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RESEARCH ARTICLE

Reinterpretation of the non-biomineralised macroalgae *Algites magnus* Teslenko, 1982 and *Algites codiumiformis* Teslenko, 1986 from the Bajocian (Middle Jurassic) of Crimea (Ukraine) as trace fossils

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ABSTRACT

As a result of the revision of the type material, two taxa of Middle Jurassic non-biomineralised macroalgae from the Crimean Peninsula (southern Ukraine), *Algites codiumiformis* Teslenko, 1986 and *Algites magnus* Teslenko, 1982, have been assigned to the trace fossils *Dactyloidites ottoi* (Geinitz, 1849) and ?*Chondrites* isp., respectively. *Algites theodosiensis* Teslenko, 1982 from Lower Cretaceous strata of Crimea, whose type material is likely lost, is synonymised with the ichnospecies *Chondrites targionii* (Brongniart, 1828).

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Introduction

Non-biomineralised macroalgae have a low preservation potential as fossils (Filipiak & Zatoń, 2016; Korde, 1993; Krings & Mayr, 2004; LoDuca et al., 2011; Pettersson et al., 2020). As a result, such finds require careful and nuanced interpretation. In the fossil record, these algae are typically represented by carbonaceous or sulphide crusts preserved on the surfaces of fine-grained rocks, such as mudstones and siltstones (Filipiak & Zatoń, 2016; Korde, 1993; Krings & Mayr, 2004; LoDuca et al., 2011; Pettersson et al., 2020).

In Ukraine, non-calcified macroalgae have been documented in Ediacaran (Ivantsov et al., 2015 and references therein) and Silurian (Ishchenko, 1984, 1985, 1986; LoDuca, 2024; Skompski et al., 2023) strata of Podillia (western Ukraine), in Aalenian (Middle Jurassic) deposits of the Crimean Peninsula (southern Ukraine) (Teslenko & Yanovskaya, 1990; Teslenko, 1982) and in Pennsylvanian (unpublished data of the author) and Sarmatian (Miocene, Neogene) deposits of the Donets Basin (eastern Ukraine) (Pimenova, 1954).

Nalyvaiko (1936) briefly described, but did not illustrate, the macroalga *Confervites fasciculatum* Brongniart, 1828 from the Upper Cretaceous marlstone succession of the southern Donets Basin. However, Savchinskaya (1982) did not confirm this report. Brown algae genus *Cystoseira* occurs in Neogene deposits of the Kerch Peninsula (southern Ukraine).

In the early days of palaeontology, many fossils now recognised as trace fossils were originally described as remains of macroalgae (Baucon et al., 2012; Mikuláš & Dronov, 2006). The so-called 'Age of Fucoids' in palaeontological history ended in 1881 (Baucon et al., 2012; Mikuláš & Dronov, 2006; Osgood, 1975), yet its influence persisted well into the following era. During this time, unequivocal ichnofossils were still often misattributed to plant remains, particularly to non-calcified macroalgae. This trend remained especially prevalent within Soviet palaeontology, possibly due to its relative isolation from global scientific developments, ideological policies, manifested, for example, in the so-called 'Lysenkoism', the 'Pavlovian session' and the campaign against 'cosmopolitanism', among others, also had a significant negative impact on science (Ivanov, 2000; Lakhtin, 1990; Sinclair, 1987). As a result, numerous new taxa of fossil non-calcified algae were described from the former USSR (see review in Korde, 1993), which are, in fact, trace fossils reflecting the activities of various animals in unconsolidated substrates.

This study focuses on the revision of *Algites magnus* Teslenko, 1982 and *Algites codiumiformis* Teslenko, 1986, taxa originally described by Teslenko (1982, 1986 and

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1987) from the Bajocian of the Crimean Peninsula, southern Ukraine, and assigned to non-calcified macroalgae. These taxa have been mentioned in the literature as macroalgae (e.g. Korde, 1993; Paperny, 2019). However, Naugolnykh (2017) suggested that *Algites codiumiformis* represents the trace fossil *Lorenzinia* Gabelli, 1900, or a closely related form, but did not substantiate this interpretation nor dispute the algal origin of *Algites magnus* and *Algites theodosiensis* Teslenko, 1982, which are also treated as trace fossils in the present study.

Material and methods

The holotypes of *Algites codiumiformis* (specimen NMNHU G-2201/01) and *A. magnus* (specimen NMNHU G-2201/68) are examined in this study; one paratype of *Algites codiumiformis* is presumably lost.

Specimen NMNHU G-2201/01 is a well-preserved trace fossil on the lower bedding plane of a yellowish-grey fine-grained sandstone. The surface hosting *Algites codiumiformis* is smooth, with minor weathering marks on the rock. In the original description (Teslenko, 1982, p. 116), the holotype number is Kr/M-7/2, but the specimen itself is catalogued as NMNHU G-2201/01.

Specimen NMNHU G-2201/68 is a trace fossil preserved on a sub-triangular slab (approximately 30 cm long and 20 cm at its widest point) of fine-grained, dense, horizontally bedded yellowish-grey sandstone. In the original description (Teslenko, 1982, p. 116), the holotype number is Kr/M-7/1, but the specimen itself is catalogued as NMNHU G-2201/68.

The specimens were collected by Dr. Yuri V. Teslenko (1924–2006) at Yanyshar Bay (=Tykha Bay) near the former town of Planers'ke (now Koktebel, on the south-eastern (Black Sea) coast of the Crimean Peninsula, southern Ukraine; Figure 1). Tykha Bay is located approximately 2.5 km east of Koktebel, bounded to the west by the Toprak-Kaya Cape and to the east by an unnamed cape separating the bay from the Provato Bay.

The specimens originate from tuffaceous sandstones of the Lower Subformation (*sensu* Teslenko & Yanovskaya, 1990) of the Karadag Formation, dated to the Bajocian (Teslenko & Yanovskaya, 1990; Teslenko, 1982, 1986). The Bajocian age (168.2 ± 1.2 to 170.9 ± 0.8 Mya; International Chronostratigraphic Chart, 2024) of *A. codiumiformis* and *A. magnus* is confirmed by the co-occurrence of the late Bajocian ammonite species *Parkinsonia parkinsoni* (Sowerby, 1821) (Teslenko & Yanovskaya, 1990).

The examined specimens likely come from one of the 0.2–0.4 m thick dense sandstone beds within the mudstone-dominated succession bearing siderite nodules, as described by Muratov (1937). This sedimentary sequence may correspond to the Middle Subformation of the Karadag Formation (*sensu* Permyakov et al., 1991) or the Lower Subformation (*sensu* Teslenko & Yanovskaya, 1990).

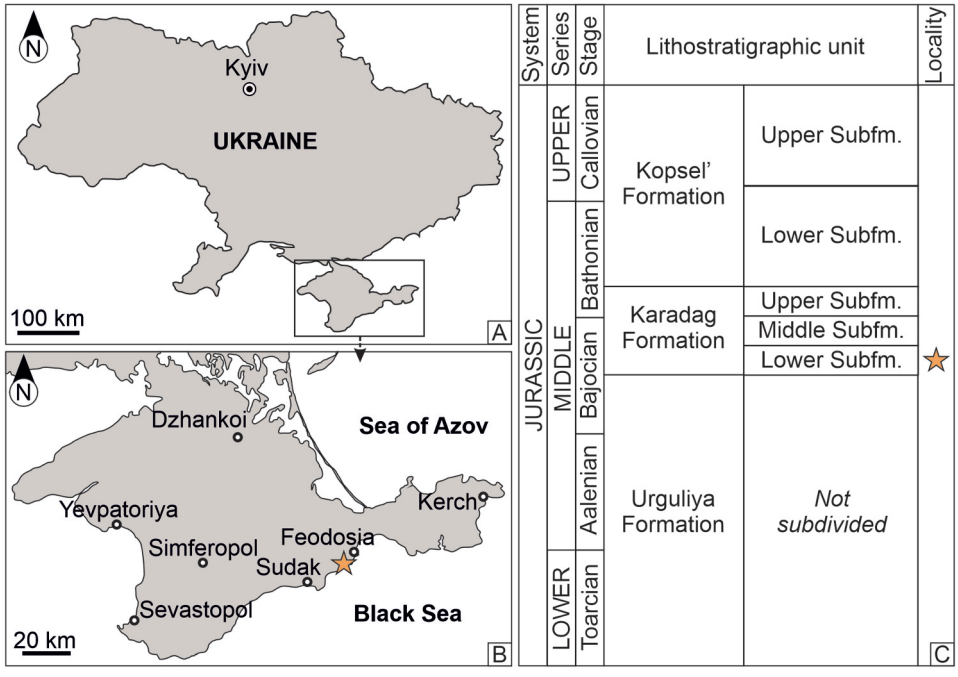


Figure 1. Geographical location (A, B) and stratigraphic position (C) of the type locality of *Algites codiumiformis* Teslenko, 1986 and *Algites magnus* Teslenko, 1982 (marked by the orange asterisks). Abbreviation: Subfm. – Subformation.

The material examined forms part of collection NMNHU G-2201 ('Middle Jurassic flora of the Crimean Peninsula') housed at the Department of Geology, National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv (acronym: **NMNHU**).

Geological setting

The area surrounding the town of Koktebel is part of the Sudak-Feodosia facies zone (Leshchukh et al., 1999; Permyakov et al., 1991) or the Sudak-Karadag facies zone (Permyakov et al., 1984; Teslenko & Yanovskaya, 1990), which encompasses the eastern portion of the Tuak Uplift and the East Crimean Synclinorium, as well as the Sudak Synclinorium and the Sudak-Karadag fold system. This zone is characterised by the presence of volcanogenic rocks and a thick succession of reef limestones (Lebedinsky & Shalimov, 1962; Moiseev, 1937; Permyakov et al., 1991; Remizov, 1962; Uspenskaya, 1969).

The Karadag Formation is primarily composed of siliciclastic and effusive rocks (Ivanik et al., 2013; Leshchukh et al., 1999; Permyakov et al., 1984, 1991; Rogov, 2004). It is subdivided into three subformations: Lower, Middle and Upper (Permyakov et al., 1984, 1991). Teslenko and Yanovskaya (1990) further divided the Karadag Formation into two subformations, with the Lower and Middle subformations likely corresponding to the Lower Subformation as defined by Permyakov et al. (1984, 1991).

The Lower Subformation (*sensu* Permyakov et al., 1984, 1991), 125–240 m thick, consists of spilite and andesite lavas, along with their tuffs, which contain rare ammonites such as *Spiroceras bifurcatum* Hyatt in Zittel, 1900 (Ivanik et al., 2013; Permyakov et al., 1991). This subformation is assigned to the late Bajocian *Spiroceras bifurcatum* Zone by Permyakov et al. (1991).

The Middle Subformation, 120 m thick, is a succession dominated by mudstones and siltstones, containing late Bajocian ammonites *Garantiana garantiana* (d'Orbigny, 1846), *Sphaeroceras brongniarti* (Sowerby, 1818), *Parkinsonia parkinsoni* (Sowerby, 1821) and *P. bigoti* Nicolesco, 1928 (Ivanik et al., 2013; Permyakov et al., 1991). This subformation corresponds to the late Bajocian *Garantiana garantiana* and *Parkinsonia parkinsoni* zones (Permyakov et al., 1991).

The Upper Subformation, which is 315–1000 m thick, consists of andesite tuffs interbedded with tuffitic sandstones. It contains late Bajocian and early Bathonian ammonites, including *Parkinsonia parkinsoni* (Sowerby, 1821), *P. orbigniana* Wetzel, 1911, *P. bigoti* Nicolesco, 1928, *Procerites (Siemiradzkia) aurigerus* (Oppel, 1857), *Calliphylloceras disputabile* (Zittel, 1869), bivalves *Nucula ventricosa* Hinds, 1843, *Leda lacryma* (Sowerby, 1824) and *Anisocardia tenera* (Sowerby, 1821) (Beznosov, 1958; Leshchukh et al., 1999; Permyakov et al., 1991; Remizov, 1962; Teslenko & Yanovskaya, 1990; Tsereteli, 1973; Tsereteli & Lominadze, 2009). This subformation is assigned to the late Bajocian *Parkinsonia parkinsoni* Zone and to the lowermost part of the Bathonian by Permyakov et al. (1991). However, the presence of *Procerites (Siemiradzkia) aurigerus* suggests that the Upper Subformation belongs exclusively to the *Procerites aurigerus* Zone, the uppermost zone of the early Bathonian (Rogov, 2004).

The Karadag Formation represents a sequence of rocks formed along the continental margin, reflecting its evolution from a phase of island-arc volcanism (upper Bajocian volcanogenic-sedimentary strata) to the relatively deep-water deposits of distal prodeltaic environments (lower Bathonian strata) (Gulyaev et al., 2023; Meijers et al., 2010; Permyakov et al., 1992; Teslenko, 1987).

Systematic Palaeontology

The rationale for the synonymy of *Algites codiumiformis* and *A. magnus* with *Dactyloidites ottoi* (Geinitz, 1849) and ?*Chondrites* isp., respectively, is given below.

Ichnogenus ***Dactyloidites*** Hall, 1886

Type ichnospecies. *Buthotrephis asteroides* Fitch, 1850; original designation.

Dactyloidites ottoi (Geinitz, 1849) (Figure 2A,B)

1849 ***Spongia ottoi* sp. nov.**: Geinitz, p. 264, pl. 12, figs. 6, 7.
1852 *Spongia ottoi* Geinitz, 1849: von Otto, p. 12, pl. 4, fig. 7.
1930 *Spongia ottoi* Geinitz, 1849: Häntzschel, figs. 1–3.
1841 *Gyrophyllites* cf. *kwassizensis* Glocker, 1841: Lehner: p. 190, pl. 17, fig. 37.
1960 ***Spongia shikokuensis* sp. nov.**: Katto, p. 324, pl. 34, figs. 10, 13.
1964 ***Häntzschelinia kolymensis* sp. nov.**: Vyalov, p. 113, fig. 2.
1964 ***Haentzschelinia pygmaea* sp. nov.**: Vyalov, p. 115, fig. 3.



Figure 2. *Dactyloidites ottoi* (Geinitz, 1849), specimen NMNHU G-2201/01, holotype of *Algites codiumiformis* (A – photo, B – schematic sketch). C – ?*Chondrites* isp., specimen NMNHU G-2201/68, holotype of *Algites magnus*. Coast of Tykha Bay near the town of Koktebel, Autonomous Republic of Crimea, Ukraine; Karadag Formation, late Bajocian, Middle Jurassic. Scale bars equal 10 mm.

1965 ***Haentzschelinia shikokuensis* sp. nov.**: Keij, pl. 28, figs. 4–7.
1965 ***Haentzschelinia labuanensis* sp. nov.**: Keij, pl. 28, figs. 2–3.
1975 *Haentzschelinia ottoi* (Geinitz, 1849): Häntzschel, p. W68, fig. 3a, b.
1981 *Haentzschelinia* sp.: Tanaka & Sumi, pl. 4, fig. 1.
1985 *Dactyloidites ottoi* (Geinitz, 1849): Fürsich & Bromley, p. 207, figs. 1–6.
1986 ***Algites codiumiformis* sp. nov.**: Teslenko, p. 95, unnumbered text-fig.
1986 *Haentzschelinia* sp.: Noda, p. 69, fig. 3.
1989 *Häntzschelinia ottoi* (Geinitz, 1849): Vyalov, pp. 73, 74.
1990 *Algites codiumiformis*: Teslenko & Yanovskaya, p. 67, text-fig. 7, pl. 1, fig. 1.
1996 *Dactyloidites ottoi* (Geinitz, 1849): Bromley, p. 133, figs. 7.7c, 7.8.
1993 *Dactyloidites ottoi* (Geinitz, 1849): Pickerill et al., p. 1072, figs. 2, 3.
1995 *Dactyloidites ottoi* (Geinitz, 1849): de Gibert et al., p. 770, pl. 91, figs. 2–4.
1997 *Häntzschelinia ottoi* (Geinitz, 1849): Seilacher, p. 48, fig. 28.
1999 *Dactyloidites ottoi* (Geinitz, 1849): López Martínez & Ardévol, p. 130, fig. 3.
2004 *Dactyloidites ottoi* (Geinitz, 1849): Agirrezabala & de Gibert, figs. 5, 6.
2004 *Dactyloidites ottoi* (Geinitz, 1849): Blissett & Pickerill, p. 348, pl. 3, fig. A.
2008 *Dactyloidites ottoi* (Geinitz, 1849): Lazo et al., p. 1, fig. 2.
2010 *Dactyloidites ottoi* (Geinitz, 1849): Srivastava et al., p. 172, pl. 1, figs. 1–3.
2011 *Dactyloidites ottoi* (Geinitz, 1849): Göhler, p. 59, figs. 2, 3.
2014 *Dactyloidites ottoi* (Geinitz, 1849): Wilmsen & Niebuhr, p. 125, figs. 3–6.
2020 *Dactyloidites ottoi* (Geinitz, 1849): Aguilar, p. 3, fig. 2.

2023 *Dactyloidites ottoi* (Geinitz, 1849): Curran & Glumac, p. 27, figs. 7, 8.

Material. One specimen (NMNHU G-2201/01), chosen by Teslenko (1986) as the holotype of *Algites codiumiformis*.

Description. Specimen NMNHU G-2201/01 is a partially preserved vertical rosette, fan-shaped trace fossil consisting of six unbranched and once-branched radial burrows preserved as a positive semirelief on the upper bedding plane of the sandstone bed. The burrows radially diverge from one point at an angle of about 30–35°. The secondary branching is at an angle of about 15°. The individual burrows are usually straight, sometimes very slightly curved, and widen slightly from the base to the distal end. The distal ends of the best-preserved burrows are rounded. The infill is passive, with a composition that does not differ from the matrix rock. The length of individual burrows is 20–30 mm, and the width of the distal ends of the burrows is 4 mm. The total width of the burrow system is 40 mm, the length is 30 mm, and the angle between the most distant individual radial burrows (the first and sixth, see Figure 2B) is approximately 180°.

Remarks. Teslenko (1986) interpreted *Algites codiumiformis* as a green alga closely related to the genus *Codium* Stackhouse, 1797. *Algites* Seward, 1894, is a formally recognised genus that includes presumably non-biomineralised fossil algae, the precise systematic classification of which remains uncertain due to the absence of preserved reproductive structures or internal features (Basson, 1972; Basson & Wood, 1970; Seward, 1894; Teslenko & Yanovskaya, 1990; Teslenko, 1982, 1986). However, LoDuca et al. (2017) restricting it to include only ribbon-like thalli with a minimum width of 0.1 mm.

The non-algal nature of *Algites codiumiformis* is supported by both the taphonomy and morphology of specimen NMNHU G-2201/01. For instance, it seems highly improbable that a non-calcified alga could have created a depression in a relatively dense psammite substrate that would have been preserved as a fossil. Additionally, no remains of carbonaceous, sulphide or iron hydroxide substances, characteristic of fossil non-biomineralised macroalgae, were found on specimen NMNHU G-2201/01. The 'attachment disc' mentioned by Teslenko and Yanovskaya (1990, p. 67) is more likely to be a poorly preserved horizontal burrow or subvertical shaft. Furthermore, no remains of the 'utricles' mentioned by Teslenko and Yanovskaya (1990, p. 67) were observed.

Dactyloidites is 'a mid-to-deep burrow system forming stellate to palmate rosettes composed of branched or unbranched actively filled spreite-bearing branches radiating horizontally to sub-horizontally from a single vertical to sub-vertical central shaft' (Boyd & McIlroy, 2016, p. 259). The morphology of specimen NMNHU G-2201/01 is consistent with this diagnosis. A comparison of the morphology of the holotype of *Algites codiumiformis* with images of *Dactyloidites ottoi* presented in Fürsich and Bromley (1985, figs. 1, 3), Pickerill et al. (1993, fig. 2), de Gibert et al. (1995, fig. 2), Agirrezabala and de Gibert (2004, fig. 5), Lazo et al. (2008, fig. 2), Wilmsen and Niebuhr (2014, figs. 3–6), Aguilar (2020, fig. 2), Curran and Glumac (2023, fig. 7), and others confirms that these taxa are morphologically identical and thus synonymous.

Occurrence. ?Triassic, Jurassic – Neogene. It is likely that the stratigraphic range of *Dactyloidites ottoi* extends down to the Carboniferous, as upper Serpukhovian deposits in the Donets Basin (Ukraine) contain trace fossils that closely resemble or may even be attributable to *D. ottoi* (Aisenverg, 1958, pl. 17, fig. 2, by the author's interpretation).

Ichnogenus ***Chondrites*** Sternberg, 1833

Type ichnospecies. *Fucoides antiquus* (Brongniart, 1828); subsequent designation by Miller (1889).

***?Chondrites* isp.**
(Figure 2C)

1982 ***Algites magnus* sp. nov.**, Teslenko, p. 116, text-fig. 2.
1990 *Algites magnus*, Teslenko & Yanovskaya, p. 68, pl. 12, fig. 1.

Material. One specimen (NMNHU G-2201/68), chosen by Teslenko (1982) as the holotype of *Algites magnus*.

Description. A system of horizontal, cylindrical, straight to slightly arched, somewhat flattened, Y-shaped branched burrows consisting of a master branch and 4 s-order branches. The burrows are unlined and preserved as convex hyporelief, as indicated by corresponding concave semirelief traces on the opposite side of the slab. The burrow diameter is 4–5 mm. Branching angles are acute to right. The burrows are actively filled with finer-grained, structureless sandy material that differs in colour from the host rock.

Remarks. Specimen NMNHU G-2201/68 interpreted as a two-dimensional burrow system similar to the ichnogenus *Chondrites* Sternberg, 1833. The ichnogenus *Chondrites* is defined as 'regularly branching tunnel system consisting of a small number of subvertical master-shafts, connected to the ancient sediment–water interface, that branches at depth to form a dendritic network. Fill can be active or passive' (Baucon et al., 2020, p. 4). Moreover, the branching angle may range from 15° to 90°, with average values typically between 30° and 60° (Fu, 1991). The burrow infill is structureless, although rare occurrences of meniscate infill have been reported (Baucon et al., 2020; Ekdale & Bromley, 1983; Knaust, 2017). The burrow diameter is generally narrow and typically remains constant within a single system (Baucon et al., 2020; Fu, 1991; Savrda & Bottjer, 1991).

Specimen NMNHU G-2201/68 exhibits characteristic morphological features typical of *Chondrites*. However, the irregular branching of the secondary branches is the only morphological feature that does not allow confident assignment of the specimen to *Chondrites*.

Taxonomic remarks on *Algites theodosiensis*

Together with *Algites magnus*, Teslenko (1982) also described a new species, *Algites theodosiensis*, originating from Berriasian (Lower Cretaceous) deposits near the city of Feodosiya in southeastern Crimea. Unfortunately, the type series of this species has not been found; it was apparently never deposited in the NMNHU. For this reason, a complete taxonomic revision of the species cannot be performed. However,

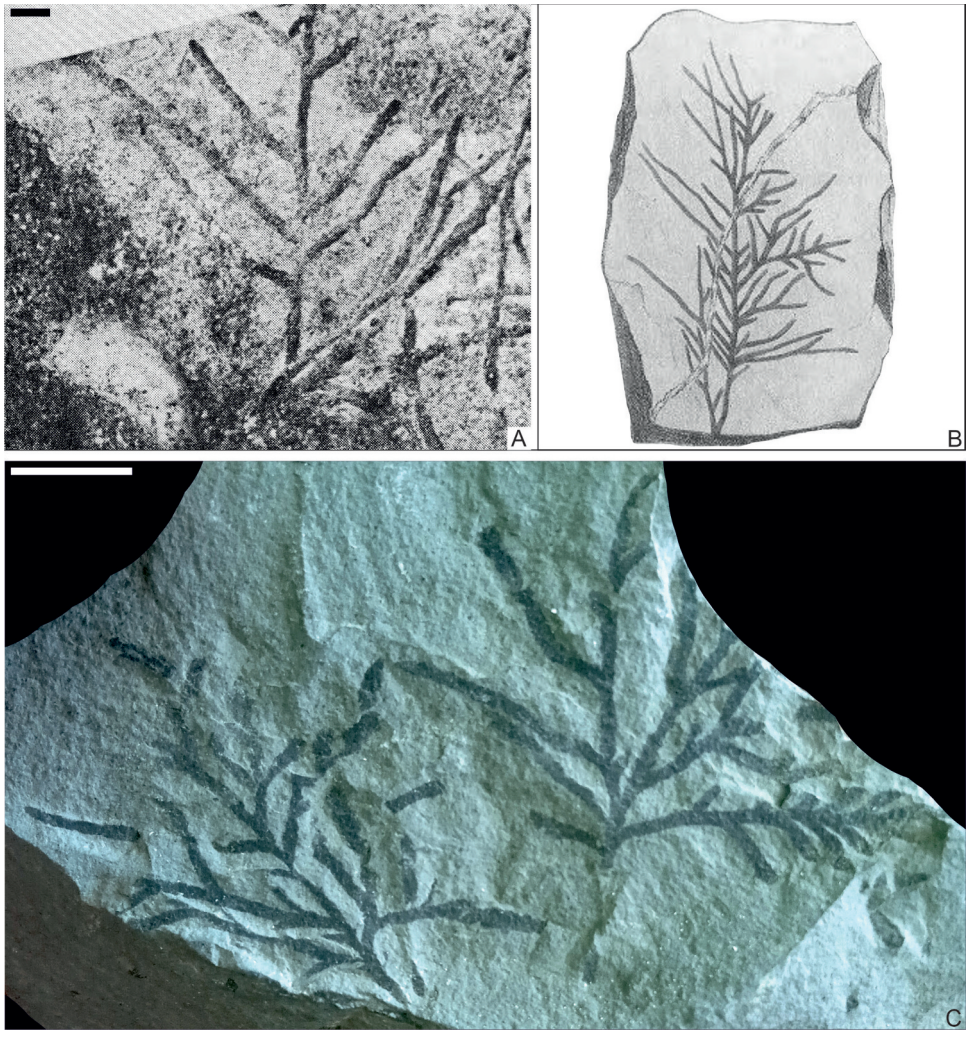


Figure 3. *Algites theodosiensis* Teslenko, 1982 and trace fossils *Chondrites*. A – Holotype of *Algites theodosiensis* (modified after Teslenko, 1982, fig. 3). B – *Chondrites targionii* (Brongniart, 1828) (reproduction of the illustration of the specimen described by Brongniart, 1828: pl. 4, fig. 6 as *Fucoides targionii*). C – *Chondrites intricatus* (Brongniart, 1823) from the Berriasian of the Feodosiya section (uncatalogued specimen from the Geological Museum of the Taras Shevchenko National University of Kyiv). Scale bars equal 10 mm.

based on the image of the holotype of this species published by Teslenko (1982, fig. 3; reproduced here in Figure 3A), it can be confidently stated that *Algites theodosiensis* is a trace fossil belonging to the ichnogenus *Chondrites* Sternberg, 1833. This interpretation is supported by the morphology of *Algites theodosiensis*, which does not differ from that of typical *Chondrites* (compare with the *Chondrites* specimens shown in Figure 3B,C). It should be noted that Teslenko (1982, p. 117) compared *Algites theodosiensis* with the 'macroalgae' *Fucoides targionii* Brongniart, 1828, which are now assigned to the ichnogenus *Chondrites*. Therefore, *Algites theodosiensis* should be referred to the ichnogenus *Chondrites* and is likely a junior synonym of the ichnospecies *Chondrites targionii* (Brongniart, 1828) (cf. Brongniart, 1828, pl. 4, fig. 6 and Figure 3B in this study). Baraboshkin et al. (2016, 2016, 2019) illustrated records of *Chondrites intricatus* (Brongniart, 1823) from the Berriasian of the Feodosiya section, which are morphologically similar to *Algites theodosiensis* (see also Figure 3C).

Discussion and concluding remarks

Teslenko (1982, 1986) and Teslenko and Yanovskaya (1990) described several new taxa from Middle Jurassic deposits of Crimea, interpreted as non-biomineralised macroalgae. These include *Algites subtilis* Teslenko, 1982, *A. codiumiformis* Teslenko, 1986 and *A. magnus* Teslenko, 1982. Of these, only *Algites subtilis* (Figure 4) can currently be reliably attributed to non-biomineralised macroalgae. However, this taxon requires further detailed study and revision. The type series of *A. subtilis* was recovered from fine-grained, shallow marine sandstone (so-called Cycadophyte-bearing Unit; according to Romanov et al., 1986) containing marine bivalves and allochthonous terrestrial plant remains. This bed lies 30–50 m below the Nyzhniy (=Lower) coal seam of the Beshui Formation (Aalenian). These strata were exposed in the former Beshui Coalfield in the Bakhchisarai Raion of southwestern Crimea, Ukraine (Romanov et al., 1986, 1987; Teslenko & Yanovskaya, 1990; Teslenko, 1982).

Teslenko (1982) did not provide a formal diagnosis of *A. subtilis* but offered a detailed description of the available specimens. Below is a translation of this description from the original Russian-language text: 'The thalli are bushy, non-calcified, and repeatedly dichotomously branched into fine segments. Their visible length is approximately 40 mm. The width of the thallus segments varies: in some, presumably older segments, it reaches up to 1 mm, while in others it does not exceed 0.3 mm. The areas at the points of dichotomy are the most expanded. The edges of the segments are



Figure 4. Type series of *Algites subtilis* Teslenko, 1982. A – holotype NMNHU G-2201/04, B – counterpart of the holotype (specimen NMNHU G-2201/02). The Beshui Coalfield near the former village of Shakhty, Bakhchisarai Raion, Autonomous Republic of Crimea, Ukraine; Beshui Formation, Aalenian, Middle Jurassic. Scale bars equal 10 mm.

smooth, although in one instance they exhibit a wavy form; here the thallus acquires a bead-like appearance. The imprints are dark brown in color, which makes them stand out clearly against the pale-colored host rock. On the dark background of certain parts of the thalli, a longitudinal fracture filled with lighter intrusive material is distinctly visible. In some cases, the fracture reaches a relatively large width, while in others it is barely noticeable. At the branching points of the thalli, the fracture either does not dichotomize at all, continuing into a wider segment, or sends a very thin small branch into an adjacent segment, which immediately disappears in the basal part of the segment' (Teslenko, 1982, fig. 115).

Dactyloidites ottoi is a fodinichnion trace fossil originated as the result of infaunal activity by a deposit-feeding organism, likely a polychaete worm, which processed sediment in search of organic material (Curran & Glumac, 2023; de Gibert et al., 1995; Fürsich & Bromley, 1985; Häntzschel, 1975; Wilmsen & Niebuhr, 2014). This ichnospecies typically occurs in shallow-water, nearshore to deltaic siliciclastic nutrient-rich environments with discontinuous sedimentation, corresponding to the distal *Skolithos* and proximal *Cruziana* ichnofacies (Agirrezabala & de Gibert, 2004; Curran & Glumac, 2023; Wilmsen & Niebuhr, 2014).

The genus *Chondrites* is a fodinichnion and chemichnion ichnogenus with a wide facies distribution, reported from both shallow- and deep-marine deposits (Baucon et al., 2020; Knaust, 2017; Seilacher, 2007). However, its greatest abundance is recorded in deep-marine settings (*Nereites* ichnofacies: Knaust, 2017; McIlroy, 2008), where it also represents a characteristic component of the *Zoophycos* ichnofacies (Buatois & Mángano, 2016; McIlroy, 2008).

Monotypic or low-diversity assemblages dominated by *Chondrites* are generally interpreted as indicators of dysoxic conditions (Bromley, 1996; Bromley & Ekdale 1984; Buatois & Mángano, 2016). Indeed, tracemakers of *Chondrites* are capable of colonising environments with oxygen levels significantly lower than those required by most other metazoans (Savrda & Bottjer, 1984). The tracemakers of *Chondrites* burrow systems are most likely asymbiotic and chemosymbiotic bivalves, as well as deposit feeder vermiform organisms (Baucon et al., 2020).

Bajocian–Bathonian trace fossils of eastern Crimea remain poorly documented. For example, Babanova (1963) reported the occurrence of a 'jellyfish' *Atollites caucasicus* Sobolev, 1957 from a siderite nodule within shale beds at Toprak-Kaya Cape, near the town of Koktebel. More recently, Gulyaev et al. (2023) correlated this section interval (Bed No. 1) with the lower Bathonian *Zigzag* Zone. Based on lithological characteristics, the shale containing *A. caucasicus* is assigned to the Kopsel' Formation, which is yielded ammonites *Oxycerites yeovilensis* (Rogov, 2004; Rollier, 1911; Stremoukhov, 1913a, 1913b; Tsereteli, 1989).

Atollites caucasicus is most likely a trace fossil and may be a junior synonym of *Gyrophyllites* Glocker, 1841 or *Kirklandia* Caster, 1945. Gerasimov (1980) described from Lower Cretaceous deposits structures similar to *Atollites caucasicus*, which he interpreted as the remains of jellyfish, *Palaeosemaeostoma rjasanense* Gerasimov, 1980. Baraboshkin et al. (2014), having studied new material of *Palaeosemaeostoma rjasanense* from the type area, concluded that this species most likely belongs to trace fossils. Vasilyuk & Tchaykovskaya (1984) compared *A. caucasicus* with the modern 'elephant ear' anemone *Bothwellia australense* Preobrazhensky, 1981, which is now recognised as a junior synonym of *Amplexidiscus fenestrafer* Dunn & Hamner, 1980 (Grebelny, 2019). However, Vasilyuk & Tchaykovskaya (1984) erroneously interpreted numerous newly collected specimens of *Atollites caucasicus* from its type area (North Caucasus, Russia) as external moulds of giant foraminiferans. Nonetheless, based on morphological and sedimentological evidence, the interpretation of *A. caucasicus* as a trace fossil, most plausibly referable to *Gyrophyllites*, appears to be the most reasonable.

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Data availability statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.31504297.

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