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A WHOLE-PLANT SPECIMEN OF THE MARINE MACROALGA *PTERIGOPHYCOS* FROM THE EOCENE OF BOLCA (VENETO, N-ITALY)

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Abstract: Uncalcified macroalgae are generally rare as fossils, and hence their past diversity and evolutionary history remain poorly resolved. The Bolca area in northern Italy has yielded abundant adpression fossils of Eocene macroalgae. However, the vast majority of specimens are detached blades and blade portions. Here, we present an almost complete thallus of the macroalga *Pterigophycos* from Bolca that consists of a squat holdfast from which leaf-like blades up to 30 cm long extend. Each blade has a midrib extending over its entire length. Proximally the lamina forms a narrow rim on each side of the midrib, but becomes wider and lobed in the lower mid-portion. In the upper three quarters of the blade the lamina consists of spathulate or wedge-shaped segments. *Pterigophycos* blades have certain features in common with the present-day *Phycodrys rubens*, *Delesseria sanguinea* (both Ceramiales, Rhodophyta), *Undaria pinnatifida*, and *Egregia menziesii* (both Laminariales, Phaeophyceae); however, the systematic affinity of the fossil remains unresolved. The fossil is suggestive of intraspecific variability in blade morphology, and thus contests the historic view that there are several different species of *Pterigophycos* in the Bolca flora.

Key words: holdfast, Rhodophyta, thallus, uncalcified macroalga, Lessini Mountains, Ypresian

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Introduction

Macroalgae (i.e., macroscopic, plant-like members of the Rhodophyta (red), Phaeophyceae (brown), and Chlorophyta (green algae)) are a major constituent of many marine ecosystems today (e.g., Round 1981, Häder and Figueroa 1997, Keith et al. 2013). The fossil record of these organisms, therefore, can provide important insights into biological and ecological processes in ancient marine ecosystems. Calcareous (biomineralizing) algae are frequently found as fossils and, consequently, are often well understood today (e.g., Riding 1991, Graham and Wilcox 2000); some are used as index fossils, facies indicators, and palaeoenvironmental proxy indicators (e.g., Dragastan et al. 1994, Kundal and Sanganwar 1998). Conversely, uncalcified macroalgae are generally rare as fossils, and hence their palaeobiodiversity and evolutionary history remain poorly resolved. The failure to more fully document uncalcified macroalgae from the geologic past is due primarily to the fact that the thalli do not normally lend themselves to preservation in any recognizable form (Taylor et al. 2009).

Fossils of uncalcified macroalgae are known from a number of Cenozoic localities throughout Europe and North America (e.g., Gardner 1923, Cockerell 1926, Kovar 1982, Krings and Butzmann 2005); however, diverse algal assemblages are exceedingly rare. The most diverse Cenozoic uncalcified algal flora (22 species in 10 genera) comes from the Monterey Formation (Miocene) of California, USA (Parker and Dawson 1965). Another fossil deposit that has yielded abundant uncalcified macroalgae is Bolca in northern Italy. This Eocene Konservat-Lagerstätte, which contains a diverse marine and terrestrial flora and fauna, is most widely known today for exquisite fish fossils (Blot 1969, Marramà et al. 2016, Friedman and Carnevale 2018). Our knowledge of the algal component of the Bolca flora stems largely from the works of Abramo Bartolommeo Massalongo (1851, 1858, 1859a, b), who described some 20 different taxa, including the genus *Pterigophycos* A.Massal. (Massalongo 1858), which accommodates relatively large, pinnate blades known exclusively from the Bolca area.

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Text-fig. 1. Massalongo's original specimens. a: *Laminarites irideaephyllus* A.Massal.; b: *Pterigophycos gazolanus* A.Massal.; c: *Pterigophycos canossae* A.Massal.; d: *Pterigophycos spectabilis* A.Massal. Reproduced from Massalongo (1858: pls 15–17). Scale bars = 1 cm.

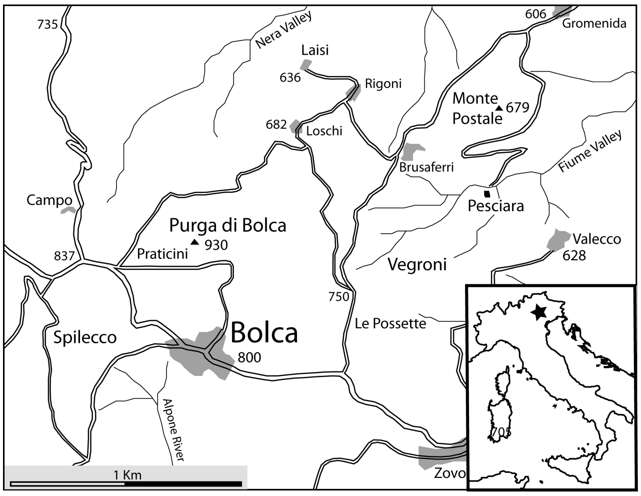
Blades of *Pterigophycos*, which Massalongo (1858) attributed to the red algae (Rhodophyta), are leaf-like, membranous, up to 40 cm long, and subtended by a stipe (Text-fig. 1b–d). They are either pinnate, or entire-margined to pinnatifid, or proximally almost entire, but sinuous to lobed in the midportion, and pinnatifid to distinctly segmented (pinnate) distally; a prominent "midrib" extends over the entire length of the blade. The lamina segments (or pinnae) are sinewy, spathulate or wedge-shaped, entire-margined, and arranged alternately to oppositely. Massalongo (1858, 1859a, b) recognized four different species of *Pterigophycos* in the Bolca assemblage, namely *P. pinnatifidus* (Sternb.) A.Massal. (≡ *Delesserites pinnatifidus* Sternb.; Sternberg 1833: 33, pl. 10, fig. 4), *P. gazolanus* A.Massal. (Text-fig. 1b), *P. canossae* A.Massal. (Text-fig. 1c), and *P. spectabilis* A.Massal. (Text-fig. 1d), all of them based on detached blades and blade portions. Whole-plant specimens that could provide information about the growth habits of these algae have not been described to date.

Here, we present a remarkable, nearly complete plant (thallus) of *Pterigophycos* from the Bolca area. The fossil demonstrates that this alga possessed a squat holdfast structure from which several blades extended. The blades are suggestive of relatively high intraspecific variability in morphology, and thus cast doubt on Massalongo's identification of four different species of *Pterigophycos* among the Bolca algae.

Geographical and geological setting

The Bolca fossiliferous area, situated in the Lessini Mountains (Verona and Vicenza provinces, northeastern Italy), is a complex of several sites (Text-fig. 2) characterized by different fossil assemblages of marine and terrestrial origin (Papazzoni et al. 2014). The most famous among the sites are the so-called Pesciara (or Pesciara cave), ca. 2 km northeast of the village of Bolca, and Monte Postale, ca. 300 m from the Pesciara. These localities have yielded the majority of the exceptional fish fossils which are all preserved in finely laminated micritic limestone. Additional fossiliferous sites include the Purga di Bolca and Vegroni, where the sediments are indicative of freshwater and brackish conditions. The Purga di Bolca consists of lignites around a volcanic neck, and contains remains of crocodiles, turtles, snakes, and plants (especially palms; see Giusberti et al. 2014a). The lignites of Vegroni have produced a variety of plants (Friedman and Carnevale 2018). Near Bolca there is yet another locality, known as Monte Solane, that has yielded abundant uncalcified macroalgae from the lower Eocene (Zorzin et al. 2011, Giusberti et al. 2014b).

The stratigraphic sequence of the Pesciara has been assigned to the Calcari Nummulitici, an informal unit of Eocene age that is widely distributed in northeastern Italy (e.g., Fabiani 1914, Sorbini 1968, Barbieri and Medizza 1969, Dal Degan and Barbieri 2005, Papazzoni and Trevisani 2006). The succession consists of a less than 20 m thick



Text-fig. 2. Map of the Bolca area, showing all the relevant fossil sites, and map of Italy, with the Bolca area marked by a star.

cyclic alternation of finely laminated micritic limestone, which is rich in fish, plant, and invertebrate fossils, and coarse-grained biocalcarenites containing a benthic fauna. The foraminifera of the fish-bearing limestone of the Pesciara have been placed in the Alveolina dainelli Zone (Papazzoni and Trevisani 2006), or the SBZ 11 Biozone (Serra-Kiel et al. 1998), which correspond to the late Ypresian (ca. 50 million years ago). The taphonomic features of the fossils, together with the sedimentology of the finely laminated deposits, suggest scarcely oxygenated bottom conditions with low hydrodynamic energy, typical of an obrution stagnation deposit (Seilacher et al. 1985, Papazzoni et al. 2014). At ‘Monte Postale’ (Fabiani 1914, 1915, Hottinger 1960, Papazzoni and Trevisani 2009, Papazzoni et al. 2014), the fossiliferous horizons of upper Ypresian limestone form the lower part of the stratigraphic succession (Vescogni et al. 2016). The Spilecco (lower Eocene; Barbieri and Medizza 1969, Papazzoni et al. 2014), Purga di Bolca, and Vegroni (middle Eocene; e.g., Nicolis 1884, Fabiani 1915, Barbieri and Medizza 1969, Medizza 1980, Sorbini 1989) successions are slightly older and younger, respectively (Papazzoni et al. 2014).

Fossils from the Bolca area have been collected and studied since the 16th century (see Sorbini 1989, Roghi et al. 2014). More than 250 fish species have been formally described and named (140 genera, 90 families, and 19 orders), including angelfish, moray eels, mackerel, sea pikes, rays, and sharks (Marramà et al. 2016). Polychaetes, jellyfish, crustaceans, corals, molluscs, cephalopods, and foraminifera were also found in the laminated layers, the latter often as fragments with signs of transport. Marine plants, such as putative red (*Delesserites* (Brongn.) Sternb., *Pterigophycos*), brown (*Postelsiopsis caputmedusae* A.Massal.; Forti 1926), and green (*Aristophycos* A.Massal.) algae, as well as marine monocots (*Halochloris* Unger; Landini and Sorbini 1996, Wilde et al. 2014, Friedman and Carnevale 2018), are the most common plant remains in the Pesciara and Monte Postale. The terrestrial vertebrate assemblage consists of tortoise shell plates, a snake (*Archaeophis proavus* Massalongo, 1859), and a two-meter-long crocodile (*Crocodylus vicetinus* Lioy, 1865), while among the numerous insects are crickets, beetles, termites, mosquitoes, dragonflies, and water bugs.

The terrestrial flora is dominated by dicots (Massalongo 1859a, Molon 1867, Meschinelli and Squinabol 1892, Fiore 1936, Gola 1941). Monocots are rare and are represented by palm leaves (*Latanites* A.Massal., *Hemiphoenicites* Vis.; Massalongo 1858, 1861, De Visiani 1864) and fruits (*Castellinia* A.Massal., *Geonomites* Vis., *Palaeospathe* Unger). Evidence of conifers is limited to remains of *Podocarpus* Pers. and *Taxodium* Rich. (Massalongo 1859a, Fiore 1936), whereas ferns, lycophytes, and sphenophytes are absent (Friedman and Carnevale 2018). Noteworthy is also the recent discovery of amber in the Pesciara (Trevisani et al. 2005, Giusberti et al. 2014b). All plant remains are well preserved, but the flora is in need of a systematic reappraisal (e.g., Massalongo 1859a, De Visiani 1864, Meschinelli and Squinabol 1892, Gola 1941, Wilde et al. 2014).

Material and methods

The fossil that forms the basis for this study is preserved as an impression with parts of the coaly substance still present on a micritic limestone matrix; it is located on a slab that is ca. 45 cm wide and 59 cm long. The specimen, which was purchased from a fossil vendor some years ago, undoubtedly comes from the Bolca area; however, it cannot be traced to any specific site in the area or source stratum. The specimen was part of the private collection of one of us (H.M.), but has been donated to the Museo dei Fossili in Bolca, Italy. The accession number 22.116 has been issued for the specimen.

Systematic palaeobotany

Phylum probably Rhodophyta

Genus *Pteridophycos* A.Massal.

***Pterigophycos* sp.**

Text-figs 3, 4

Material. MB 22.116, housed in Museo dei Fossili in Bolca, Italy.

Description. The adpressed thallus is 470 × 380 mm in size and consists of a squat structure, in vivo probably dome-shaped, of width 17 mm and height 20 mm, dark-brown to blackish in color, and covered by a thick layer of organic material (Text-figs 3a, b, 4a, c). Extending from this structure are seven blades, three large ones (denoted B1–3 in Text-fig. 3a), one medium-sized (denoted B4 in Text-fig. 3a), and at least three small ones (denoted B5–7 in Text-fig. 4a). Extending from the squat structure are also several linear elements (white arrow in Text-fig. 3a, Text-fig. 4a, c), which are up to 30 mm long and 1–2.5 mm wide, and characterized by a central strand of opaque matter which is less than 0.5 mm wide. Two of the elements are slightly bent. Delicate, linear organic remains (less than 0.5 mm wide) occur in the area between these two elements.

Two of the large blades are orientated in the same direction. The largest blade (B1) is 300 mm long (excluding

Text-fig. 3. **a:** ***Pterigophycos*** **sp., whole-plant specimen, coll. No. 22.116, larger blades denoted B1–4 (for details, see text), scale bar = 2 cm; b: Close-up of blades B1 and B2, which resemble** ***P. spectabilis*** **A.Massal. and** ***P. canossae*** **A.Massal., respectively; c: Close-up of blade B3 resembling** ***P. canossae*****; d: Close-up of blade B4 resembling** ***P. gazolanus*** **A.Massal. or** ***Laminarites irideaephyllus*** **A.Massal. Scale bars = 1 cm unless otherwise stated.**

Text-fig. 4: ***Pterigophycos*** **sp., details of specimen in Text-fig. 3a. a: Blades B5–7; b: Close-up of (a), focusing on attachment of small blades B5–7 to holdfast structure; c: Detail of holdfast with several linear elements extending from proximal portion; d: Detail of blade B2, showing midrib and spathulate lamina segments; e: Detail of blade B1, showing lowermost, smallest lamina segments; f: tiny bivalve shell on stipe of blade B1, scale bar = 5 mm; g: Detail of blade B2, showing proximal beginning of lamina segmentation. Scale bars = 1 cm unless otherwise stated.**

stipe) and 93 mm wide. The stipe is cylindrical, 40 mm long and 3.4 mm wide, slightly curved, and physically connected to the squat structure via a slightly enlarged (swollen) base that is 4.5 mm wide (Text-fig. 4c). The proximal portion of the lamina is up to 10 mm wide and extends laterally along the continuation of the stipe in the form of a rim on both sides that successively becomes wider and lobed (Text-fig. 4a, e). Approximately 90 mm from its proximal onset, the lamina expands and becomes up to more than 15 mm wide. Above this part, the lamina consists of individual segments (pinnae), which are spathulate, cuneate, or wedge-shaped, and typically possess a wide, rounded apex (upper right-hand side of Text-fig. 3b). Segments are arranged oppositely, and emerge perpendicularly from a 5–6 mm wide midrib. The distance between two segments is on average 3–4 mm. The midrib is pronounced in the proximal part of the blade, but becomes less distinct distally. The lamina segments occur in the form of brownish impressions (with little or none of the coaly substance left) that do not reveal any details of the surface texture or internal organization. The lowermost lamina segments are ca. 25 mm long and up to 8 mm wide; the narrowed base is 4 mm wide. Segments more distally are larger, up to 66 mm long and 20 mm wide. In the distal third of the blade, segments appear to be more densely spaced and become broader and more imbricate to the extent that they overlap. The distalmost lamina segments are up to 28 mm wide. On the stipe of the blade a tiny bivalve shell is located, 5 mm long and 4 mm wide, and characterized by radial striations (Text-fig. 4f).

The second blade (B2) is 250 mm long and 70 mm wide (left-hand side of Text-fig. 3b). The cylindrical stipe is 60 mm long and 3.4 mm wide, somewhat curved, and attached to the squat structure via a slightly enlarged base. The lamina in the proximal portion of the blade is 6–7 mm long and 4.5–7 mm wide. Slightly above, the lamina starts to become segmented (Text-fig. 4g); segments are inverse spathulate and have a wide, rounded apex (Text-fig. 4d). They emerge from the midrib perpendicularly and at distances of 3–4 mm, and are oppositely arranged. The midrib itself is pronounced and 2–3 mm wide. The lamina segments are brownish impressions; no information on surface texture or internal organization is visible, precisely as in blade B1 (see above). While the proximal lamina segments are only ca. 18 mm long, up to 6.5 mm wide, and have a constricted base basis ca. 4 mm wide, those in the midportion of the lamina are distinctly larger, namely up to 43 mm long and 18 mm wide. Segments in the distal third of the blade are more densely packed and distinctly imbricate.

The third blade (B3) is 300 mm long and 90 mm wide (Text-fig. 3c). The stipe is 4 mm wide, and dark brown to black in color. The lamina starts to expand approximately 55 mm above the base of the stipe. Lamina segments are linear to inverse spathulate, and possess a wide, rounded apex. They appear to be attached to the midrib in a rather irregular pattern, with the individual segments overlapping each other in all directions, thus making it almost impossible to decipher the precise dimensions and determine the mode of attachment to the midrib. The midrib appears pronounced and is visible up to the apex.

The medium-sized blade (B4) is 145 mm long and 60 mm wide (Text-fig. 3d). The stipe is 4.5 mm wide, dark-brown to black in color. The expansion of the lamina starts approximately 35 mm above the base of the stipe. The proximal lamina is up to 7 mm wide. Lamina segments start to appear in the midportion of the blade. They are imbricate, linear to slightly spathulate, and have a rounded apex. The midrib is distinct, 3 mm wide and dark-brown to blackish in color, as is the stipe. Conversely, the lamina segments are brownish impressions. Lamina segments are up to 32 mm long and 12 mm wide.

Text-fig. 5. Reconstruction drawing of *Pterigophycos* sp. thallus growing on a rock surface (blades slightly simplified, details deemphasized).

The small blades (B5–7) are up to 100 mm long and 35 mm wide (Text-fig. 4a, b). They overlap each other and are folded to the extent that their morphology is difficult to discern. The stipes are up to 25 mm long and 4.5 mm wide. No evidence of a pronounced midrib and lamina segments in the upper portions of the blades has been found; however, the lamina appears to be laterally incised or lobed.

Discussion

The famous Eocene Konservat-Lagerstätte, Bolca [NB: A Monte Bolca (or Mount Bolca), as one often sees on museum labels and in older literature, does not exist. There is only the village of Bolca] has yielded, and continues to yield, a remarkably diverse fauna and flora comprised of both marine and terrestrial elements (Friedman and Carnevale 2018). The most impressive specimens of plant fossils are complete palm fronds, which today are on display in numerous museums in Italy and abroad. However, the vast majority of Bolca plant fossils preserve dispersed simple or pinnate leaves, seeds (Massalongo 1850, 1858, 1859b, 1861, De Visiani 1864, Fiore 1932), and remains of marine macroalgae.

Morphology, comparisons, and biology

The fossil described in this study is a significant exception among the algal fossils from the Bolca area because it preserves a nearly complete thallus (Text-fig. 3a). Macroalgal fossils from Bolca normally consist of detached blades or blade portions, with only a few exceptions (e.g., Wilde et al. 2014: fig 1a). The thallus can satisfactorily be assigned to the fossil genus *Pterigophycos* based on striking similarities in blade size and basic morphology when compared to specimens figured by Massalongo (1859b: pl. 15–17; refigured here in Text-fig. 1b–d).

The squat structure from which the blades all emerge (Text-fig. 4a, c) was likely an effective holdfast affixing the thallus to the substrate, probably rocks or submerged driftwood. The narrow, slightly curved elements that extend from the lower half of the holdfast (Text-fig. 4a) could be outgrowths (haptera) that aided in securing the thallus to the substrate, or alternatively are the stipes of old blades which had been ripped off or had already wilted and decayed.

The lamina segments of the blades all appear to be complete; however, they are often folded and overlaying each other to the extent that it is difficult, or even impossible to determine their dimensions and morphology. The lamina appears to have been thin. Conversely, the holdfast, stipes, and midrib regions of the blades are distinctly darker than the lamina segments; moreover, the coaly substance is usually still (partly) in place. This suggests that these parts of the thallus were differently organized and more complex internally. The lamina of the largest blade (B1) proximally appears in the form of a narrow rim on either side of the midrib, but rapidly becomes wider and shows an increasingly sinuous to lobed margin (right-hand side of Text-fig. 4a). Further up the blade, the lamina consists of segments which are spathulate or wedge-shaped, and gradually increase in size towards the distal tip of the blade (right-hand side of Text-fig. 3b). Blade B1 closely resembles *Pterigophycos canossae* (Text-fig. 1c) in overall appearance, although the lower lamina segments of the latter are on average larger and more constricted at the base, and the midrib terminates in a single large, heart-shaped terminal segment. On the other hand, blade B2 (left-hand side of Text-fig. 3b) is more similar in basic morphology to *P. spectabilis* (Text-fig. 1d). However, the lamina segments in the latter form are more prominently constricted proximally. Moreover, there is no proximal rim-like lamina in *P. spectabilis*, and the blade shows what appear to be veins or strands of mechanical cells that extend from the midrib into the lamina segments. Finally, *P. spectabilis* is characterized by a large terminal lamina segment, identical to that in *P. canossae*, which is not present (not preserved?) in any of the blades of the fossil described here.

The presence of veins or vein-like strands in the lamina segments of Massalongo's *Pterigophycos spectabilis* specimen (Text-fig. 1d), as well as in his *P. gazolanus* fossils (Text-fig. 1b), is an interesting feature that might be used to challenge the attribution of these fossils to the algae. However, there are several present-day macroalgae, such as certain members of the red algal genus *Delesseria* J.V.Lamour. (Ceramiales, Rhodophyta), that possess leaf-like blades with pronounced venation, which functions in stabilization and is effective in the translocation of organic substances (e.g., Hartmann and Eschrich 1969, Raven 2003). Strands of specialized cells effective in long-distance transport are also known to occur in various larger brown algae (Phaeophyceae; see Raven 2003, Graham et al. 2009).

Blade B3 (Text-fig. 3d) and the small blades B5–7 of the fossil presented in this study are difficult to compare with Massalongo's *Pterigophycos* specimens because very little of their morphology is revealed. However, the presence of a rim-like lamina in the proximal portion of B3 is reminiscent of *P. canossae*. Blade B4 (Text-fig. 3d) probably represents a young and still developing blade with densely spaced, partly overlapping lamina segments. This could suggest that the lamina segments differentiated before the midrib elongated. Blade B4 in fact is somewhat similar to a leaf with an incised margin and a distinct midrib. If found detached, and depending on whether the blade is interpreted as pinnate with partially fused segments, or as entire and with a strongly sinuous to deeply incised margin, B4 could be interpreted either as a small specimen of *P. gazolanus* (Text-fig. 1b) or as belonging to *Laminarites irideaephyllus* A.Massal., another macroalga described from the Bolca area by Massalongo (1858: pl. 17, fig. 1; refigured here in Text-fig. 1a). However, B4 is shorter and wider than blades of *L. irideaephyllus*. It is noteworthy that Massalongo (1858) regarded *L. irideaephyllus* as largely conforming to *Pterigophycos* in regard to morphology and blade margin undulation/incision. However, secondary veins, which are visible in *P. gazolanus* (Text-fig. 1b), are lacking in *L. irideaephyllus* and B4.

The individual blades of the thallus described here can be attributed to at least two of the taxa described and figured by Massalongo (1858) from the Bolca area. Thus, the thallus supports the hypothesis advanced by Massalongo (1858) that the various blade types he had formally described as species of *Pterigophycos* may belong to one biological species. This author regarded *P. canossae* (Text-fig. 1c) as an intermediate form between *P. spectabilis* (Text-fig. 1d) and *P. gazolanus* (Text-fig. 1b), and *P. pinnatifidus* (Sternberg 1833: 33, pl. 10, fig. 4) as a young *P. spectabilis*. If this is accurate, then it is possible that *Pterigophycos* produced blades that were entire-margined and similar to *Laminarites irideaephyllus* (Text-fig. 1a) when young, but became subdivided into individual segments as they matured and the lamina expanded. An alternative interpretation views the different blade morphologies as adaptations. Blades of thalli growing in stagnant or calm water were perhaps less incised or subdivided into individual lamina segments than the blades of thalli that occurred in habitats dominated by strong water currents (see Palaeoecology below). Finally, Massalongo (1858) speculated that vegetative proliferation occurred in *Pterigophycos*, namely that the individual lamina segments detached from the midrib as the blades atrophied, became dispersed, and eventually grew into new thalli elsewhere. However, there is currently no evidence for this mechanism in *Pterigophycos*.

Present-day morphological similitudes

We are not aware of any present-day uncalcified macroalga that corresponds to *Pterigophycos* in thallus morphology (Text-fig. 5), and thus could be used to infer the systematic affinities of the fossil. Massalongo (1858) compared *P. gazolanus* with the present-day red alga *Phycodrys rubens* (L.) Batters (as *Delesseria sinuosa* J.V.Lamour.) of the Delesseriaceae (Ceramiales, Rhodophyta) (Batters 1902). *Phycodrys rubens* is characterized by blades that resemble leaves, even as far as the existence of a midrib and pairs of lateral veins. The blades sometimes produce lateral extensions of the lamina (e.g., Bradbury et al. 1859: fig. 45) that resemble the lamina segments in *Pterigophycos*. Similar lateral outgrowths from the blade have also been recorded in other species of *Phycodrys* Kütz. (Stewart 1976). The type species of the genus *Delesseria*, *D. sanguinea* (Hudson) J.V.Lamour., is constructed of branches arising from a discoid holdfast and bearing spirally arranged, leaflike blades that are ovate-lanceolate in outline. Each blade consists of a short stipe and a monostromatic (i.e., having cells in a single layer) lamina with an undulating margin. A prominent midrib divides the blade into two halves and gives off veins on both sides that run to the lateral margins. Blades of *D. sanguinea* are only slightly similar to the intermediate blade B4 of the fossil in regard to overall shape, except that the latter is deeply incised, whereas *D. sanguinea* is largely entire (Wynne and Saunders 2012). Moreover, no evidence of lateral veins has been found in the fossil lamina segments. However, lateral veins are present in several of the *Pterigophycos* specimens figured by Massalongo (see Text-fig. 1b, d).

Another present-day alga that bears some resemblance to the fossil is *Undaria pinnatifida* (Harv.) Suringar, a member of the family Alariaceae (Laminariales, Phaeophyceae). This kelp produces segmented blades with a distinct midrib, and subtended by a stipe and fibrous holdfast; blades may grow to 1 m long (Okamura 1915, Shibneva and Skriptsova 2012). The blades are similar in basic morphology to the blades in *Pterigophycos*. However, *U. pinnatifida* produces single blades extending from the holdfast, while the fossil demonstrates that several blades were given off from the holdfast structure in *Pterigophycos*. A second member of the Alariaceae that may be compared with the fossil is *Egregia menziesii* (Turner) Aresch., a perennial kelp characterized by a holdfast from which typically a single main stipe arises (known as the rachis) that may be branched or unbranched and up to 15 m long (Abbott and Hollenberg 1976, Henkel and Murray 2007, Burnett and Koehl 2019). The rachis is lined with lamina segments 2–8 cm long on either side. The appearance of mature *E. menziesii*, lined with lamina segments along the main stipe, makes it obvious why it is commonly known as the feather boa kelp (Blanchette et al. 2002). The lateral outgrowths can range from broadly ovate to spathulate to highly dissected and fringed; these variations are observed even within local populations and seem to mostly depend on the position of the segments on the axis (Henkel and Murray 2007).

Palaeoecology

Very little information on the palaeoecology of *Pterigophycos* can be obtained from the fossils. Moreover, little is known about the quality of the habitats in which these algae grew. Most marine macroalgae are exposed to mechanical forces in the form of water currents and water motion (Denny 1988, Koehl et al. 2008), which may damage the thalli or dislodge them from their substrate (Koehl and Wainwright 1977, Carrington 1990). The strength of these forces depends on the size and shape of the alga, and the speed and direction of the water movement (Vogel 1994, Denny et al. 1985). The relative water force affecting each individual is reduced if the algal thalli occur in dense stands or aggregations (Koehl and Alberte 1988, Johnson 2001, Gaylord et al. 2007). Moreover, blade morphology affects the drag force imposed by the water flow (Johnson and Koehl 1994). It is possible to envisage, therefore, that blade segmentation in *Pterigophycos* was effective in reducing drag forces in moving water. Furthermore, the resistance of an alga to mechanical deformation depends on the stiffness of its parts. The prominent midrib in the *Pterigophycos* blades could have provided mechanical support. Unfortunately, the specimens available do not provide information on the internal organization of the blades. Size and shape of macroalgae can change considerably as they grow and reproduce, and many species grow and reproduce primarily when water currents are weakest and water motion is slow (Johnson and Koehl 1994, Koehl 1999, Wolcott 2007, Demes et al. 2013). Seaweeds less than 50 cm tall and relatively flexible usually bend down into the slowly moving water near the substrate (Koehl and Wainwright 1977); however, they appear to break under relatively low stress and tension (Delf 1932). Moreover, the form of an algal thallus is known to correlate with nutrient-uptake abilities, and photosynthetic and respiration rates, as well as susceptibility to herbivory. For example, net photosynthetic rates of filiform blades or lamina segments are greater than those of spathulate laterals (Henkel and Murray 2007 and references therein). Macroalgae with flat, strap-like blades dominate in habitats exposed to rapidly flowing water, whereas those with wide, ruffled "undulate" blades are more frequent in sheltered sites (Koehl and Alberte 1988, Koehl et al. 2008). The shape of the blade appears to be a plastic trait, with changes being induced by mechanical stress (Koehl et al. 2008).

Extant *Delesseria sanguinea* grows in intertidal and subtidal areas, attached to rock surfaces or other algae (Maggs and Hommersand 1993, Bunker et al. 2017, Guiry 2021). *Egregia menziesii* commonly occurs along rocky shores from the intertidal down to 20 m depth (Abbott and Hollenberg 1976, Henkel and Murray 2007). Due to the shape and robust nature of the thallus, whiplash motion from blades has been reported to have significant impact on the intertidal community structure and diversity (Tillin and Budd 2002). The large number of algal remains preserved in the Bolca area could suggest that these organisms grew in large numbers and dense stands, which would reduce the adverse effects of the water currents. It is also possible, however, that recurrent catastrophic events (e.g., strong water currents) destroyed numerous thalli all at once, the parts of which were eventually deposited and became fossilized.

Conclusions

The Bolca Konservat-Lagerstätte represents a rare window into a series of marine to terrestrial palaeoenvironments in the early Eocene of the Tethys. The remarkable fossil diversity reflects a fortuitous combination of taphonomic factors and a reef setting in a region interpreted as an ancient biodiversity hotspot (Friedman and Carnevale 2018). However, plant fossils from Bolca usually occur as fragmentary remains providing limited information on plant stature (physiognomy), palaeobiology, and palaeoecology. This is especially true of the marine macroalgae. The fossil presented in this study, in conjunction with specimens figured previously by Massalongo

(1858), therefore, gives a rare glimpse of the growth habit and intraspecific variability of a Bolca alga attributable to the little-known genus *Pterigophycos*. We are well aware of the fact that the new information from this specimen strongly suggests the need for taxonomic revision of the genus *Pterigophycos*. However, many of the more than 1,000 macroalgal fossils from Bolca kept in various museum collections in Italy and abroad have not been critically evaluated to date. A thorough analysis of these fossils to assess the record of *Pterigophycos* and revise the taxon thoroughly is beyond the scope of this article, but will be presented in due course elsewhere. Moreover, we believe that information on thallus morphology can also be obtained from other Bolca algae by piecing them together from disarticulated parts. The reconstruction of an increasing number of whole-plant taxa provides a template to interpret newly discovered parts of these algae with regard to their position in the thallus and their function. Although Bolca fossils have been intensively studied for almost 200 years, new and heretofore understudied specimens can still provide plenty of opportunities to refine and advance the broader discussion of life in these Eocene palaeoecosystems.

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