Zitteliana

An International Journal
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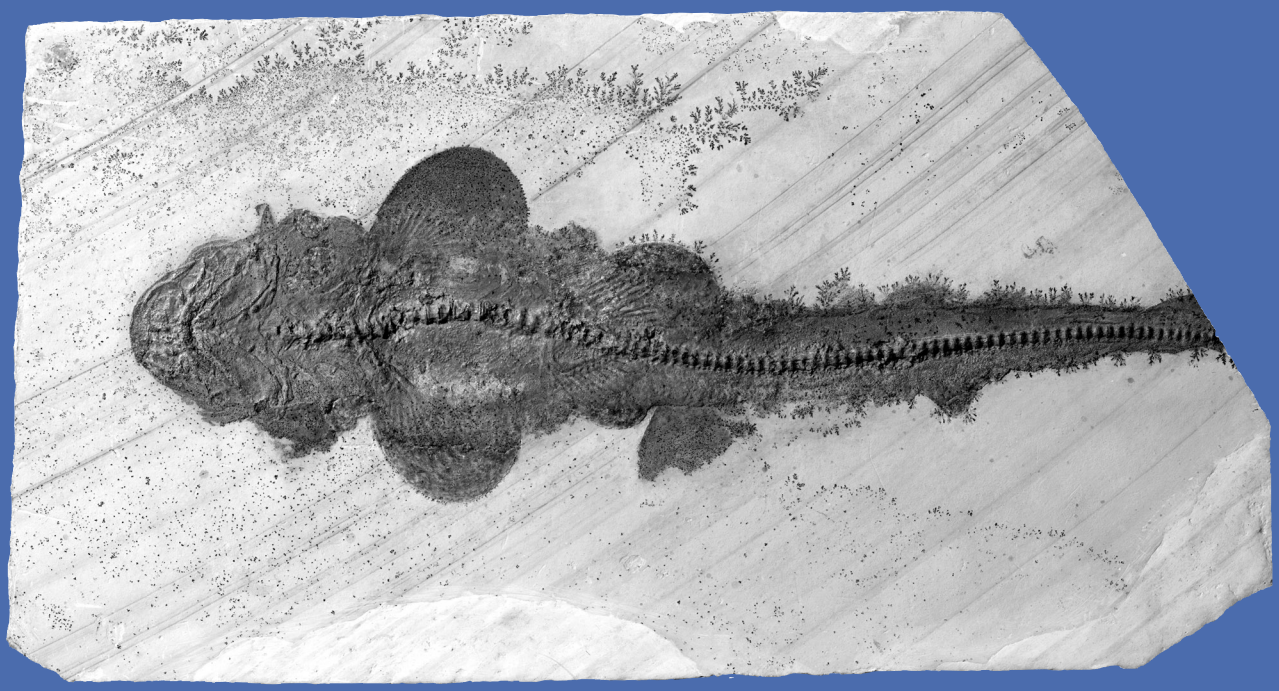
Series A/Reihe A
Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

44



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EDITORIAL NOTE

As of in 2003, the journal *Zitteliana* is published in two series.

Series A: *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) replaces the former „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). The numbering of issues is continued (last published: Heft 43, 2003).

Series B: *Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) continues the previous „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627).

Instructions for authors are included at the end of this volume.

HINWEIS DES HERAUSGEBERS

Vom Jahr 2003 an erscheint die Zeitschrift *Zitteliana* in zwei Reihen.

Die *Reihe A*: *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) ersetzt die bisherigen „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). Die Bandzählung (zuletzt erschienen: Heft 43, 2003) wird fortgesetzt.

Die Reihe B: *Abhandlungen der Bayerischen Staatssammlung für aPaläontologie und Geologie* (ISSN 1612-4138) führt die bisherige „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627) fort.

Hinweise für Autoren beider Reihen sind am Ende dieses Bandes enthalten.

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Für den Inhalt der Arbeiten sind die Autoren allein verantwortlich.
Authors are solely responsible for the contents of their articles.

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Cover illustration: *Phorcynis catulina* Thiollière, 1854 (BSP 1990 XVIII 51) from the lower Tithonian of Zandt / Denkendorf (Bavaria), ventral view, 25 cm. Photograph: G. Janßen (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Umschlagbild: *Phorcynis catulina* Thiollière, 1854 (BSP 1990 XVIII 51) aus dem unteren Tithon von Zandt / Denkendorf (Bayern), Ventralansicht, 25 cm. Foto: G. Janßen (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

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Bassonia hakelensis (Basson) nov. comb., a rare non-calcareous marine alga from the Cenomanian (Upper Cretaceous) of Lebanon

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Abstract

A nearly complete specimen of the Cenomanian (Late Cretaceous) non-calcareous alga *Bassonia hakelensis* (Basson) nov. comb. is reported from the Haqel fish beds in Lebanon. *Bassonia hakelensis* was originally described under the name *Algites hakelensis* Basson, 1972. Based on the distinctive morphology of the thallus, we find it compelling to exclude this species from *Algites* Seward, 1894, and assign it to a new genus, for which the name *Bassonia* nov. gen. is introduced. *Bassonia hakelensis* displays morphological characters also found in certain extant rhodophytes, but assignment to any particular extant taxon is impossible because important features required today in order to establish the systematic position of an alga cannot be determined.

Key words: *Algites* Seward, *Bassonia* nov. gen., fossil non-calcareous alga, Haqel fish beds, Late Cretaceous, *Pithyopsis tasmanica* (Sonder) Falkenberg (Ceramiales, Rhodomelaceae)

Kurzfassung

Aus den Haqel Fischschiefern (Cenoman, Oberkreide) im Libanon wird ein nahezu vollständiges Exemplar der unkalzifizierten Alge *Bassonia hakelensis* (Basson) nov. comb. vorgestellt. *Bassonia hakelensis* ist ursprünglich unter dem Namen *Algites hakelensis* Basson, 1972 beschrieben worden. Aufgrund der charakteristischen Thallusmorphologie halten wir es für angebracht, diese Art von *Algites* Seward, 1894 abzugrenzen und in eine neue Gattung zu stellen, für die der Name *Bassonia* nov. gen. eingeführt wird. *Bassonia hakelensis* besitzt morphologische Merkmale, die auch bei einigen modernen Rotalgen zu finden sind; eine Zuordnung des Fossils zu einem bestimmten modernen Taxon ist allerdings nicht möglich, da wesentliche, für die Bestimmung von Algen generell erforderliche Merkmale nicht erhalten sind.

Schlüsselwörter: *Algites* Seward, *Bassonia* nov. gen., fossile unkalzifizierte Alge, Haqel Fischschiefer, Oberkreide, *Pithyopsis tasmanica* (Sonder) Falkenberg (Ceramiales, Rhodomelaceae)

1. Introduction

Based on the biological and ecological significance of algae in many aquatic environments today (Round 1981; Graham & Wilcox 2000), a detailed knowledge of their fossil record, evolution, and the roles they played in biological and ecological processes in the past is important in understanding the evolutionary history of ancient and modern aquatic ecosystems. Fortunately, the fossil record of algae is copious, and many ancient forms are increasingly well-understood relative to their geographical distribution, stratigraphical range, paleobiology and -ecology. Certain groups of microalgae, charophyte oogonia (gyrogonites), and the remains of calcareous macroalgae from marine and brackish environments are especially abundant and diverse in the fossil record because their thick walls and/or calcium-based skeletons are readily preserved (e.g., Flügel 1977; Tappan 1980; Riding & Voronova 1985; Riding 1991; Taylor & Taylor 1993; Brooke & Riding 1998; Aguirre et al. 2000). On the other hand, non-calcareous macroalgae are comparatively rare as fossils, which is primarily the result of the fact that fossilization potential of the delicate algal bodies is low; they are preserved only where the depositional environment provided ideal conditions for fossilization (e.g., reduced rates of decomposition, relatively stagnant water, and/or quick embedding) and may sometimes yield exquisite fossils. The fossil record of non-calcareous macroalgae throughout geological time includes spectacular, anatomically preserved Late Neoproterozoic algae from the Doushantuo Formation in South China (Xiao et al. 2004 and literature cited therein), various compressed algal thalli from the Lower Cambrian Kaili Biota (Guizhou Province) in China (Yang et al. 2001a, 2001b) and Middle Cambrian Burgess Shale (British Columbia) in Can-

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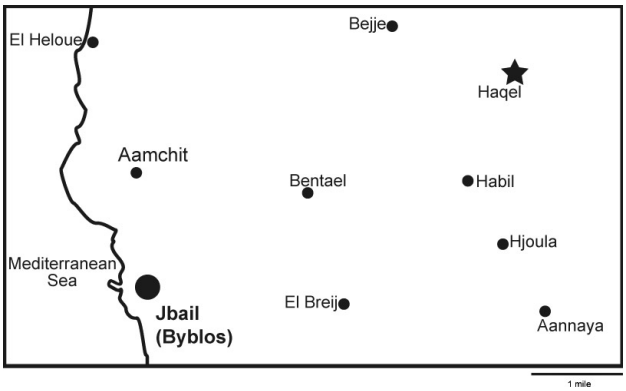
ada (Walcott 1919), the famous Ordovician Lake Winnipeg (Canada) algal flora (Fry 1983), *Powysia* from the Ludlovian (Upper Silurian) of Wales (Edwards 1977), *Thalassocystis* from the Silurian of Michigan (Taggert & Parker 1976), *Drydenia, Hungerfordia,* and *Enfieldia* from the Devonian of New York (Fry & Banks 1955), *Valmeyeraphycus, Chenilleophycus,* and *Phascolophyllaphycus* from the Mississippian of Illinois (Leary 1986), and a diverse Tertiary algal flora (22 species in 10 genera) from the Monterey Formation (Miocene) of California (Parker & Dawson 1965). A more complete fossil record is required, however, in order to reconstruct the evolutionary history of non-calcareous macroalgae, and assess the roles that these plants played in the biology and ecology of ancient aquatic ecosystems. Thus, every new find represents a significant piece of information that deserves thoughtful consideration.

Here we present the first nearly complete specimen of the rare Cenomanian (Late Cretaceous) alga *Bassonia hakelensis* (Basson, 1972) nov. comb. from the famous Haqel fish beds in Lebanon. Although fossils from Haqel have been collected and studied intensively for more than 100 years, we are aware of only two fragmentary specimens of this alga that have been described and figured to date (Basson 1972). *Bassonia hakelensis* was originally placed in the vaguely defined form genus *Algites* Seward, 1894 (i.e. *Algites hakelensis* Basson, 1972); however, we believe that the distinctive morphology of the thallus does not permit retention of this alga in *Algites*, but rather requires establishment of a better circumscribed, new genus, for which the name *Bassonia* nov. gen. is introduced. The diagnosis for *B. hakelensis* (Basson) nov. comb. is emended. Finally, some hypotheses are offered on the systematic affinities of *B. hakelensis*.

2. Geological Setting, Material, and Methods

Bassonia (al. *Algites*) *hakelensis* has to date exclusively been reported from the middle (top of the Lower) Cenomanian sublithographic limestone deposits at Haqel, a village approximately 12 km to the East of the ancient city of Byblos (today Jbail) in Lebanon (Textfig. 1). The limestone deposits are situated within an area of massive Cretaceous shelf sediments containing nerineids, rudists, and orbitolinids, which are indicative of a warm and shallow sea. The limestone was deposited in small basins, only a few hundred meters across, which are believed to have had their tectonic origins at the intersection of block fault systems. The fossiliferous layers are always accompanied by breccia-like deposits, which rest unconformably on the basin slopes and represent the initial phase of the basin filling; it is believed that they were the result of a series of localized ocean-bottom landslides. The fossiliferous layers, in contrast, indicate slower deposition in a subsequent stagnant stage. Detailed information on the geology and sedimentology of Haqel and vicinity can be found in Hückel (1970) and Gayet et al. (2003). The limestone deposits at Haqel are particularly famous for their over 70 genera (with approximately 350-400 kinds) of exquisitely preserved fish, including box fishes, coelacanths, sharks, sting rays, and chimaeras, but have also yielded a wealth of other animal fossils such as molluscs, annelids, crustaceans, and echinoderms (e.g., Fraas 1878; Lewis 1878; Dames 1886; Alessandrello & Teruzzi 1986; Gayet et al. 2003 and literature cited therein). The quality of the fossils is almost unique; it even surpasses that seen in the fossils from the famous Konservat Lagerstätten at Monte Bolca (Italy) and Solnhofen (Germany). Taphonomic studies suggest that the abundance of well-preserved animal fossils may have been the result of periodic surface algal blooms (Gayet et al. 2003). Marine plants from Haqel have not been reported to date, with the exception of two foliose macroalgae, i.e. *Algites hakelensis* (Basson 1972) and *Delesserites libanensis* (Basson 1981).

The specimen described here is reposited in the paleobotanical collection of the Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany) under acquisition number 1983-I-8. It was photographed on low-speed orthochromatic film (Macophot Ort 25 ISO); to increase contrast, cross-polarized light was used.



Textfigure 1: Map of the Jbail (Byblos) region in Lebanon. Asterisc (*) indicates the position of the village Haqel

3. Systematic Paleontology

Algae

Rhodophyta *Incertae sedis*

Genus *Bassonia* nov. gen.

Generic diagnosis: Fossil marine non-calcareous macroalga, attached to substrate by circular holdfast; long shoots monopodially organized, producing determinate short shoots that bear long, spine-like outgrowths.

Type species: *Bassonia hakelensis* (Basson, 1972) Krings et Mayr

Etymology: The genus is named after Dr. P. W. Basson who originally described this alga from the Haqel fish beds in Lebanon.

Bassonia hakelensis (Basson, 1972) nov. comb.
Pl. 1, Figs 1-6

Basionym: *Algites hakelensis* Basson, 1972. Basson, P. W. (1972): *Algites hakelensis* sp. nov., a Cretaceous foliose alga from Lebanon, American Midland Naturalist 88, pp. 506-511, figs 1, 2.

Holotype: Basson 1972: fig. 1. Specimen #16403, reposited in the paleontological collection of the Department of Geology, American University of Beirut, Beirut, Lebanon

Paratype: Specimen 1983-I-8 (Pl. 1, Figs 1-6), reposited in the paleobotanical collection of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

Emended diagnosis: Holdfast ~1 cm in diameter; thallus >15 cm high; main long shoot massive, semirigid in appearance, >0.5 cm in diameter, producing second-order long shoots at irregular intervals; second-order long shoots terminally widened, unbranched or branched; short shoots bud- to branchlet-like, up to 1 cm long, directed upwardly, bearing one to several (usually two to five) robust outgrowths that give thallus a spiny appearance; branchlet-like short shoots may display central band consisting of carbonaceous material, outer regions preserved only as stained impressions; outgrowths undivided, spine-like, entire-margined, up to 1.8 cm long, basally up to 1.5 mm wide, possessing long tapering tips, arising directly from band of carbonaceous material in center of short shoots, and appearing as if their proximal portions were embedded in outer region of shoot.

Locality: Sublithographic limestone deposits at Haqel, ~12 km to the East of Jbail (Byblos), Lebanon

Age: Middle Cenomanian (early Late Cretaceous)

Description: The algal thallus (Pl. 1, Fig. 1) is ~19 cm long; it is preserved as a stained impression with some remains of brownish to black carbonaceous material still present. The plant was attached to the substrate by a circular holdfast, approximately 1 cm in diameter (Pl. 1, Fig. 2); it cannot be determined from the specimen whether the holdfast originally was discoidal or (hemi-)spherical. The thallus is more or less monopodially organized, with a massive main long shoot, semirigid in appearance, that measures between 0.9 (proximally) and 0.4 (distally) cm wide; the shoot was probably more or less cylindrical *in vivo*. At irregular intervals, the main long shoot produces second-order long shoots, which are up to 7 cm long and 0.7 cm wide and similar in appearance to the main long shoot. The individual second-order long shoots are typically slightly widened terminally (Pl. 1, Figs 2, 3). Large, spine-like outgrowths (?trichoblasts [trichoblast = a uniseriate, usually colorless structure of limited growth in the red algae (Rhodophyta)]) up to 1.5 cm long with broad bases and bent in an upward direction are sporadically given off by the main and second-order long shoots (e.g., Pl. 1, Fig. 6 [large arrows]). Numerous determinate, bud- to branchlet-(or column-)like short shoots extend from the long shoots; however, a consistent distribution pattern of short shoots is not recognizable, with the exception of the proximal thallus portion where they appear to be in spiral arrangement (Pl. 1, Figs 4, 5). The short shoots are up to 1 cm long and 0.4 cm wide, undivided or once divided, and always directed upwardly (Pl. 1, Figs 3-6). It is interesting to note that, in the branchlet-like short shoots, brownish or black carbonaceous material is present only in the form of a distinct, relatively broad central band (Pl. 1, Figs 3, 6 [small arrows]), whereas the outer (peripheral) regions of the shoots are preserved only as stained impressions; in bud-like short shoots, this feature is less distinct. The short shoots bear one to several (usually two to five) robust spine-like outgrowths (?trichoblasts), up to 1.8 cm long, which give the whole thallus a spiny appearance. The outgrowths are undivided, entire-margined, up to 1.5 mm wide basally, and possess long tapering tips (Pl. 1, Figs 2, 3, 6). They arise directly from the band of carbonaceous material that occurs in the center of the short shoots, and thus often look as if their proximal portions were deeply embedded in the outer region of the shoot (Pl. 1, Figs 3 [small arrows], 6).

4. Discussion

Bassonia hakelensis is one of only two non-calcareous macroalga species recorded to date for the Haqel fish beds. The second species is *Delesserites libanensis* Basson, a form that closely resembles members from the extant rhodophyte genus *Delesseria* Lamouroux (Ceramiales, Delesseriaceae) (Basson 1981). Apart from the fossil presented here, only four slabs with specimens of *B. hakelensis* have been discovered, i.e. two figured by Basson (1972: figs 1, 2), and two yet unpublished fragments, which are still in the possession of the owners of the Haqel outcrop (pers. commun. P. Abi Saad, Nov. 2003). Among these fossils, our specimen is by far the best preserved and most complete, nicely displaying several features of the alga that were previously unknown, including the circular holdfast (Pl. 1, Fig. 2), subdivision of the thallus in long- and determinate short-shoots (Pl. 1, Figs 1, 3-6), distinct band of carbonaceous material in the center of the short shoots (Pl. 1, Fig. 6 [small arrows]), and the arrangement and insertion of spine-like outgrowths on the shoots (Pl. 1, Figs 2, 3, 6). We hypothesize that the almost perfect preservation of our specimen is due to the fact that it represents a relatively young thallus, which somehow became detached entirely from its place of growth and quickly deposited; all other specimens of *B. hakelensis* display several-times-branched distal thallus portions of much larger (older) individuals.

Bassonia hakelensis cannot be referred to any extant group of algae with certainty due to the fact that important features required in order to accurately establish the systematic position of an alga (e.g., thallus color, pigment composition, reproductive structures, and stages of the life cycle) cannot be determined. Given that these features loom large in algal systematics today, the problem of incompleteness of the fossil unfortunately places serious constraints on interpretation. Nevertheless, Basson (1972) suggests that *B.* (al. *Algites*) *hakelensis* may represent a member of the red algae (Rhodophyta) based on similarities in basic structure between the fossil and members of the extant rhodophyte genera *Callophyllis* Kützing (Cryptonemiales, Callymeniaceae), *Polycoelia* J. Agardh (Cryptonemiales, Callymeniaceae), and *Callilepharis* Kützing (Gigartinales, Rhodophyllidaceae). On the other hand, this author also notes a certain resemblance of *B. hakelensis* to members of the phaeophyte genus *Stypopodium* Kützing (Dictyotales, Dictyotaceae). However, we concur with Basson only with respect to the observation that there exist similarities in basic structure between *B. hakelensis* and certain extant red algae. Basson's material is fragmentary and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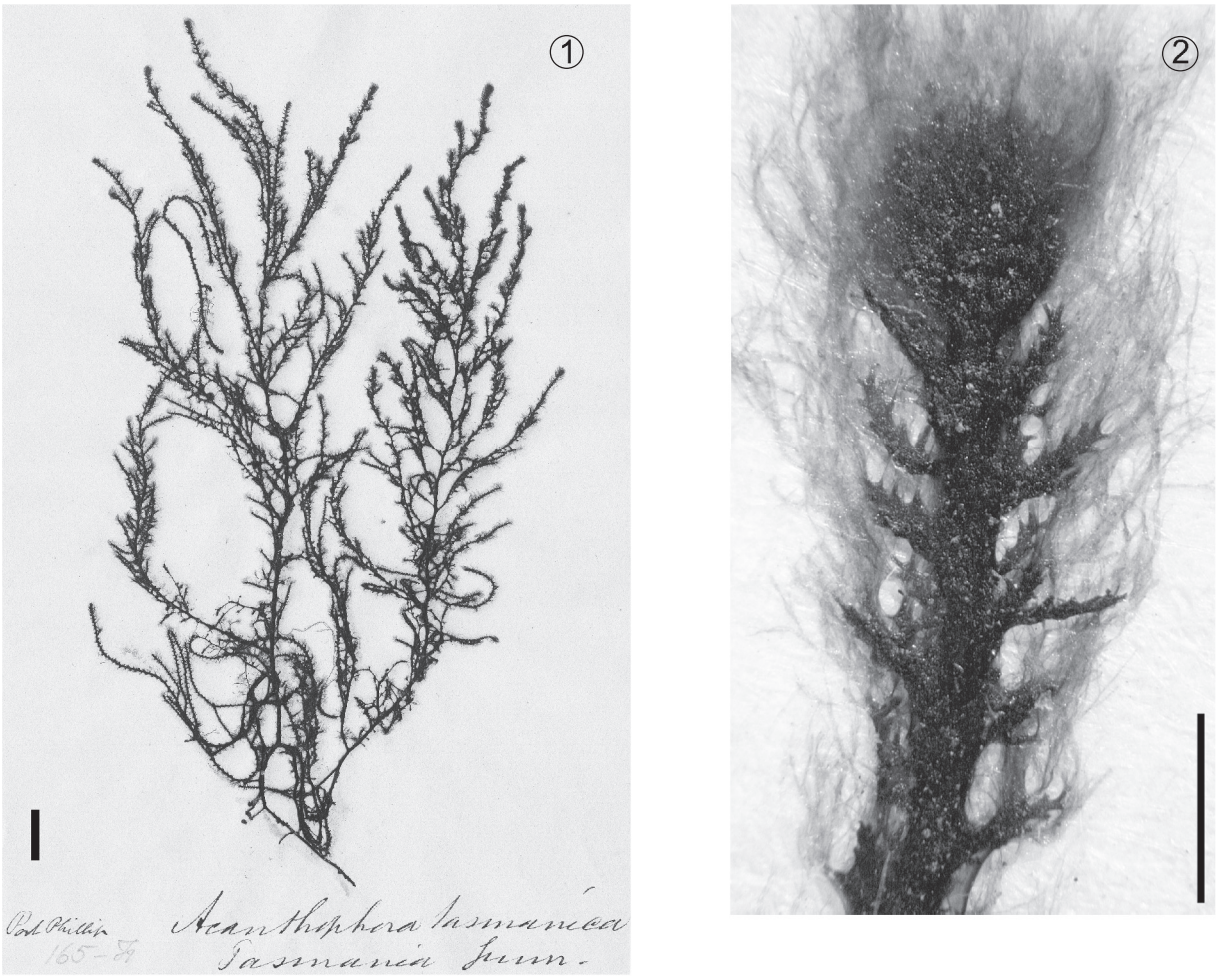


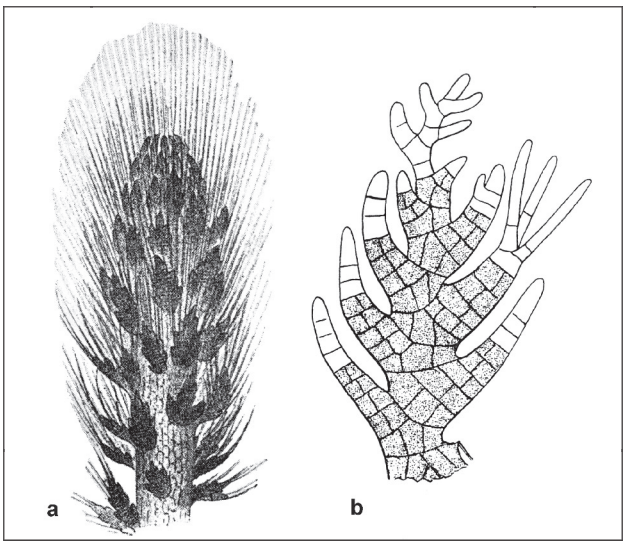
Plate 2: *Pithyopsis tasmanica* (Sonder) Falkenberg from Tasmania; specimen number A2792 (written on the sheet: *Acanthophora tasmanica* Sonder, which is the old name of this alga), reposited in the collection of the Sektionen för Kryptogambotanik, Naturhistoriska Riksmuseet, Stockholm, Sweden.
Fig. 1: Thallus; scale bar = 1 cm.
Fig. 2: Distal portion of a long shoot with numerous short shoots that bear trichoblasts; scale bar = 1 mm.

rather imperfectly preserved, and his considerations relating to correspondences between the fossil and the above listed genera of extant algae become questionable in light of the additional data on morphology obtained from the specimen presented here. Members of *Stypopodium* possess thalli in the form of clusters of fan-shaped blades (Nizamuddin & Aisha 1996), and those seen in species of *Calliblepharis, Callophyllis,* and *Polycoelia* are composed of flat, leaf-like blades that are palmately or irregularly arranged (Kylin 1956: p. 230 and 300, and figs 170A and 233A); thus, representatives from these extant genera of algae are considerably different habitually from *B. hakelensis.* Rather, we suggest that another extant rhodophyte, not taken into consideration by Basson in his original study, may represent a more plausible modern model organism for comparison: *Pithyopsis tasmanica* (Sonder) Falkenberg from the *Polysiphonia* group of the Rhodomelaceae (Ceramiales) (cf. Falkenberg 1901; Kylin 1956: p. 506/507). This alga occurs exclusively along the costs of southern Australia and Tasmania. It possesses erect, branched, and rather robust thalli, up to 25 cm high (Pl. 2, Fig. 1). The long shoots pro-

Left side: Plate 1: *Bassonia hakelensis* (Basson) Krings et Mayr from the middle Cenomanian (Upper Cretaceous) of the Haqel fishbeds in Lebanon; paratype; specimen number 1983-I-8, reposited in the paleobotanical collection of the Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.
Fig. 1: Overview; scale bar = 1 cm.
Fig. 2: Detail from Fig. 1, showing a second-order long shoot; scale bar = 1 cm.
Fig. 3: Detail from Fig. 1, showing the widened terminal portion of a second-order long shoot with three short shoots bearing spine-like outgrowths; note that the outgrowths are given off by the central band of carbonaceous material, and thus appear to be deeply embedded in the outer region of the shoot [small arrows]; scale bar = 0.5 cm.
Fig. 4: Detail from Fig. 1, showing the proximal portion of the thallus with circular holdfast; scale bar = 1 cm.
Fig. 5: Detail from Fig. 1, showing short shoot arrangement in the proximal portion of the main long shoot; scale bar = 1 cm.
Fig. 6: Detail from Fig. 1, showing portion of a second-order long shoot with two short shoots and a spine-like outgrowth extending directly from the long shoot [large arrows]; small arrows indicate dark band of carbonaceous material in the center of one of the short shoots; scale bar = 0.5 cm.

duce numerous short shoots in ¼ spiral arrangement, which are often directed upwardly and bear several long, undivided trichoblasts (Pl. 2, Fig. 2; Textfig. 2a). Although *B. hakelensis* is much larger and more massive in all parts than *P. tasmanica* (compare Pl. 1, Fig. 1 to Pl. 2, Fig. 1), the close resemblance, in particular with regard to the arrangement and basic structure of the short shoots and spine-like outgrowths/trichoblasts, is striking (compare Pl. 1, Figs 2, 3 to Pl. 2, Fig. 2 and Textfig. 2a). Unfortunately, the fossil does not display any anatomical details, and hence there exists no way to determine whether the similarity to *P. tasmanica* is superficial and restricted to the overall appearance of certain macromorphological features, or comparable internal organization of the thallus occurs. A close biological relationship between *B. hakelensis* and *P. tasmanica* seems unlikely, however, because the former taxon is many times larger in all parts than the latter, which suggests a fundamentally different internal organization. For example, the short shoots in *P. tasmanica* are tiny structures, up to 0.7 mm long and consisting of only a relatively small number of cells (Falkenberg 1901 and Textfig. 2b), whereas those seen in *B. hakelensis* (Pl. 1, Figs 3-6) are larger structures, up to 1 cm long and 0.4 cm wide, that display internal differentiation into a peripheral and inner region recognizable as a dark band of carbonaceous material in the center of the shoot (Pl. 1, Fig. 6 [small arrows]).

Based on the uncertainties with regard to the biological affinity of his fossils, Basson (1972) refrained from assigning the alga to any single extant taxon, nor did he establish a new genus of fossil algae; rather, the alga was provisionally placed in *Algites* Seward, 1894, and the name *Algites hakelensis* Basson, 1972 introduced. The form genus *Algites* was established for fossils that "…in all probability belong to the class Algae, but which, by reason of the absence of reproductive organs, internal structure, or characters of trustworthy nature in the determination of affinity, cannot be referred with any degree of certainty to a particular recent genus or family" (Seward 1894: p. 4). Over the years, *Algites* has become a "waste-basket taxon" for all sorts of enigmatic adpression fossils that are similar in basic structure to algae, but lack distinctive features, which renders it difficult to identify their biological affinities. Thus, *Algites* seems to represent an appropriate repository for the alga from Haqel; however, the complement of macromorphological features gathered from the specimen presented here now permits the characterization of *Bassonia hakelensis* and the distinctive morphology of the whole plant in greater detail. Moreover, certain characteristic features of this fossil alga are strikingly similar to those observed from the extant rhodophyte genus *Pithyopsis*. Since *B. hakelensis* is today more fully understood than most other fossils assigned to *Algites*, we find it justified to exclude this species from *Algites* and assign it to a new, better circumscribed genus, for which the name *Bassonia* is introduced. *Bassonia hakelensis* is provisionally placed in the Rhodophyta based on the fact that this form is characterized by macromorphological features that are also known to occur in extant red algae. We admit, however, that indisputable evidence for a rhodophycean affinity of *B. hakelensis* is missing.



Textfigure 2: *Pithyopsis tasmanica* (Sonder) Falkenberg, redrawn from Falkenberg (1901). **a**: Terminal region of a long shoot with numerous short shoots that bear trichoblasts. **b**: A single short shoot.

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5. References

Aguirre, J., Riding, R. & Braga, J. C. (2000): Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. – Paleobiology, **26**: 651-667.

Alessandrello, A. & Teruzzi, G. (1986): *Eunicites phnicius* n. sp., a new fossil polychaete annelid of the Cenomanian of Hakel, Lebanon. – Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale de Milano, **127**: 321-325.

Basson, P. W. (1972): *Algites hakelensis* sp. nov.: a Cretaceous foliose alga from Lebanon. – American Midland Naturalist, **88**: 506-511.

Basson, P. W. (1981): Late Cretaceous alga, *Delesserites libanensis* sp. nov. – Review of Palaeobotany and Palynology, **33**: 363-370.

Brooke, C. & Riding, R. (1998): Ordovician and Silurian coralline red algae. – Lethaia, **31**: 185-195.

Dames, W. (1886): Über einige Crustaceen aus den Kreideablagerungen des Libanon. – Zeitschrift der Deutschen Geologischen Gesellschaft, **38**: 551-575.

Edwards, D. (1977): A new non-calcified alga from the upper Silurian of mid Wales. – Palaeontology, **20**: 823-832.

Falkenberg, P. (1901): Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeresabschnitte. – Fauna und Flora des Golfes von Neapel, Bd. 26; Berlin (R. Friedländer und Sohn), xvi + 754 pp.

Flügel, E. [Ed.] (1977): Fossil Algae; Berlin/Heidelberg (Springer), xiii + 375 pp.

Fraas, O. (1878): Aus dem Orient. II. Theil. Geologische Beobachtungen am Libanon; Stuttgart (E. Schweizerbart'sche Verlagsbuchhandlung), 136 pp.

Fry, W. L. (1983): An algal flora from the Upper Ordovician of the Lake Winnipeg region, Manitoba, Canada. – Review of Palaeobotany and Palynology, **39**: 313-341.

Fry, W. L. & Banks, H. P. (1955): Three new genera of algae from the Upper Devonian of New York. – Journal of Paleontology, **29**: 37-44.

GAYET, M., BELOUZE, A. & ABI SAAD, P. in collaboration with ARMAND, A. & GAUDANT, O. (2003): Liban – Mémoire du temps. Les poissons fossiles; Méolans-Revel (Éditions DésIris La Fresquière), 158 pp.

GRAHAM, L. E. & WILCOX, L. W. (2000): Algae; Upper Saddle River NJ (Prentice Hall), xiii + 640 pp.

HÜCKEL, U. (1970): Die Fischschiefer von Haqel und Hjoula in der Oberkreide des Libanon. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **135**: 113-149.

KYLIN, H. 1956. Die Gattungen der Rhodophyceen; Lund (CWK Gleerups Förlag), xv + 673 pp.

LEARY, R. L. (1986): Three new genera of fossil noncalcareous algae from Valmeyeran (Mississippian) strata of Illinois. – American Journal of Botany, **73**: 369-375.

LEWIS, E. R. (1878): The fossil fish localities of the Lebanon. – Geological Magazine, **5**: 214-220.

NIZAMUDDIN, M. & AISHA, K. (1996): An emendation to the genus Stypopodium Kütz., and its new species from the coast of Pakistan. – Pakistan Journal of Botany, **28**: 127-141.

PARKER, B. C. & DAWSON, E. Y. (1965): Non calcareous marine algae from California Miocene deposits. – Nova Hedwigia, **10**: 273-295.

RIDING, R., [Ed.] (1991): Calcareous Algae and Stromatolites; Berlin/Heidelberg (Springer), x + 571 pp.

RIDING, R. & VORONOVA, L. (1985): Morphological groups and series in Cambrian calcareous algae. – In: TOOMEY, D. F. & NITECKI, M. H. (Eds), Paleoalgology. Contemporary Research and Applications; Berlin/Heidelberg (Springer), 56-78.

ROUND, F. E. (1981): The Ecology of Algae; Cambridge MA (Cambridge University Press), 653 pp.

SEWARD, A.C. (1894): The Wealden Flora. Part 1. Thallophyta - Pteridophyta. – Catalogue of the Mesozoic plants in the Department of Geology, British Museum (Natural History); London (Stephen Austin and Sons), xl + 179 pp.

TAGGERT, R. E. & PARKER, L. R. (1976): A new fossil alga from the Silurian of Michigan. – American Journal of Botany, **63**: 1390-1392.

TAPPAN, H. (1980): The Paleobiology of Plant Protists; San Francisco CA (W. H. Freeman and Company), xxi + 1028 pp.

TAYLOR, T. N. & TAYLOR, E. L. (1993): The Biology and Evolution of Fossil Plants; Englewood Cliffs NJ (Prentice Hall), xxii + 982 pp.

WALCOTT, C. D. (1919): Middle Cambrian algae. Cambrian Geology and Paleontology IV. – Smithsonian Miscellaneous Collections, **67**: 217-260.

XIAO, S., KNOLL, A. H., YUAN, X. & PUESCHEL, C. M. (2004): Phosphatized multicellular algae in the Neoproterozoic Doushantuo Formation, China, and the early evolution of florideophyte red algae. – American Journal of Botany, **91**: 214-227.

YANG, R. D., MAO, J. R. & ZHAO, Y. L. (2001a): Branching macroalgal fossils of the Early-Middle Cambrian Kaili Formation from Taijiang, Guizhou Province, China. (In Chinese with English abstract). – Acta Geologica Sinica, **75**: 121-135 .

YANG, R. D., MAO, J. R. & ZHAO, Y. L. (2001b): New macroalgal fossils from Middle Cambrian Kaili Biota in Guizhou Province, China. – Acta Botanica Sinica, **43**: 742-749.