUR AND ENVIRONMENT

Arthrodendron borberensis has a distinctly layered wall. We speculate that agglutinated grains were attached to both sides of a primary organic matrix. On the inner surface of the test wall, there is an inner finely grained, dark layer that is composed of silica and clay minerals, which may correspond to the original inner organic lining. The silica was most likely deposited on the inner organic lining. Protrusions of the chamber inner wall and fill that extend to the host rock (Fig. 5C) may be primary morphological features or secondary ones caused by compaction of the test.

Arthrodendron borberensis lived within the mud as shallow infauna, or on the muddy surface of the sea floor. The infaunal mode of life is proven by the trace fossil Paleodictyon preserved on the same bedding plane, which has a hexagonal net that runs directly above one of the chambers (Fig. 4B). Paleodictyon is a three-dimensional burrow system composed of a horizontal hexagonal network connected to the sea floor surface by vertical shafts. Preservation of the hexagonal net requires an erosive event that exhumes the net (Seilacher, 1977). Moreover, articulated and disarticulated chambers of Arthrodendron are present in the mud layer beneath the hosting sandstone bed (Fig. 4E). It is possible that Arthrodendron also lived on the sediment surface after exhumation. It was killed by a weak turbiditic current that deposited the host sandstone bed. The test was plastic, as shown by the deformation by trace fossils (Fig. 3E), overlapping, and compaction of the chambers.

The foraminiferal assemblage recovered from washed residues of sample C11 (Fig. 2) collected in the immediate proximity of the *Arthrodendron* bed consists entirely of agglutinated forms. The foraminiferal assemblage is completely dominated by tubular foraminifera (mostly *Rhizammina* with rare *Psammosiphonella*) and broken fragments of *Arthrodendron*. Nontubular forms make up less than 10% of the assemblage, and include single specimens of *Psammosphaera* sp., *Ammodiscus peruvianus* Berry, and *Paratrochammina* sp. Moreover, *Bathysiphon* sp. is present in the beds above the *Arthrodendron*-bearing bed (Fig. 2). Concentration of tubular specimens is a feature that is typical of turbiditic deposits (Kaminski *et al.*, 1988).

The trace fossil assemblage from the Arthrodendron-bearing bed and a few underlying beds (Fig. 2) includes *Paleodictyon* isp., *?Thalassinoides* isp., *Helminthopsis* isp., *"Arthrophycus" strictus* (Ksi kiewicz), *Ophiomorpha annulata* (Ksi kiewicz), *Scolicia* isp., *Halopoa* isp., *Nereites irregularis* (Schafhäutl), and *Planolites* isp. This assemblage is typical of the deep-sea *Paleodictyon* subichnofacies of the *Nereites* ichnofacies (Seilacher, 1974; Uchman and Wetzel, 2011), similar to the other trace fossil assemblages of the Pagliaro Formation (Uchman, 2007). Thus, the micropalaeonological and ichnological data point to a deep-sea turbiditic environment, but above the calcium compensation depth (CCD) as suggested by the calcareous character of the shales.

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