

**A TAXONOMIC, PHYLOGENETIC AND BIOGEOGRAPHIC
STUDY OF THE GENUS ACANTHOPHORA
(RHODOMELACEAE, RHODOPHYTA)**

YDE S.D.M. DE JONG¹, CREUSA HITIPEUW² &
WILLEM F. PRUD'HOMME VAN REINE¹

SUMMARY

A cladistic analysis, based on a taxonomic revision is carried out for 7 *Acanthophora* species using 19 characters. Hypotheses on species affinities are based primarily on morphological characters. Because most species show only few distinctive characters, emphasis was placed on features of spine development, either in relation to vegetative or to reproductive structures. Global distribution of 7 *Acanthophora* species: viz. *A. aokii*, *A. dendroides*, *A. muscoides*, *A. nayadiformis*, *A. pacifica*, *A. ramulosa*, and *A. spicifera*, shows a discontinuous pattern. Although widely distributed species are present (*A. muscoides* and *A. spicifera*), a disjunct distribution of other species occurs in the Pacific (*A. aokii*), Indian Ocean (*A. dendroides*), East-Atlantic region (*A. ramulosa*), and the Mediterranean and Red Sea (*A. nayadiformis*). Information on the historical background of the species distribution can be inferred from the obtained phylogenetic tree.

Key words: *Acanthophora*, Rhodomelaceae, Rhodophyta, biogeography, phylogenetics, seaweeds, taxonomy.

INTRODUCTION

In order to illustrate the use of phylogenetic systematics for the interpretation of species relationships and in an attempt to clarify its taxonomy and biogeography, a study was carried out on the red seaweed genus *Acanthophora* J.V. Lamour. The phylogenetic and biogeographical information obtained in this study will be used to outline a general historical biogeographical hypothesis of the Atlantic Ocean by the reconstruction of a general area cladogram. For this more general purpose phylogenies of different groups of well-defined, unrelated seaweed genera, each represented by several morphologically distinguishable species, are needed (De Jong & Prud'homme van Reine, 1997).

The genus *Acanthophora*, a member of the family Rhodomelaceae (Ceramiales, Rhodophyta), was chosen for phylogenetic and biogeographical analysis, because of the presence of a limited number of (mostly) restrictedly distributed, morphologically variable, but distinct species, which are considered to form a monophyletic group of algae (Falkenberg, 1901).

- 1) Rijksherbarium/Hortus Botanicus, P.O. Box 9514, 2300 RA Leiden, The Netherlands.
- 2) Jalan Mutiara No. 68, Ambon 97123, Indonesia.

Table 1. Accepted names and synonyms in the genus *Acanthophora*. Type specimens are between square brackets.

Accepted name	References
<i>Acanthophora</i> J.V. Lamour. [CN] Type species: <i>Acanthophora thieryi</i> (J.V. Lamour.) J.V. Lamour. (now: <i>Acanthophora spicifera</i> (Vahl) Børgesen) New name for: <i>Fucus acanthophorus</i> J.V. Lamour. Tribus Chondriae acanthophorae	Lamouroux, 1805: 61; 1813: 132; Vahl, 1802: 44; C. Agardh, 1822: 361; Børgesen, 1910: 201, f. 18–19
<i>Acanthophora aokii</i> Okamura [SAP n° 15]	Okamura, 1934: 35, t. 318, f. 15–17
<i>Acanthophora dendroides</i> Harv. [MICH 1319] Heterotypic synonym: <i>Acanthochondria falckenbergii</i> Weber Bosse	Harvey, 1855: 538, n° 68; Weber-van Bosse, 1911: 30
<i>Acanthophora muscoides</i> (L.) Bory [LD 94/068.9765, n° 38011] Basionym: <i>Fucus muscoides</i> L. Homotypic synonym: <i>Chondria muscoides</i> (L.) C. Agardh Heterotypic synonyms: <i>Fucus acanthophorus</i> auct. non J.V. Lamour., Turner <i>Chondria muscoides</i> var. <i>B turneri</i> C. Agardh <i>Acanthophora militaris</i> J.V. Lamour. <i>Acanthopora delilei</i> auct. non J.V. Lamour., Harv.	Linnaeus, 1735: 1161; Turner, 1808: 68, t. 32; Lamouroux, 1813: 132, t. 4, f. 4–5; C. Agardh, 1822: 361–362; Bory, 1828: 156; Harvey, 1853: 18
<i>Acanthophora nayadiformis</i> (Delile) Papenf. [LD 1001.5a] Basionym: <i>Fucus nayadiformis</i> Delile Heterotypic synonyms: <i>Fucus acanthophorus</i> auct. non J.V. Lamour., Turner <i>Acanthophora delile</i> J.V. Lamour. <i>Chondria delile</i> (J.V. Lamour.) C. Agardh <i>Cystoseira acanthophora</i> Delle Chiaje	Turner, 1808: 68, t. 32; Delile, 1813: 292, t. 56, f. 1; Lamouroux, 1813: 132; C. Agardh, 1822: 363; Delle Chiaje, 1829; Papenfuss, 1968: 96
<i>Acanthophora pacifica</i> (Setch.) Kraft [UC 261336] Basionym: <i>Cladhymania pacifica</i> Setch.	Setchell, 1926: 102; Kraft, 1979: 123
<i>Acanthophora ramulosa</i> (Lindenb.) Kütz. [L 939.6-14] Basionym: <i>Acanthophora ramulosa</i> Lindenb. ex Kütz. Homotypic synonyms: <i>Chondria ramosissima</i> Lindenb. in herb. <i>Acanthophora muscoides</i> var. <i>ramosissima</i> Lindenb. ex Sond.	Kützing, 1843: 437; Sonder, 1871: 18; Steentoft, 1967: 136, f. 2–3, t. 2
<i>Acanthophora spicifera</i> (Vahl) Børgesen [C 124/93, n° 10] Basionym: <i>Fucus spiciferus</i> Vahl Heterotypic synonyms: <i>Fucus acanthophorus</i> J.V. Lamour. <i>Acanthophora thieryi</i> (J.V. Lamour.) J.V. Lamour. <i>Chondria acanthophora</i> C. Agardh <i>Acanthophora antillarum</i> Mont. ex Kütz. <i>Acanthophora thieryi</i> f. <i>gracilis</i> P. Crouan & H. Crouan <i>Chondria muscoides</i> auct. non L., Mont. <i>Acanthophora intermedia</i> P. Crouan & H. Crouan <i>Acanthophora orientalis</i> J. Agardh <i>Acanthophora spicifera</i> f. <i>orientalis</i> (J. Agardh) Weber Bosse <i>Acanthophora spicifera</i> var. <i>orientalis</i> (J. Agardh) Zaneveld <i>Acanthophora orientalis</i> var. <i>wightii</i> (J. Agardh) Sond. <i>Acanthophora wightii</i> J. Agardh <i>Acanthophora spicifera</i> f. <i>wightii</i> (J. Agardh) Weber Bosse	Vahl, 1802: 44; Lamouroux, 1805: 61, t. 30, f. 1; 1813: 132; C. Agardh, 1822: 363; Montagne, 1842: 43; J. Agardh, 1863: 821; Kützing, 1865: 27, t. 75, f. d–g; P. Crouan & H. Crouan in Mazé & Schramm, 1878: Sonder, 1879: 81; Weber-van Bosse, 1923: 348; Børgesen, 1910: 201; Zaneveld, 1959: 25

MATERIALS AND METHODS

Observations were done on herbarium material. For light microscopical study herbarium specimens were stained in a 1% solution of aniline blue and mounted in Karo. The present morphological descriptions and distributional accounts are based on herbarium specimens and on literature. Herbarium abbreviations follow Holmgren et al. (1990).

A data matrix of 7 species and 19 characters of *Acanthophora* was compiled by translating qualitative morphological characters into multistate or additive binary codes. Phylogenetic analysis was carried out searching for character parsimony, as available in PAUP v. 3.1.1 (Swofford, 1993), using the exhaustive search option. Character-state changes in the resulting cladogram were evaluated using MacClade v. 3.0.4 (Maddison & Maddison, 1992). To solve character polarity, *Chondria* C. Agardh was used as an out-group.

Based on the cladistic results, a biogeographical analysis was carried out by simply substituting taxa with distribution areas. Additionally, the information on the paleogeology is used in combination with the topology of the cladogram in order to explain the present distribution of the *Acanthophora* species.

ACANTHOPHORA

Acanthophora J.V. Lamour. 1813. — Type species: *Acanthophora spicifera* J.V. Lamour. (= *Fucus acanthophorus* L.; *Acanthophora thierrii* J.V. Lamour.; see below.)
Acanthochondria Weber Bosse 1911.

Plants cartilaginous or membranaceous, consisting of alternate or irregularly divided, erect, terete or flattened branches of indeterminate growth and similar but shorter branches of determinate growth, having a cortex composed of small polygonal cells. Axes articulated, polysiphonous with 5 periaxial cells, heavily corticated by parenchymatous dividings. Attachment small to large discoidal, often lobed holdfast, in some species rhizoidal. *Determinate branches* and often also the indeterminate axes spirally arranged, with short, spine-like, polysiphonous branchlets, often appearing in tufts. *Trichoblasts* monosiphonous and deciduous, only present at branch apices and on sterile segments.

Dioecious. Cystocarps ovoid to urceolate, developed in the axils of spine-like branchlets and located at their bases, containing tufts of pear-shaped carpospores on simple gonimoblasts, radiating from a basal placenta. Spermatangia developed on trichoblasts of spine-like branchlets, flattened and in disk-like clusters, in hyaline, flat, circular to irregular sori, with sterile cell margins. Tetraspores tetrahedrally divided, lodged in swollen, often spinous stichidia.

Notes — The reproductive as well as vegetative structures are apparently rather uniform throughout the genus. Within the genus antheridia have first been described and figured for *A. spicifera* (Askenasy, 1888, as *A. orientalis*). Antheridia were also found by Børgesen (1918) on the same species. Antheridia in *Acanthophora* are very similar to the antheridial structures in *Chondria*, formed on the first lateral of the trichoblasts, appearing as a flat disk-shaped body, most often with a rather irregularly formed circumference and a margin composed of large, oblong, thick-walled trans-

parent cells. Inside these, both surfaces are densely covered by spermatocysts. In the middle of the antheridial strand a system of filaments is subdichotomously ramified in the same plane (Fig. 41).

During the present study, antheridia were observed in four species (not in *A. aokii* and *A. ramulosa*). They also occur in *A. pacifica*. The structures were found to be very similar to those described for *Chondria*, and no difference has been observed among the species. The carposporophyte consists of simple filamentous gonimoblasts (Fig. 40) enclosed in a pericarp.

Notes on nomenclature — The genus *Acanthophora* was established by Lamouroux (1813: 132) to accommodate his *Fucus acanthophorus* described as a new species in 1805, and renamed *A. thierii* in 1813. Lamouroux also included other species under the same genus, i.e., *A. delilei*, based on Delile's species *Fucus nayadiformis* from the Mediterranean and *A. militaris* recorded as a new species from the Antilles. Most species of *Acanthophora* were originally grouped under the genus *Chondria* C. Agardh (1817). This genus shares many features with *Acanthophora*, including a cartilaginous texture, a cylindrical thallus, a distinct axial cell issuing 5 periaxial cells and the gross morphology of reproductive structures. *Acanthophora* and *Chondria*, however, differ in the form of the branchlets which in *Chondria* are club- or spindle-shaped and are constricted or tapered at the bases, while *Acanthophora* has spine-like branchlets. Details of the morphology of reproductive structures are also slightly different. Fritsch (1945) described that sporangia in most *Chondria* species are developed in the apical depression of club-shaped branchlets, and that the initial cell produces 3 cover cells. *Acanthophora* has sporangia arranged in stichidial ramuli.

After world-wide reviewing the genus, it can be concluded that 7 species of *Acanthophora* are present (Table 1). Two species originally placed in *Acanthophora*, viz. *A. arborea* Harv. (1860) from Australia and *A. tasmanica* Sond. (1871) from Tasmania (also recorded in Hooker, 1860), were later classified into other genera by Falkenberg (1901): *Chiracanthia arborea* (Harv.) Falkenberg and *Ptyopsis tasmanica* (Sond.) Falkenberg, respectively. According to Kylin (1956) these taxa belong to non-related and widely separated groups of the Rhodomelaceae. These two species were excluded from this study (Table 2).

Kraft (1979) transferred *Cladhymenia pacifica* to the genus *Acanthophora*, mainly on the basis of the presence of spines. We have not seen material of this species. Although spine-like spurs on cystocarps also occur in some *Chondria* species (Gordon-Mills & Womersley, 1987) we have followed Kraft in not considering these as real vegetative spines.

Table 2. Excluded names in the genus *Acanthophora*.

Previous name	Corrected name	References
<i>Acanthophora arborea</i> Harv.	<i>Chiracanthia arborea</i> (Harv.) Falkenb.	Harvey, 1860; Falkenberg, 1901; Kylin, 1956
<i>Acanthophora tasmanica</i> Sond.	<i>Ptyopsis tasmanica</i> (Sond.) Falkenb.	Sonder, 1871; Falkenberg, 1901; Kylin, 1956

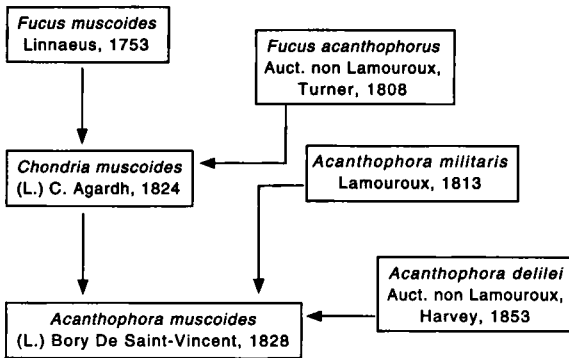


Fig. 1. Nomenclatural complexity in *Acanthophora muscoides* (L.) Bory.

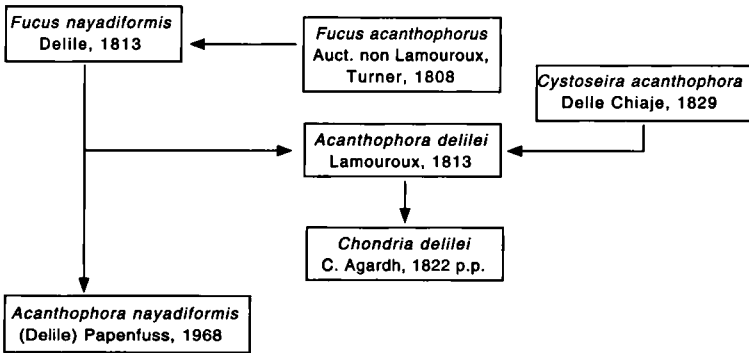


Fig. 2. Nomenclatural complexity in *Acanthophora nayadiformis* (Delile) Papenf.

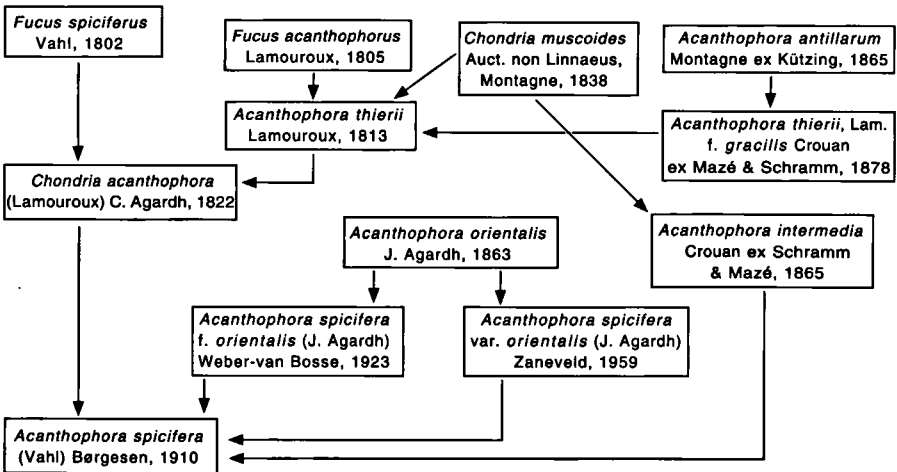


Fig. 3. Nomenclatural complexity in *Acanthophora spicifera* (Vahl) Børgesen.

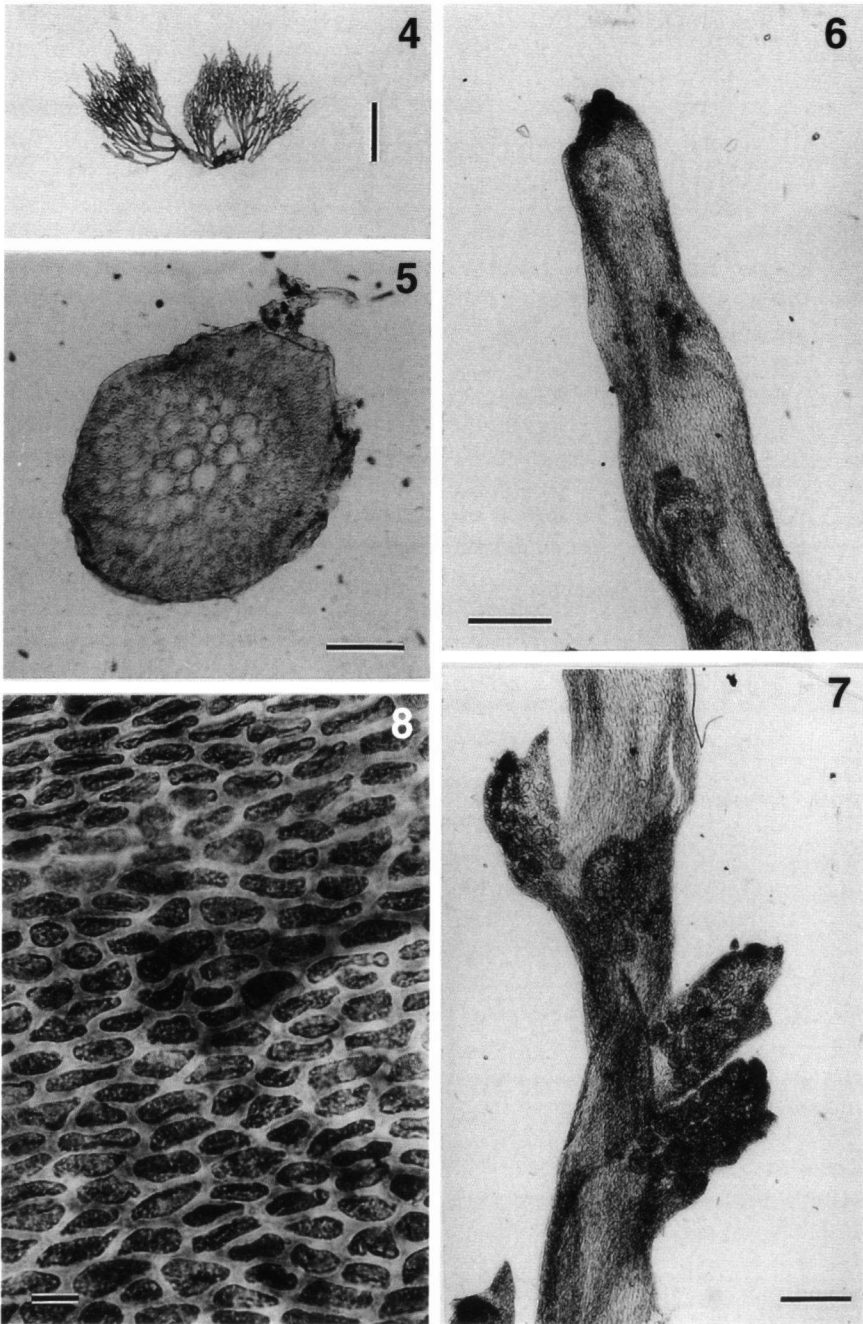


Fig. 4–8. *Acanthophora aokii* Okamura. — 4. Habit; *SAP 15* (bar = 10 mm). — 5. Cross section of erect axis; *SAP 15* (bar = 200 μ m). — 6. Rounded apex; note minute spine-like ramuli; *SAP 15* (bar = 200 μ m). — 7. Stichidial ramuli bearing tetrasporangia (arrow); *SAP 15* (bar = 200 μ m). — 8. Surface view of epidermal cells type; *SAP 15* (bar = 20 μ m).

KEY TO THE SPECIES

- 1a. Plants always small, 2–3 cm tall; covered by very minute spine-like ramuli on both main axes and branches **1. *A. aokii***
 b. Plants usually more than 3 cm tall; covered by conspicuous spines 2
 2a. Main axes flattened **5. *A. pacifica***
 b. Main axes cylindrical 3
 3a. Plants sparingly branched; spines lacking or – if present – only in very low numbers or solitary on main axes; on indeterminate branches spines are crowded and become smaller towards the apex; spines on the branchlets mostly grouped at the apices **7. *A. spicifera***
 b. Plant densely branched and bushy; spine-like branchlets present on all branches 4
 4a. Stolonerous 5
 b. Plants not stoloniferous 6
 5a. Determinate branches constricted at the bases; apices rounded, with 1 or 2 spines **2. *A. dendroides***
 b. Determinate branches not constricted at the bases; apices blunt, covered with many spines **4. *A. nayadiformis***
 6a. Determinate branches not subtended by a spine and having a characteristic ovoid to cylindrical shape, without a clear basal constriction **6. *A. ramulosa***
 b. Determinate branches usually subtended by a spine and constricted at the bases **3. *A. muscoides***

1. *Acanthophora aokii* Okamura — Fig. 4–8, 42

Acanthophora aokii Okamura 1934: 35, t. 318, f. 15–17; Cordero 1981: 203, f. 199, 200, 207; T. Yoshida et al. 1985: 266; P.C. Silva et al. 1987: 60 (as *aoki*). — Type: *SAP n° 15*, from Taiwan (Aoki).

Plants very small, 2 to 3 cm high, main axes 0.5–1 mm wide, cylindrical, rather soft in texture and purplish red, erect, fastigiate, with rounded apex and attached by a flat disk. Axes naked in proximal parts; distal parts covered by spirally arranged, scattered, very short, spine-like branchlets (Fig. 4, 6). Branching alternate-dichotomous; indeterminate branches covered like distal parts of axes, determinate branchlets (ramuli) compressed in apical parts of indeterminate branches, covered by minute spines only, 20 µm broad, thus seemingly naked. In cross section of axes 5 periaxial cells can be observed (Fig. 5), surrounded by epidermal cells, which are rounded in surface view (Fig. 8). *Stichidia* globose to oblong, formed at the apex of ramuli, devoid of spines or sometimes furnished with a single spine, seemingly axillary. *Tetraspores* scattered, tetrahedral (Fig. 7).

Distribution — Pacific Ocean (Fig. 42).

Note — Only few specimens were available for this study. The description was mainly based on that of Okamura and the observation of the type material. Until now, gametangia of this species are not known.

Specimens examined: *SAP n° 15* (tetrasporic); *NY 5261*, Ryukyu Isl., Yonaguni (tetrasporic).

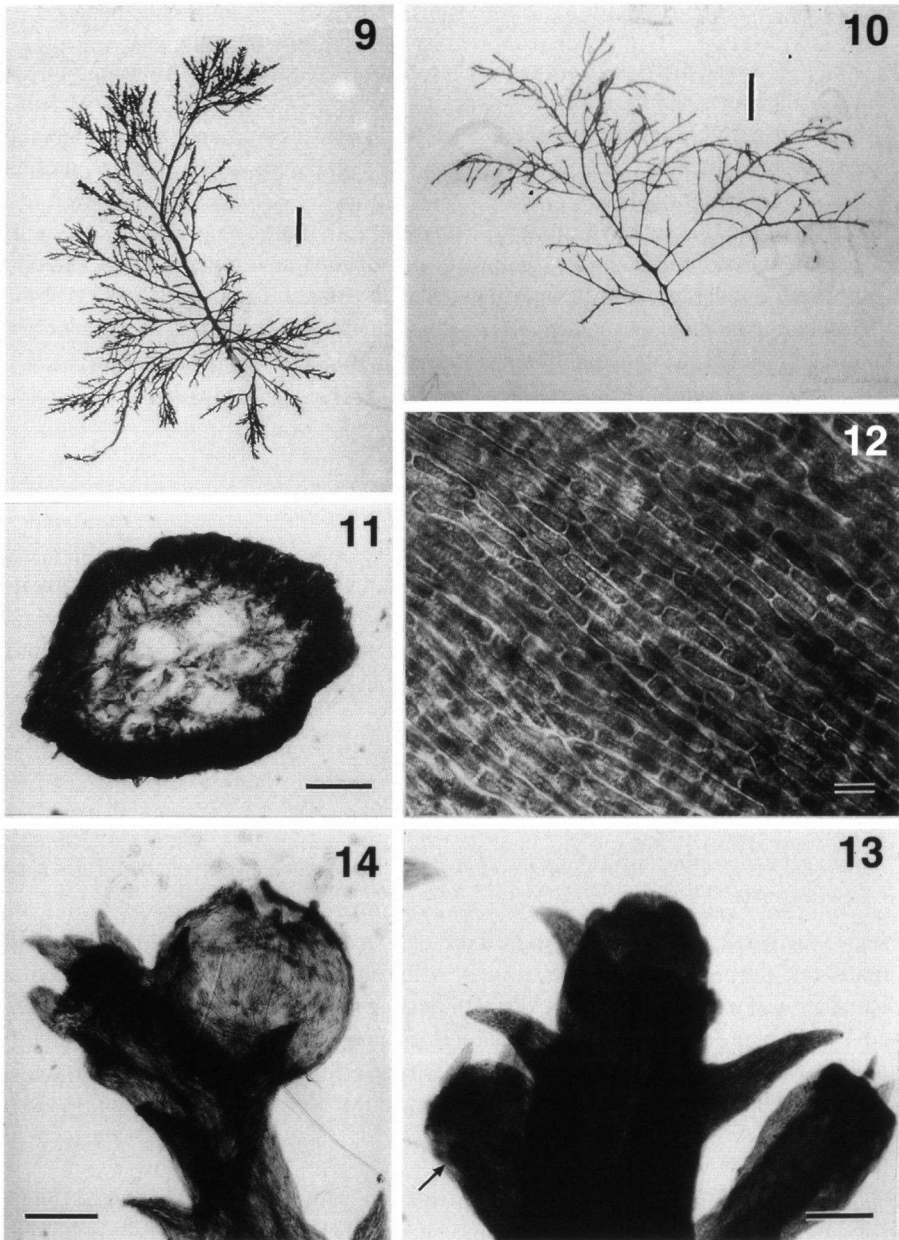


Fig. 9–14. *Acanthophora dendroides* Harv. — 9. Habit; *MICH 1319* (bar = 10 mm). — 10. Habit of male plant; L 938.303-84 (bar = 10 mm). — 11. Cross section of erect axis shows large periaxial cells; *MICH 1319* (bar = 200 μ m). — 12. Surface view of epidermal cells; *MICH 1319* (bar = 20 μ m). — 13. Rounded apex; note several broad spines on apex and stichidia borne on the branches (arrow); *MICH 1319* (bar = 200 μ m). — 14. Globular cystocarp; L 941.98-165 (bar = 200 μ m).

2. *Acanthophora dendroides* Harv. — Fig. 9–14, 43

Acanthophora dendroides Harv. 1855: 538, no. 68; J. Agardh 1863: 818; Harv. 1855: 538; De Toni 1903: 820; Weber Bosse 1923: 348; Okamura 1932: 140; Børgesen 1934a: 22; 1934b: 47; P.L. Anand 1943: 38; Lucas & Perrin 1947: 254; Durair. 1961: 15; Jaasund 1976: 137; G. W. Lawson 1980: 32; P. C. Silva et al. 1996: 468. — Type: *MICH 1319*, from Rottneest Island, Australia. *Acanthochondria falkenbergii* Weber Bosse 1911: 3. — Syntypes: *Weber-van Bosse s.n.* (L 938.303-85), *Weber-van Bosse s.n.* (L 938.303-84).

Plants 15–20 cm high, robust, purplish, tough in texture, pyramidally ramified on all sides (Fig. 9). Plant attached by a lobed disk, with stolons spreading from the main axes. Main axes terete, 0.8–0.9 mm wide, with only few spiny outgrowths, but branches and branchlets spinous. Apices of main axes rounded (Fig. 13). Branches and branchlets constricted at their bases, not subtended by a spine. Spines continuously spread at the end of determinate branches, 0.4–0.5 mm broad. Axial cells very distinct, with 5 periaxial cells, exceeding the axial cell in size (Fig. 11). In surface view, epidermal cells elongated (Fig. 12). *Stichidia* spineless, regularly developed on setaceous rachis of apices of ramuli. *Tetraspores*, terminal in stichidia, tetrahedrally divided. *Cystocarps* globose, sessile on spinous ramuli (Fig. 14). Male plants smaller than female plants (Fig. 10), *spermatangia* borne on branchlets, disk-like (flattened), margins composed of large, oblong, thick-walled transparent cells.

Distribution — Indian Ocean (Fig. 43).

Specimens examined: *MICH 1319*; L 938.303-85, Weber-van Bosse; L 941.98-165, Weber-van Bosse (cystocarpic); L 938.303-84, Weber-van Bosse (spermatangial); *NY 5261* (tetrasporic).

3. *Acanthophora muscoides* (L.) Bory — Fig. 1, 15–20, 44

Acanthophora muscoides (L.) Bory 1828: 156; J. Agardh 1863: 816; Grunow 1868: 92; Mazé & Schramm 1870–1877: 246; Dickie 1875: 148; De Toni & Levi-Morenos 1888: 31; De Toni 1895: 31; 1903: 818; Børgesen 1918: 264; 1937: 348; M. Howe 1920: 569; W.R. Taylor 1928: 165, t. 26, f. 7, t. 34, f. 9; 1931: 27; 1943: 161; 1960: 620, t. 72, f. 3; 1964: 8; 1969: 186; W.R. Taylor & Rhyne 1970: 15; Okamura 1932: 140; Yamada 1944: 44, 45; V.J. Chapm. 1963: 188; Díaz-Piferrer 1966: 65; Ferreira & Pinheiro 1966: 65; A.B. Joly 1967: 446; Oliviera Filho 1967: 172; Steentoft 1967: 136; W.D. Richardson 1975: 134; Isaac 1967: 80; Jaasund 1976: 137, f. 278; Dawes 1976: 151; G. W. Lawson 1980: 32; Trono & Ganzon-Fortes 1980: 97, f. a–b; 1988: 182, f. 130; Cordero 1981: 202, f. 204; G. W. Lawson & D.M. John 1982: 1, 2, t. 5, f. 7–8; 1987: 297, t. 48, f. 7–8; C.K. Tseng 1983: 142, t. 74, f. 1; Seagrief 1984: 3; J.H. Price et al. 1986: 4; T. Yoshida et al. 1985: 266; P.C. Silva et al. 1987: 60; Coppejans & Prud'homme 1992: 189; Verheij & Prud'homme 1993: 443, t. 15, f. 1; P.C. Silva et al. 1996: 469. — *Fucus muscoides* L. 1735: 1161. — *Chondria muscoides* C. Agardh 1822: 361; 1824: 209, excl. var. Mont. 1838–1842: 43. — Neotype (Bory 1828: 156): LD 94/068.9765 (n° 38011), from Ascension Isl.

Fucus acanthophorus auct. non J.V. Lamour.: Turner 1808: 68, t. 32, p.p. — *Chondria muscoides* var. *B. turneri* C. Agardh 1822: 362; 1824: 209. — *Acanthophora militaris* J.V. Lamour. 1813: 132, t. 4, f. 4–5. nom. nud.; C. Agardh 1822: 367 [spec. inquir.]; 1824: 210; Grev. 1830: 54; Kütz. 1849: 859 [spec. inquir.]; 1865: 28, t. 76, type: CN.

Acanthophora delilei auct. non J.V. Lamour.: Harv. 1853: 18 [excl. syn.]; G. Murray 1889: 17. — Type: not existing (or TCD: Harvey's material).

Plants 6–16 cm high, main axes 0.7–1 mm wide, cartilaginous and reddish to purple, attached to the substrate by a flat disk-like holdfast with erect shoots growing upwardly. Fronds cylindrical, bipinnate, subdichotomous to alternate and irregularly branched, apically tapered to a rounded tip (Fig. 15, 16, 18, 19). Terminal branches crowded

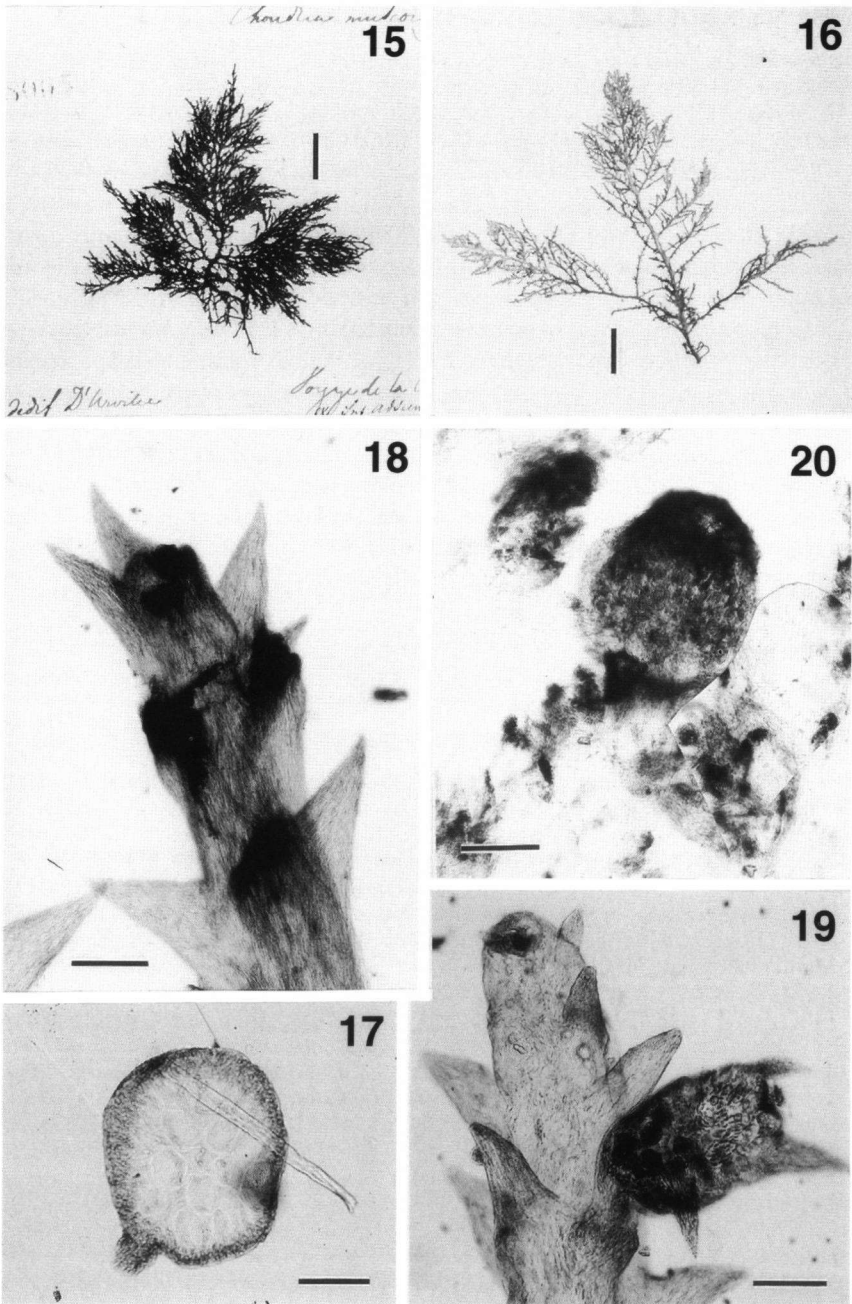


Fig. 15–20. *Acanthophora muscoides* (L.) Bory. — 15. Habit; LD 94/068.9763 (bar = 10 mm). — 16. Habit of male plant; PH s.n. (bar = 10 mm). — 17. Cross section of erect axis with large periaxial cells; L 37.1341 (bar = 200 μ m). — 18. Roundish apex with many long spines; LD 38005 (bar = 200 μ m). — 19. Stichidial ramuli bearing tetrasporangia; LD 38005 (bar = 200 μ m). — 20. Urn-shaped cystocarp bearing carpospores; MICH 4962/31 (bar = 200 μ m).

with short spines which are spirally arranged on indeterminate branches as well as on the blunt determinate branches. *Branches* usually subtended by a spine and constricted. Lower parts naked except for the numerous scars of detached branches. *Ramuli* mostly have spines, from their base upward, 0.3–0.4 mm broad. In *cross section axial cells* small and rounded, 90 µm in diameter, surrounded by 5 periaxial cells, medulla distinct, two to three cells thick (Fig. 17). Cortex composed of 2 layers of very small rounded cells. Epidermal cells elongated, fibre-like. Tetrasporangia borne in spinous *stichidial ramuli* which arise from all parts of the determinate branches, often also found at apices of branchlets bearing ramuli. *Tetraspores* tetrahedral. *Cystocarps* on short branchlets, sessile, ovate to urn-shaped with large ostiole (Fig. 20). *Spermatangia*, disk-like (flattened), margin composed of large, oblong, thick-walled transparent cells; bearing numerous spermatial cells.

Distribution — Atlantic Ocean, Indian Ocean, Pacific Ocean, Red Sea, West Indies (Fig. 44).

Note — There was confusion about the type specimen of this species. Material in the Linnaeus collection (microfiche 1274/nº 111, as *Fucus muscoides*) is not acceptable as type. The figure shows a *Gracilaria* species. After Linnaeus, C. Agardh was the first author who applied the name *muscoides* to his genus *Chondria* and referred it to the Linnaean species *Fucus muscoides*. Therefore Agardh's specimen, *Chondria muscoides* from Brazil, inscribed "*Chondria muscoides* Ag. ad oras Brasiliam & ex mus. Paris dedit Desfontaines", deposited in small fragments at the herbarium of Lund is proposed as neotype here. Specimen LD 38005 from Ascension is not an Osbeck specimen, and thus not to be accepted as type material.

Specimens examined: L 939.23-33, Senegal (tetrasporic); PH 46715, La Parguera, Puerto Rico, Almodovar (tetrasporic); L 938.92-102, Antilles, Kützing; PH s.n., Guanica, Puerto Rico, Almodovar (spermatangial); L 371391, Florida, Dawes (tetrasporic); MICH 14962, Martinique, Hamel; MICH 12728, Columbus Isl., Panama; LD 94/068.9763 (nº 38005), Ascension, D'Urville; LD 94/068.9765 (nº 38011), Brazil, Desfontaines (neotype).

4. *Acanthophora nayadiformis* (Delile) Papenf. — Fig. 2, 21–27, 45

Acanthophora nayadiformis (Delile) Papenf. 1968: 96 ['*najadiformis*']; Meñez & A.C. Mathieson 1981: 13, 47; Giaccone 1970: 71; G.W. Lawson 1980: 32; Giaccone et al. 1985: 676; Athanas. 1987: 90; P.C. Silva et al. 1996: 469. — *Fucus nayadiformis* Delile 1813: 148 [= 292]; 1826: t. 56, f. 1. — Type: LD 1001.5a, Alexandria.

Acanthophora delilei J.V. Lamour. 1813: 132 ['*delilii*'], nom. nud.; Decne. 1841: 185; 1842: 358; Grev.; 1830: 54; J. Agardh 1842: 147; Kütz. 1843: 437, t. 52, f. 4; 1849: 858; Zanardini 1858: 256; J. Agardh 1863: 817; Kütz. 1865: 27, t. 75, f. a–c; Falkenb. 1879: 275; 1901: 227, t. 22, f. 2–3; Ardiss. 1883: 351; Picc. 1884: 322; De Toni & Levi-Morenos 1888: 33; De Toni & Paol. 1888: 7; G. Murray 1889: 17; De Toni 1903: 819; Muschl. 1908: 213; Preda 1909: 252, f. 76; Funk 1927: 445, f. 45; 1955: 140; Børgesen 1933: 134; 1934b: 47; 1935: 60; 1939: 121; P.L. Anand 1943: 35, f. 25; Feldmann 1951: 107; Durair. 1961: 71, t. 32; Boudour. & M. Perret 1977: 73. — *Chondria delilei* (J.V. Lamour.) C. Agardh 1822: 363 ['*delilii*'] nom. illeg.; 1824: 209; Mont. 1842: 43, as *delilii*. — Type: PC Alexandria and Suez (not specified).

Cystoseira acanthophora Delle Chiaje 1829.

Fucus acanthophorus auct. non J.V. Lamour.: Turner 1808: 68, t. 32, p.p.

Plants 10–12 cm high, main axes 1.3–1.5 mm wide, cartilaginous, erect, cylindrical, attached to the substratum by rhizoids, producing stolons from the most basal part of the main axis, and also from the axils of the spines. *Thallus* irregularly branched,

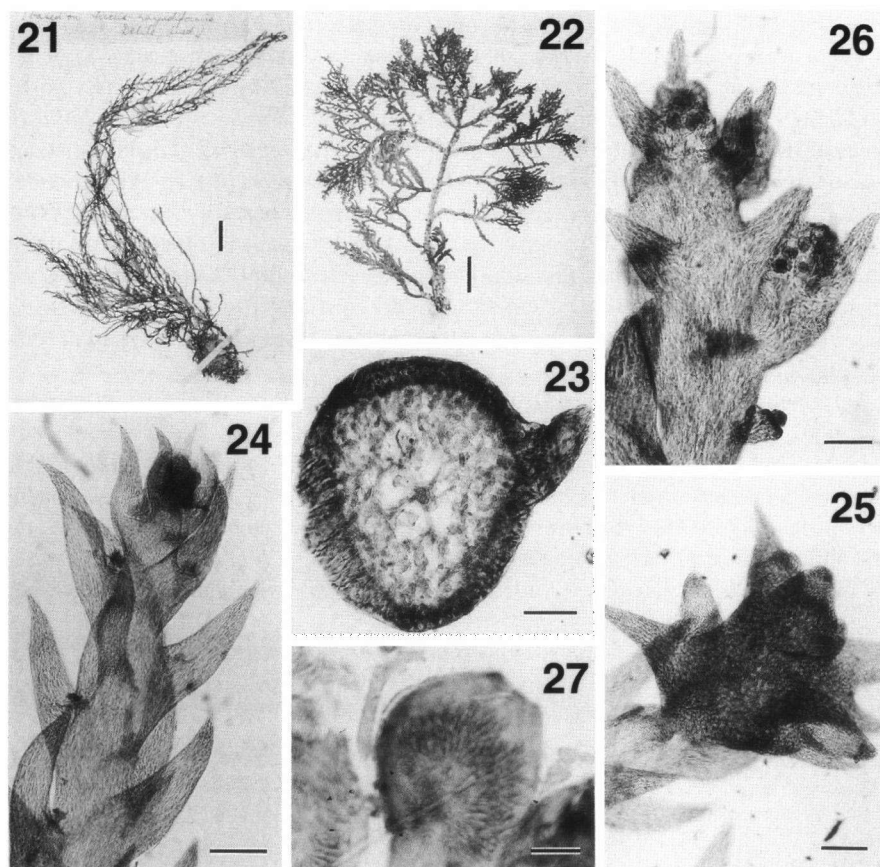


Fig. 21–27. *Acanthophora nayadiformis* (Delile) Papenf. — 21. Habit; LD 1001.5a (bar = 10 mm). — 22. Habit of male plant; PH s.n. (bar = 10 mm). — 23. Cross section of erect axis with large periaxial cells; LD 1001.5a (bar = 200 μ m). — 24. Apical part with many long spines; LD 1001.5a (bar = 200 μ m). — 25. Propagule, spike cone-shaped; L 965.316-274 (bar = 200 μ m). — 26. Stichidial ramuli bearing tetrasporangia; HBG 24/1482 (bar = 200 μ m). — 27. Urn-shaped cystocarp bearing carpospores; HBG 18/182 (bar = 200 μ m).

alternate or secund with spinous outgrowths on the main axes, covered with secondary branches above, often pinnate or bipinnate with smaller ramuli (Fig. 21, 22). *Branches* not constricted. Determinate branches subtended by a spine. *Ramuli* either naked or with few widely spaced, perpendicularly placed spines or irregularly covered with alternate spines, 0.1–0.3 mm broad, sometimes lengthened into new branches (Fig. 24). *Cross section of the axis* showing five periaxial cells enveloped by soft tissues (Fig. 23). Cortical cells partly smaller towards the periphery. Epidermal cells elongated, fibre-like. Vegetative propagation by means of specialised *propagules* (Fig. 25) (Cecere et al., 1994), borne at the distal ends of the main axes, lateral branches and branchlets. Propagules deciduous, swollen, dark bodies, derived from the transformation of apical parts of branches of any order, and detectable because of their dark colour due to the contents of floridean starch granules; resembling swollen spiked cones when mature,

protruding from the axillary region of typical spirally arranged spines, curving downward and attaching to the substrate. *Stichidia* borne on the bases of short lateral branches, globose, spineless on surface, but apices blunt with many spines. *Tetraspores* formed throughout these stichidial ramuli, tetrahedrally divided. *Cystocarps* sessile, urn-shaped, borne on ramuli (Fig. 27). *Spermatangia* disk-like structures (more or less flattened), margin composed of large, oblong, thick-walled transparent cells.

Distribution — Atlantic Ocean, Black Sea, Mediterranean Sea, Indian Ocean, Red Sea (Fig. 45).

Note — The presence of propagules in this species is easily detectable in herbarium specimens, because of their darker colour.

Specimens examined: *LD 1001.5a*, Alexandria; *LD 1001.5b*, Egypt; L 939.194-936, Alexandria; *HBG 18/182* (cystocarpic); *PH s.n.*, Key West (spermatangial); *HBG 24/1482* (tetrasporic); *NY 5261*, Key West (tetrasporic); *LD 238b* (tetrasporic).

5. *Acanthophora pacifica* (Setch.) Kraft — Fig. 43

Acanthophora pacifica (Setch.) Kraft 1979: 123–135. — *Cladhymenia pacifica* Setch. 1926: 102.
— Type: UC 261336 (*Sechell 5220*), Tahiti, reef at Aru point, June 27, 1992 (not seen).

Plants of 3–10 cm height, growing in gregarious clumps, cartilaginous, with colours ranging from reddish-yellow to a deep reddish-brown, anchored to solid substrate by fleshy, fluted holdfasts, above which both erect and semi-prostrate, stoloniferous, axes issue. Stolons attached by secondary disciform holdfasts. Main axes proximally subterete for 4–6 mm, diameter 1–3 mm. The flattened erect parts range from 1–4 mm in width and 200–600 µm in thickness and branch mainly from the margins. Apices pyramidal and beset with a few short unbranched or sparingly branched trichoblasts. *Branches* either short determinate spirally produced spines or indeterminate laterals, often with pinnate or subdichotomous branching. Spines occur on the faces of the blades, as well as on the margins. In the sections cut near the apex of the main axes 5 distinct periaxial cells occur, surrounded by parenchymatous inner cortical cells and a single layer of pigmented outer cortical cells, 1.5–6 times longer than broad. Tetrasporangial *stichidia* solitary or in dendroid clusters along the margins of the blades. Several *tetrasporangia* formed in a whorl at each tier of the stichidia, sporangia measure 100 µm. Cystocarps formed in the axils of spines, probably sessile and globose. Spermatangial clusters plate-like, developed on a trichoblast of which the basal 1–2-celled part persists as the uniseriate stalk of the disk; margin of 1–2 layers of sterile cells. Description based on Kraft (1979).

Distribution — Pacific Ocean (Tahiti, Hawaii) (Fig. 43).

Note — The transfer of this species to the genus *Acanthophora* was mainly based on the presence of spirally arranged spines. However, occasionally spines do also occur in *Chondria* species. These are usually described as spurs, from which the cystocarps arise. According to Gordon-Mills & Womersley (1987) the observation by Kraft (1979) that spines of *A. pacifica* originate from the abaxial side of a basal cell of a trichoblast, is probably not pertinent to the situation in other *Acanthophora* species. They suggest that in *A. spicifera* the spines develop directly from the whole trichoblast which is highly modified. In that case the spines are directly comparable to the pointed spurs at the base of cystocarps in several *Chondria* species which also develop from modified fertile trichoblasts.

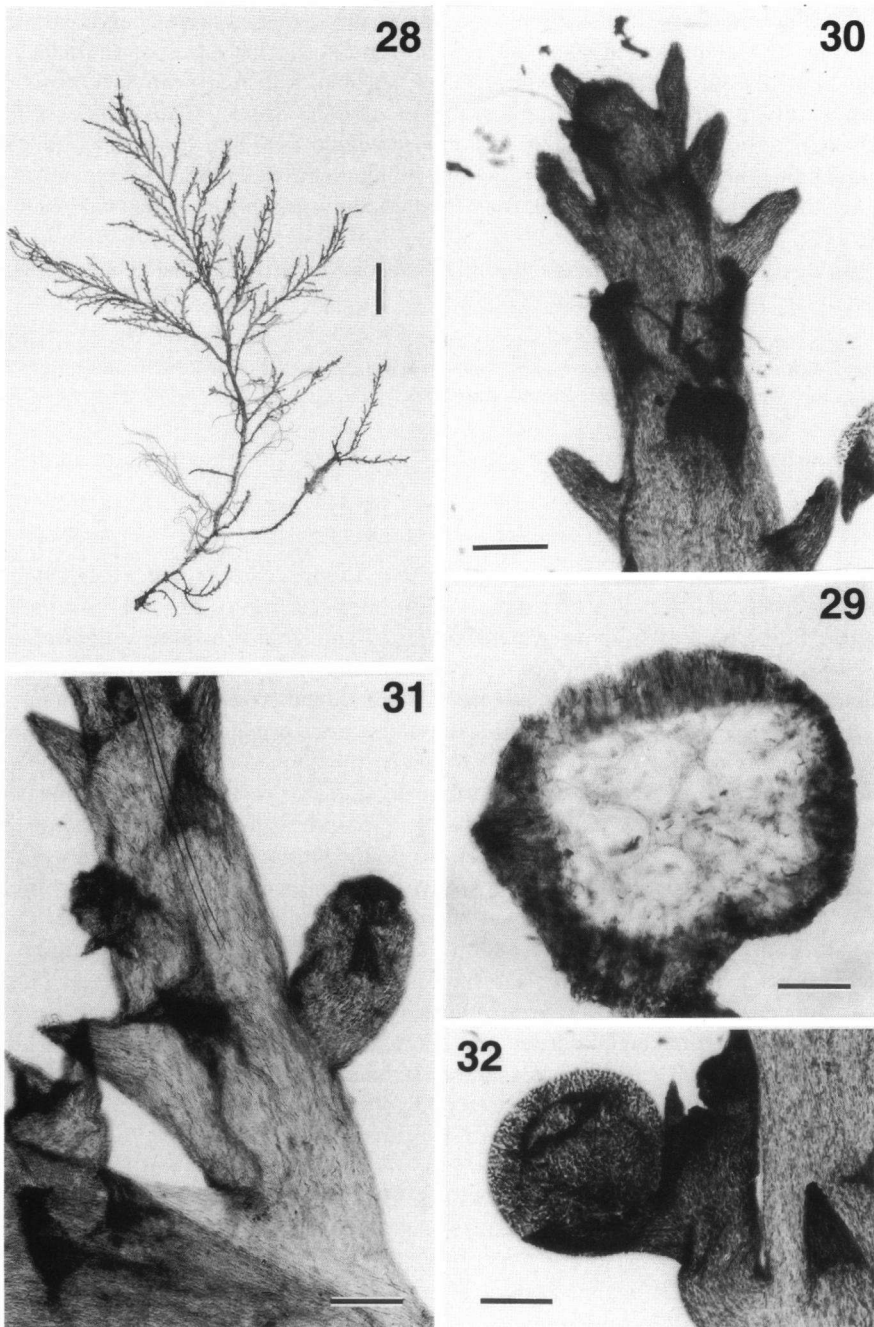


Fig. 28–32. *Acanthophora ramulosa* Lindenb. ex Kütz. — 28. Habit; L 939.6-14 (bar = 10 mm). — 29. Cross section of erect axis with large periaxial cells; C 1124/93 (bar = 200 μ m). — 30. Rounded apex; BR 127.2.816 (bar = 200 μ m). — 31. Stichidia borne on ramuli (bar = 200 μ m). — 32. Globose cystocarp bearing carpospores; BR 127.2.816 (bar = 200 μ m).

6. *Acanthophora ramulosa* Lindenb. ex Kütz. — Fig. 28–32, 42

Acanthophora ramulosa Lindenb. ex Kütz. 1843: 437; 1849: 858; 1865: 27, t. 76, f. a–c; Steentoft 1967: 136, f. 3, t. 2, f. 2; G.W. Lawson & D.M. John 1982: 316, t. 50, f. 5; 1987: 297, t. 51, f. 5; J.H. Price et al. 1986: 5.

Acanthophora muscoides var. *ramosissima* Lindenb. ex Sond. 1871: 18. — *Chondria ramosissima* Lindenb. in herb. — Type: L 939.6-14 (isotypes in HBG and C), from Angola.

Plant bushy, 10–20 cm high, robust. Main axes 1.2–1.3 mm wide, cartilaginous and deep pink in colour, attached with lobed, rather flattened disciform holdfast. Apices blunt. Fronds piramidally ramified on all sides (Fig. 28, 30). Branches many times irregularly divided and covered by spine-like branchlets. Determinate branches not subtended by a spine. Terminal branches short, in many cases developing into rather wrinkled and spineless ramuli in which tetrasporangia formation is incipient (Fig. 31). Insertion of branches constricted. Older parts of plants naked, with side branches ovoid to cylindrical, and strongly reminiscent of those in *Chondria*. The apical parts tipped with at most one or two spines (Fig. 30). Spines on indeterminate and determinate branches, 0.1–0.2 mm broad. Epidermal cells elongated in surface view. Five distinct periaxial cells present with 2 layers of parenchymatous cells towards the periphery (Fig. 29). *Stichidia* resembling ordinary branchlets, globose to cylindrical, spineless or, more generally, with one to two spines. *Tetraspores* terminal. *Cystocarps* urn-shaped to ovoid (Fig. 32) borne on a short stalk and usually subtended by a spine.

Distribution — Atlantic Ocean (Angola, São Tomé) (Fig. 42).

Note — *Acanthophora ramulosa* is often included in *A. muscoides* because of a morphological similarity (e.g., De Toni, 1903; Agardh, 1863). Steentoft (1967), however, compared these species and concluded that *A. ramulosa* should be considered as a separate species. After study of the type specimen from Angola, the present writers agree with Steentoft regarding *A. ramulosa* as different from *A. muscoides* because of the morphology of stichidia (wrinkled/spineless stichidia in *A. ramulosa* and spiny in *A. muscoides*) and the distribution of spines. Unfortunately there is no material available from other localities.

Specimens examined: L 939.6-14, Kützing; C L124/93; BR 127.23.816; HBG 43/1482, all Angola.

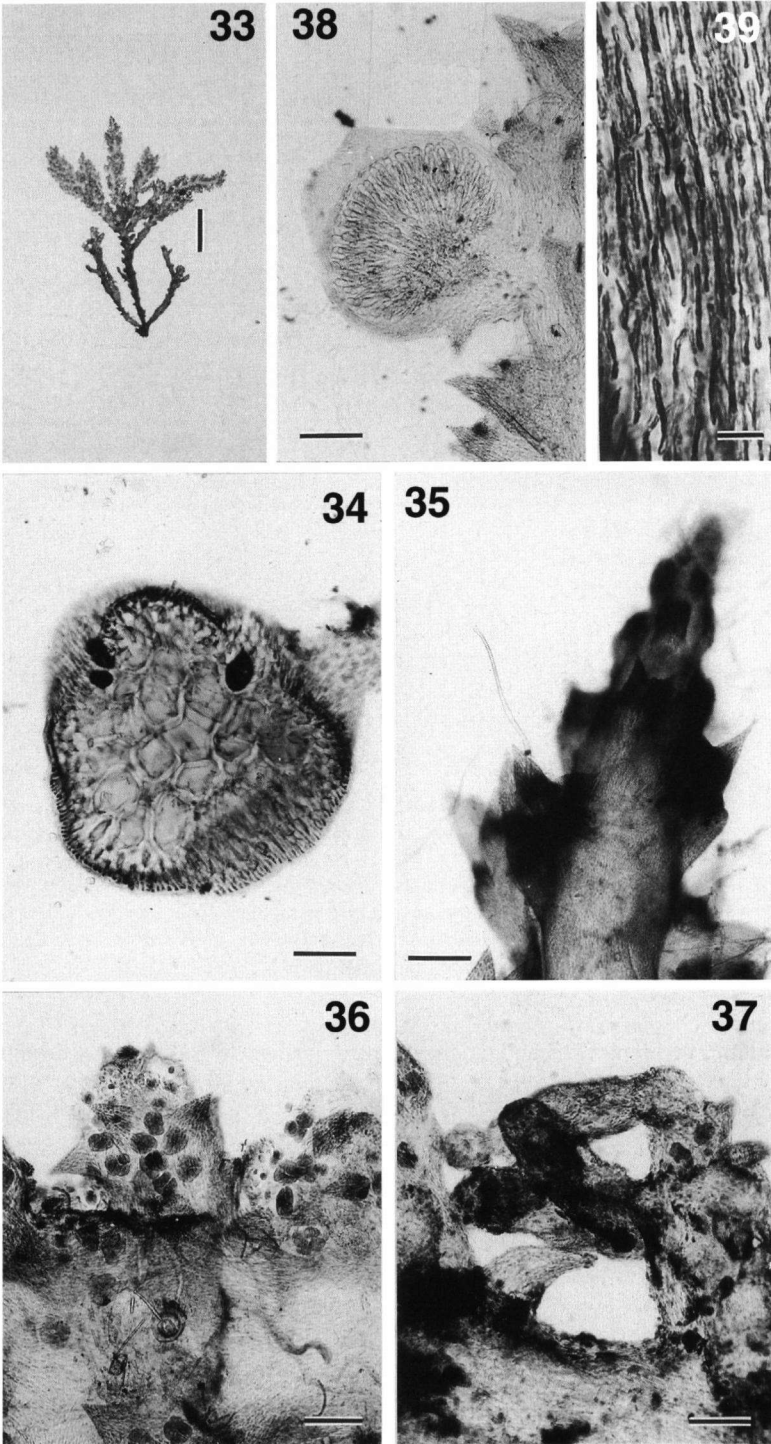
7. *Acanthophora spicifera* (Vahl) Børgesen — Fig. 3, 33–39, 46

Acanthophora spicifera (Vahl) Børgesen 1910: 201, f. 18–19; 1918: 259, f. 253–258; 1936: 94; 1937: 348; 1945: 61; 1953: 56; M. Howe 1918: 520; 1920: 569; Weber Bosse 1923: 347, f. 131, 132; W.R. Taylor 1928: 165, t. 26, f. 5, 6, t. 34, f. 7; 1931: 27; 1939: 16; 1940: 559; 1941: 99; 1943: 161; 1954: 105; 1960: 620, t. 71, f. 3, t. 72, f. 1, 2; 1962: 61; 1969: 186; 1976: 98; 1977: 14; W.R. Taylor & Arndt 1929: 658; W.R. Taylor & Bernat. 1969: 39; W.R. Taylor & Rhyne 1970: 15; P.L. Anand 1943: 37; Fritsch 1945: 556, f. 204E; E.Y. Dawson 1954: 456, f. 61, a–b; Womersley 1958: 158; Rodriguez 1959: 279; Durair. 1961: 71, t. 19, f. 2–6; V.J. Chapm. 1963: 143, f. 148; Kim 1964: 165; A.B. Joly 1965: 236, t. 54, 55, f. 651, 680–683; 1967: 446; M.M. Ferreira & Pinheiro 1966: 65; Oliviera Filho 1967: 172; 1969: 172; Steentoft 1967: 138; Trono 1968: 293; 1969: 87; 1986: 279, f. 91; Womersley & A. Bailey 1970: 337; W.D. Richardson 1975: 134; Dawes 1976: 151, f. 74; C. Hoek et al. 1972: tabel 15; Jaasund 1976: 137, f. 276; G.W. Lawson 1980: 32; Trono & Ganz.-Fort. 1980: 99, f. a; 1988: 183, f. 131, A, B; Zhang & Xia 1980: 62, f. 10, 11; Cordero 1981: 203, f. 201, 203, t. 26, A; Meñez & Calumpong 1981: 381; G.W. Lawson & D.M. John 1982: 317, t. 51, f. 1, 2; 1987: 298, t. 48, f. 1, 2; Cribb 1983:

- 105; C.K. Tseng 1983: 142, t. 74, f. 2; T. Yoshida et al. 1985: 266; J.H. Price et al. 1986: 5; P.C. Silva et al. 1987: 60; C.W. Schneid. & Searles 1991: 431; Coppejans & Prud'homme 1992: 189; Verheij & Prud'homme 1993: 444, t. 15, f. 2; M.J. Wynne 1995: 301; P.C. Silva et al. 1996: 470. — *Fucus spiciferus* Vahl 1802: 44. — Type: C 124/93 (n° 10), from Key West, Florida.
- Fucus acanthophorus* J.V. Lamour. 1805: 61, t. 30, 31, f. 1. — *Acanthophora thierrii* J.V. Lamour. 1813: 132 ['thierii']; Grev. 1830: 54; Kütz. 1843: 437, t. 52, f. 5; 1849: 858; 1865: 27, t. 75, f. h-1; Harv. 1847: 34 [excl. syn.]; 1853: 17, t. 14A, f. 1-3; J. Agardh 1863: 819; Schramm & Mazé 1865: 56; Grunow 1868: 92; Mazé & Schramm 1870-1877: 247; Zanardini 1872: 138; Dickie 1875: 148; De Toni & Levi-Morenos 1888: 33; G. Murray 1889: 17; F. Schmitz 1889: 13; De Toni 1903: 820; Pilg. 1911: 303. — *Chondria acanthophora* C. Agardh 1822: 363; 1824: 209. — Type: CN.
- Acanthophora antillarum* Mont. ex Kütz. 1865: 27, t. 75, f. d-g; sensu Mazé & Schramm 1870-1877: 247; sensu De Toni 1903: 821; sensu M. Howe 1920: 569; sensu Cribb 1983: 106. — *Acanthophora thierrii* J.V. Lamour. forma *gracilis* P. Crouan & H. Crouan ex Mazé & Schramm 1870-1877: 247, G. Murray 1889: 17. — Type: L 938.92-97, loc. Cuba.
- Chondria muscoides* auct. non L.: Mont. 1842: 43; Kütz. 1849: 859; 1865: 27, t. 77, f. a-c; De Toni & Levi-Morenos 1888: 33. — *Acanthophora intermedia* P. Crouan & H. Crouan ex Schramm & Mazé 1865: 57; Mazé & Schramm 1870-1877: 247. — Type: unknown.
- Acanthophora orientalis* J. Agardh 1863: 821; Kütz. 1865: 28, t. 77, f. d, e; Sond. 1871: 18; Picc. 1886: 81, 90; Askenasy 1888: 48, t. 9, f. 11, 12; De Toni & Levi-Morenos 1888: 33; Falkenb. 1901: 226; De Toni 1903: 822; Weber Bosse 1914: 287; C.K. Tseng 1935: 102; Papenf. 1943: 92; Seagrief 1984: 3; G.W. Lawson 1980: 32. — *Acanthophora spicifera* forma *orientalis* (J. Agardh) Weber Bosse 1923: 348. — *Acanthophora spicifera* var. *orientalis* (J. Agardh) Zaneveld 1959: 25, 106. — Types: LD 4/062.9778 (n° 38079-38081), loc. Mariana Isl., coll. J. Agardh.
- Acanthophora wightii* J. Agardh 1863: 821; De Toni & Levi-Morenos 1888: 33; De Toni 1903: 822. — *Acanthophora orientalis* J. Agardh var. *wightii* J. Agardh ex Sond. 1879: 81. — *Acanthophora spicifera* (Vahl) Børgesen forma *wightii* (J. Agardh) Weber Bosse 1923: 348. — Type: LD and TCD, loc. India.

Plants up to 20 cm high, sparingly branched, wide spreading, or somewhat bushy, cartilaginous, attached to the substrate by a large lobed disk from which several erect axes rise (Fig. 33). Main axes quite thick, 2.2 mm wide, spines absent or scarce, with alternately or irregularly divided terete branches of indeterminate growth and shorter branches of determinate growth, often subtended by a spine. Branching irregular to radial, rather sparse below and often more abundant above. Branches not constricted, partly or completely spirally covered with spine-like ramuli, spines mostly found in the upper part of the determinate branches. Apices of plants pointed, protruded in the form of a pyramid with dense spines, the latter 0.5–0.8 mm broad and getting smaller in size towards the apex (Fig. 35). When fully grown, trichoblasts protrude and seemingly envelop the apical part of the plant. Trichoblasts dichotomous, borne on the tips of branches and branchlets. Cross section of the axis shows a central cell surrounded

Fig. 33–39. *Acanthophora spicifera* (Vahl) Børgesen. — 33. Habit of male plant; PH s.n. (bar = 10 mm). — 34. Cross section of the erect axis with large periaxial cells; L 0128 (bar = 200 µm). — 35. Apical part with many spines, note the arrangement of spinous branchlets becoming smaller toward the apex; L 1050 (bar = 200 µm). — 36. Stichidia borne on ramuli; L 1050 (bar = 200 µm). — 37. A different form of stichidia, spineless and protruding from the spinous ones; PH s.n., from Gabon (bar = 200 µm). — 38. Urn-shaped cystocarp bearing carpospores; L 514685 (bar = 200 µm). — 39. Surface view of epidermal cells; C 124/93 (bar 20 = µm).



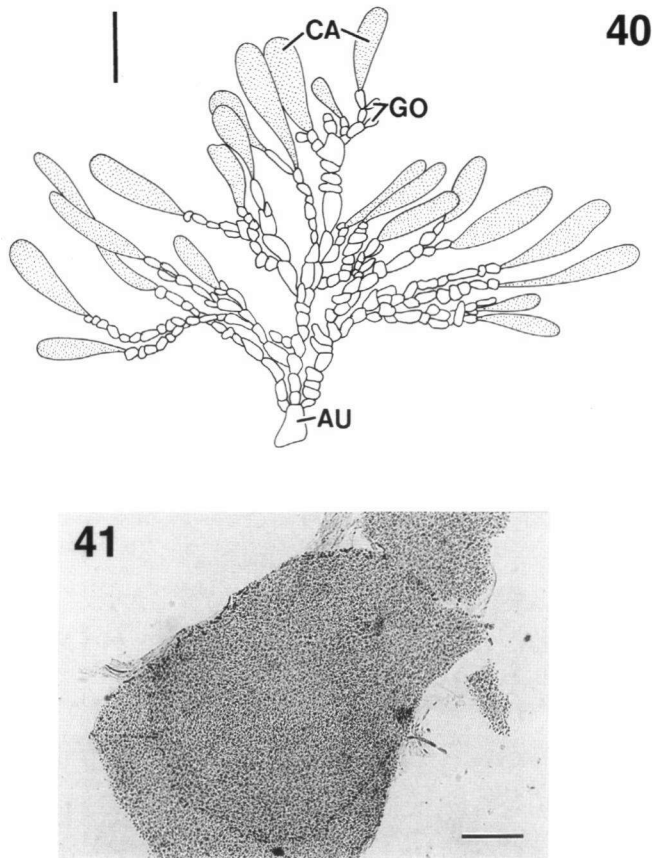


Fig. 40 & 41. Carposporophyte and antheridia of *Acanthophora*. — 40. Carposporophyte. AU = Auxiliary cell (or fusion cell), CA = carpospores, GO = gonimoblast. Notice the four-celled filament developing from auxiliary cells (bar = 10 μ m). — 41. Antheridial body with a sterile cell margin and numerous spermatangia on the surface (bar = 100 μ m).

by 5 distinct periaxial cells and small, rounded cortical cells, gradually diminishing in size towards the periphery (Fig. 34). Fibre-like epidermal cells (Fig. 39). *Stichidial ramuli* short at the bases of branches and elongated at the upper ends (Fig. 36, 37). *Tetraspores* tetrahedral, developed in abundance throughout as well as terminal on stichidial ramuli bearing spines. *Spermatangial* cluster plate-like, developed on a trichoblast of which the basal cell persists as the stalk of the disk, margin composed of large, oblong, thick-walled clear cells. *Cystocarps* urn- or pear-shaped (Fig. 38), sessile in the axils or near the bases of spine-like branchlets.

Distribution — Atlantic Ocean, Caribbean, Indian Ocean, Pacific Ocean, Red Sea (Fig. 46).

Note — *Acanthophora spicifera* can be distinguished from other species by the absence of spine-like branchlets located on the main axes. This seems to be the main distinctive character of this species. However, in practice, careful study of the type

specimen and specimens from different geographical localities, occasionally revealed solitary spines among branchlets on the main axes. This creates confusion with other species. Comparing spine distribution on the main axes of *A. spicifera* with respect to other species (*A. muscoides*, *A. nayadiformis*, *A. ramulosa*), the abundance of the spines is a remarkably clear character, because in the latter group spines occur in high density on the main axes. Other distinctive characters of *A. spicifera*, concerning the distribution of spines on the branchlets (mostly at the apices) and the arrangement of spines on the indeterminate branches (getting smaller in size toward the apical parts) should also be taken into consideration.

Specimens examined: *C* 124/93 (n° 10); *LD* 4/062.9778 (n° 38079-38081), Manilam, J. Agardh (tetrasporic); *L* 938.92-97, Cuba; *L* 0950, *L* 1050, SW Sulawesi, Verheij (tetrasporic); *L* 514685, Bay Negros, Oriental Philippines; *PH* s.n., Yabucoa, Puerto Rico, Morrill (spermatan-gial); *L* 939.6-122, Isl. Maurice, De Robilland; *L* 939.6-35, Nosi-be, Madagascar; *L* 943.68-297, Terne, Mahe, Seychelles; *L* 959.8-029, Gulf of Carpentaria, N.T. Australia; *L* 939.271-74 (n° 19146), New Caledonia; *L* 965.321-492, Hawaii, Bailey; *L* 164.921-40, Guadalcanal-Kopiu, Solomon Islands.

DISCUSSION

Study of the literature and observations on actual specimens reveal that few substantial diagnostic features can be found leading to a better understanding of species delimitation within the genus *Acanthophora*.

Despite the similarity in species characters, several diagnostic features are proposed for species delimitation.

Vegetative characters

Branching

In general the spirally arranged branching pattern does not vary within the genus *Acanthophora*. Nevertheless, ramification is different between some species which can either be caused by ecological factors or can be a differentiating feature between species: the ramification in *A. muscoides* seems to be more dense than in *A. spicifera*. Insertion of branches can differ between species. In contrast to other *Acanthophora* species, branches of *A. spicifera*, *A. nayadiformis* and *A. pacifica* are not constricted at their bases.

Spine development

The main character differentiating *Acanthophora* from its related genus *Chondria* is the presence of spines. There may be confusion, however, when *Chondria* species are beset with pointed spurs, from which cystocarps may arise (Gordon-Mills & Womersley, 1987). The spine arrangement is quite different among the species. *Acanthophora spicifera* lacks spines on the main axes. The branches issuing from these main axes in that species have no spiny branchlets at their base, as is the rule in most other species. Moreover, the spines in *A. spicifera* are mostly found at the upper end of the branchlets, the arrangement of spines is dense, and spines become smaller towards the apices.

Acanthophora muscoides and *A. nayadiformis* belong to a group of species in which isolated spines are found on main axes, while branches issue from the axils of spines

as adventitious branches (Falkenberg, 1901). Branchlets in these species mostly have spines developed from their basis upward. Additionally, branches and branchlets are in general subtended by a spine and the apical parts are tipped with several spines of uniform size.

Acanthophora ramulosa has well developed branches of indeterminate growth bearing numerous spines. The branchlets are of two kinds: in younger parts of the plants they resemble simple, short elongated branches, whereas in older parts of the main axes they bear spines. Neither branches nor branchlets develop from the axils of spines.

In *Acanthophora dendroides*, spines are found on the main axes. Incidentally, especially near the apical parts of the branches and branchlets, short spines are present. Moreover, the spines are quite broad at their base compared to other species.

Acanthophora aokii has spike-like shoots spirally wound around both branches and main axes. The spines are minute and solitarily scattered, and the apical parts are not covered by spines.

The flattened thalli of *Acanthophora pacifica* are beset with spirally produced spines (Kraft, 1979).

Attachment

The attachment structure is generally similar amongst all species. Nevertheless, character polymorphism is present for the basal disk. *Acanthophora muscoides*, *A. aokii*, and probably also *A. pacifica* have flat disciform holdfasts, while other species (*A. spicifera*, *A. ramulosa* and *A. dendroides*) have lobed disciform holdfasts. In *A. nayadiformis*, the attachment is composed of a rhizoidal holdfast, whereas the simple attachment disks described in literature for the genus can be observed in the field only in sporelings (Cecere et al., 1994). Stolons do occur in *A. dendroides*, *A. nayadiformis* and *A. pacifica*, but have not been observed in the other *Acanthophora*-species.

Reproductive characters

All *Acanthophora* species are dioecious, although for *A. aokii*, gametophytic specimens are not known.

Tetrasporangial stichidia

Tetrasporangia are developed in stichidial ramuli bearing spines in *A. spicifera*, *A. pacifica* and *A. muscoides*. In the other *Acanthophora* species the stichidia are without spines, or spines are scarce. Additionally, the distribution of tetrasporangia within the stichidia is quite variable. In *A. spicifera*, for instance, where stichidial bodies are short, tetrasporangia are developed near the base, while in longer stichidia the tetrasporangia are developed near the tip. In *A. muscoides*, tetrasporangia are often also formed in the tips of branchlets bearing the fertile ramuli. Tetrasporangial stichidia are present from the base to the apex of the indeterminate branches, but the tetrasporangia occur mostly near the tip of the stichidial ramuli.

In *A. aokii*, stichidia are globular or oblong and occupy the tip of ramuli which often bear one terminal spine; *A. nayadiformis* has spineless and globose stichidia with tetrasporangia distributed throughout; *A. dendroides* has ovate and not very spiny stichidia, but also with tetraspores distributed throughout. In *A. ramulosa*, tetrasporangia occupy the terminal part of short, wrinkled, spineless, determinate branches

and tetrasporangia mostly occur at the tip of stichidial ramuli. The determinate branchlets of *A. pacifica* that become tetrasporangial stichidia, remain terete and form tetrasporangia in each tier of the central axial filament of these stichidia.

Cystocarps

Most of the *Acanthophora* species have sessile cystocarps borne on determinate branchlets. *Acanthophora spicifera* has subsessile cystocarps formed in the axil of spine-like branchlets, while cystocarps of *A. ramulosa* are borne on short stalks. Cystocarp morphology is also different between the species, but mostly it is urn-shaped. *Acanthophora spicifera* has urn- to pear-shaped cystocarps, while cystocarps are (sub)-globose in *A. dendroides* and probably also in *A. pacifica*.

Propagules

Acanthophora nayadiformis is known to be capable of forming small branches from the apical part of the indeterminate branches which serve vegetative propagation. Propagules resemble swollen spike cones containing floridean starch granules (Cecere et al., 1994). Propagules have not been observed in other species studied here. However, Petrocelli (pers. comm.) observed propagules in *A. spicifera* and expects them also to be present in other species.

Geographical distribution

A survey of distribution of all species, as based on available publications and notes on distribution on herbarium vouchers, resulted in distribution maps for the *Acanthophora* species (also: Hitipeuw, 1996).

Acanthophora spicifera has a wide geographical distribution (Fig. 46) in the warmer regions of the West Indies, Caribbean, West Africa, Indian Ocean and Indo-Pacific regions. In the northern part of the Atlantic Ocean this species has only been reported from Biarritz (Børgesen, 1918). So far there are no records of the species from the Mediterranean. However, recently *A. spicifera* was found at several localities of the Red Sea coast of Eritrea (Ateweberhan, pers. comm.). This species was also recorded from the most southern part of the Atlantic Ocean (Harvey, 1847). Harvey doubted, however, the occurrence of *A. spicifera* on the Falkland Islands since this species is normally distributed in warmer regions. He wondered if there could be any mistake in the habitat or identification. There are no records from the east side of the Pacific Ocean.

Like *A. spicifera*, *A. muscoides* has a wide geographical distribution (Fig. 44). Most records are from the West Indies and the Caribbean region, and the northern and southern Indian Ocean. In the southern part of the Atlantic Ocean, this species is distributed from West to East. *Acanthophora muscoides* is not recorded from the Red Sea and the Mediterranean or from North Atlantic regions, nor from the eastern coast of the Pacific Ocean.

Acanthophora nayadiformis occurs throughout the Mediterranean and the Red Sea. This extends to the northern part of the Indian Ocean (Fig. 45). According to herbarium specimens, this species also occurs in Florida.

The distribution area of *A. dendroides* is the Indian Ocean, including the north-western part of Australia (Fig. 43). The species is also recorded from Indonesia.

Acanthophora aokii was first recorded from Taiwan and seems to have a limited distribution in the West Pacific (Fig. 42).

Acanthophora ramulosa appears to have a geographic distribution in the South-East Atlantic region. Steentoft (1967) stated that this species is apparently endemic to the Gulf of Guinea (Fig. 42).

Acanthophora pacifica is only known from Tahiti and Hawaii, both in the Pacific Ocean (Fig. 43).

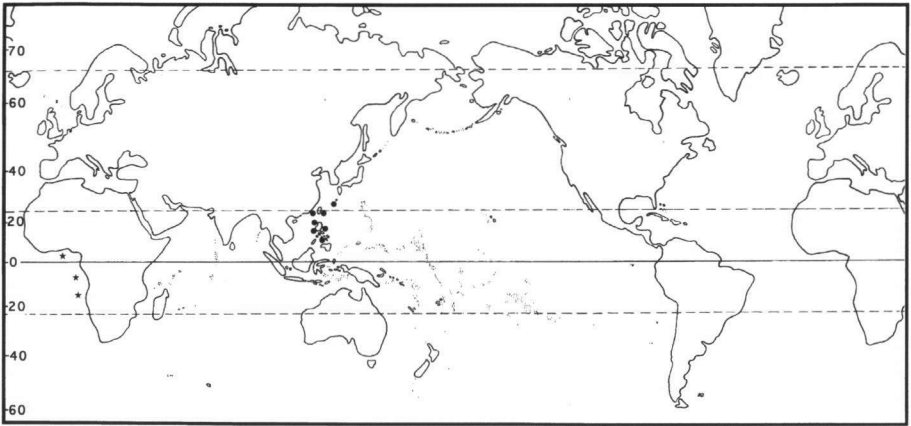


Fig. 42. Geographical distribution map of *Acanthophora aokii* Okamura (●) and *A. ramulosa* Lindenb. ex Kütz (★).

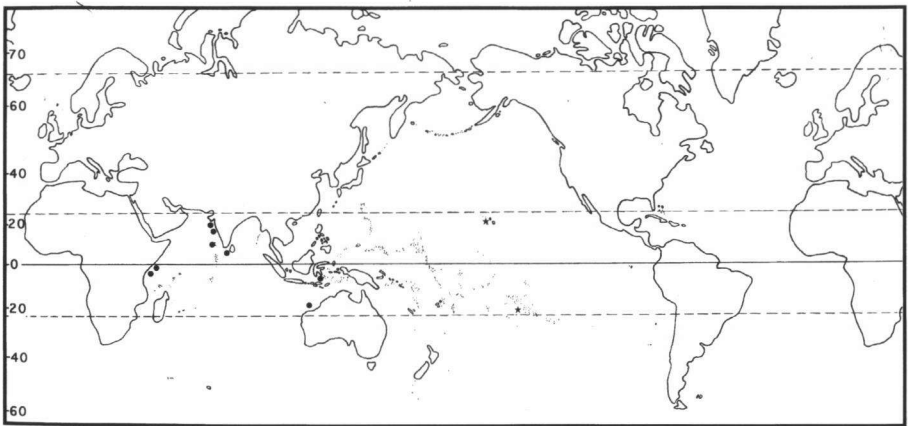


Fig. 43. Geographical distribution map of *Acanthophora dendroides* Harv. (●) and *A. pacifica* (Setch.) Kraft (★).

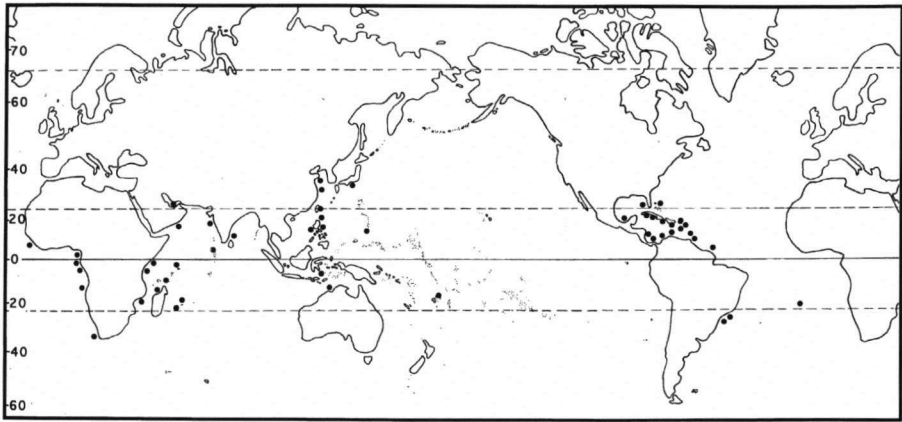


Fig. 44. Geographical distribution map of *Acanthophora muscoides* (L.) Bory.

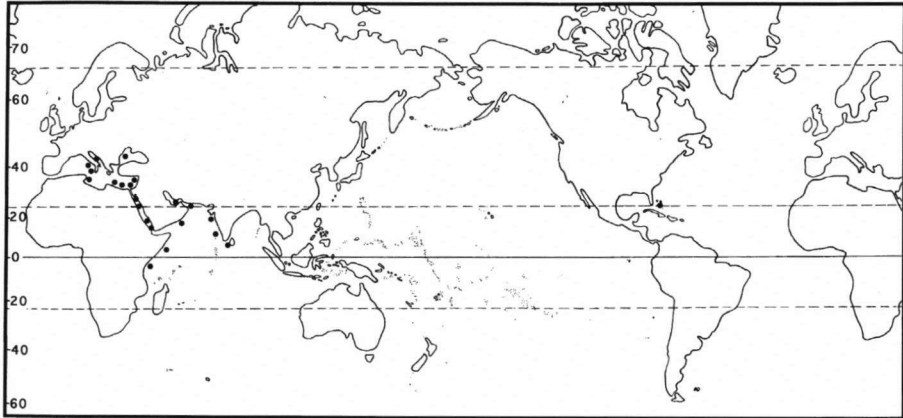


Fig. 45. Geographical distribution map of *Acanthophora nayadiformis* (Delile) Papenf.

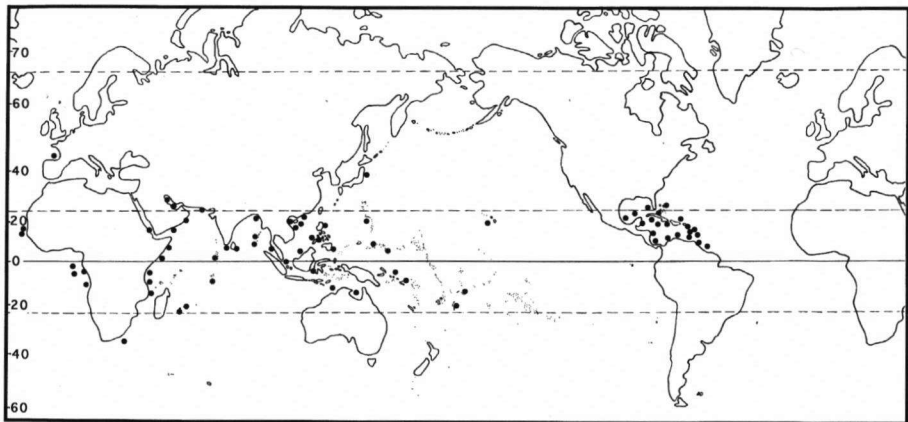


Fig. 46. Geographical distribution map of *Acanthophora spicifera* (Vahl) Børgesen.

Phylogenetic analysis

Based on the published descriptions and detailed observations on type material and other specimens of *Acanthophora*, 19 characters were selected and used for phylogenetic analysis (Table 3). A majority of these characters is based on features of the spines. However, characters based on aspects of reproduction, dimensions, vegetative structures were – when available – incorporated in the analysis as well.

Table 3. Morphological characteristics selected for phylogenetic analysis of *Acanthophora*.

1. Prostrate system (holdfast)	0 = flat disk, 1 = lobed disk, 2 = rhizoids
2. Size of fronds	0 = small (< 5 cm), 1 = medium (5–12 cm), 2 = large (> 12 cm)
3. Width of main axes	0 = < 1mm, 1 = 1–2 mm, 2 = > 2 mm
4. Branches	0 = terete, constricted at the base, 1 = terete, not constricted, 2 = flattened
5. Spines on indeterminate branches	0 = present, 1 = absent or scarce
6. Determinate branches	0 = subtended by a spine, 1 = not subtended by a spine
7. Size of spines	0 = narrow (< 0.1 mm), 1 = medium (0.1–0.3 mm), 2 = wide (> 0.3 mm), 3 = no spines
8. Position of spines on determinate branches	0 = at the end, 1 = from base (continuously) to the end 2 = irregular, solitary and scattered, 3 = no spines
9. Ultimate branches (ramuli)	0 = spiniferous, 1 = spineless/wrinkled, 2 = both, 3 = other forms (clavate, fusiform)
10. Form of apices	0 = pointed, 1 = blunt, 2 = round, 3 = depressed
11. Arrangement of spines at the apex	0 = spineless, 1 = 1 or 2 spines, 2 = many spines (more than 2)
12. Stichidia	0 = spiniferous, 1 = spineless, 2 = ovate, with few spines
13. Position of stichidia on determinate branches	0 = throughout ramuli, 1 = at the base, 2 = at the apex
14. Position of tetrasporangia in stichidia	0 = scattered, 1 = terminal, 2 = both
15. Form of cystocarp	0 = urn-shaped, 1 = pear-shaped, 2 = globose
16. Position of cystocarp	0 = sessile, 1 = subsessile, 2 = on short stalks
17. Texture	0 = cartilaginous, 1 = rather soft
18. Form of epidermal cells	0 = elongated/fibre like, 1 = rounded
19. Stolons	0 = absent, 1 = present

Table 4. Data matrix of character states of *Acanthophora*.

Characters:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Species																			
<i>A. aokii</i>	0	0	0	0	0	1	0	2	0	2	0	1	2	0	?	?	1	1	0
<i>A. dendroides</i>	1	2	0	0	0	1	2	0	0	2	1	2	2	1	2	0	0	1	1
<i>A. muscoides</i>	0	1,2	0	0	0	0	2	1	0	1	2	0	0	1	0	0	0	0	0
<i>A. nayadiformis</i>	2	1	1	1	0	0	1	2	2	1	2	1	1	0	0	0	0	0	1
<i>A. pacifica</i>	0	0,1	2	2	0	1	1	0	0	0	2	0	0	0	2	0	0	0	1
<i>A. ramulosa</i>	1	1,2	1	0	0	1	1	0	1	1	1	1	0	1	0	2	0	0	0
<i>A. spicifera</i>	1	1,2	2	1	1	1	2	0	0	0	2	0	0	2	0,1	1	0	0	0
<i>Chondria</i> sp.	0,1	0,1,2	0,1,2	0	0,1	1	3	3	3	1,2,3	0	1	2	0	0,1	0	0	0,1	0,1

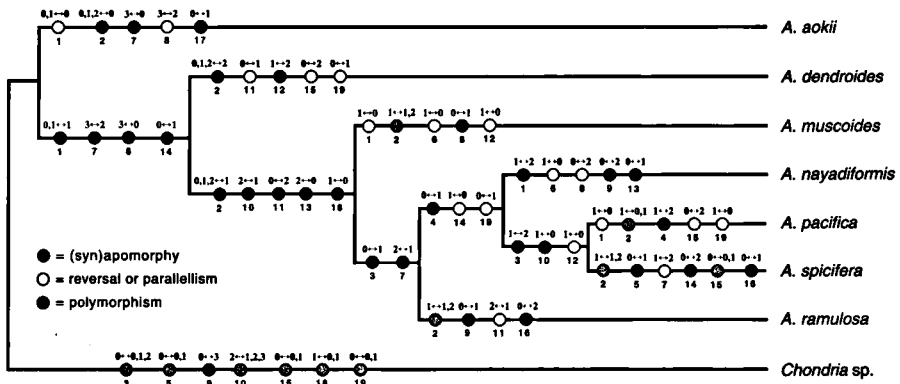


Fig. 47. Single most parsimonious cladogram of *Acanthophora* (L = 62, CI = 0.82, g₁ = 0.22), showing the distribution of character-state changes (numbers below the circles) of the characters (numbers above the circles).

Usually the species are not polymorphic for the characters selected for the data matrix, so the differences between the species are unambiguous.

The genus *Chondria* is used as an outgroup in the phylogenetic analysis because of similarities in morphological and reproductive structures, like the number of periaxial cells, features of antheridial bodies and carpogonial branches. The result of the phylogenetic analysis is one single most parsimonious tree as shown in Figure 47.

It can be noticed (Table 4 & Fig. 47) that characters separating *Chondria* from *Acanthophora* are the absence of spinous outgrowth on the branches (char. 5, 7, 8) and the shape of determinate branches (char. 9, 10). *Acanthophora aokii* seems to be most closely related to *Chondria*. Characters that distinguish this species from the remaining *Acanthophora* species are a small frond size (char. 2) and a membranaceous texture (char. 17). *Acanthophora dendroides* is characterised by having a cystocarp of distinct globular shape, a relatively small thallus with narrow main axes (char. 15), and ovate stichidia with few spines (char. 12). *Acanthophora aokii* and *A. dendroides* both have no spines at the apical part (char. 10). Moreover, the cladogram shows a clade of *A. ramulosa*, *A. nayadiformis*, *A. spicifera* and *A. pacifica* closely related by sharing characters of spine size (char. 7) and sizes of the main axes (char. 3). These species have a sister group relationship with *A. muscoides* due to a broad range of characters (chars 2, 10, 11, 13, 18).

When names of species in the cladogram are replaced by names of areas in which they occur (Fig. 48), it shows a first branch separating the West Pacific *A. aokii* from the remaining *Acanthophora* species, and a next grouping which separates *A. dendroides* distributed in the Indian Ocean from *A. muscoides*, *A. ramulosa*, *A. nayadiformis*, *A. spicifera* and *A. pacifica* from the Atlantic Ocean, Mediterranean, Red Sea and more widely distributed species. Subsequent split-offs can be recognised. *Acanthophora spicifera* and *A. muscoides* both are wide-spread tropical species; *A. ramulosa* is probably endemic to a restricted region on the West African coast, *A. nayadiformis* is a typical floral element of the Mediterranean, and *A. pacifica* is restricted to the central Pacific.

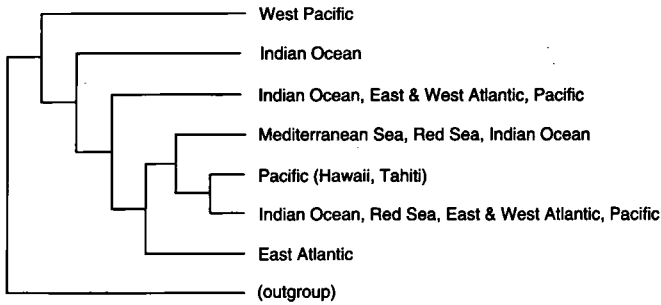


Fig. 48. Area cladogram of the genus *Acanthophora* showing the division of distribution areas related to the phylogeny of the species (Fig. 47).

CONCLUSIONS

Based on morphological observations of type specimens and a critical survey of the literature, a recognition of seven species of *Acanthophora*: *A. aokii*, *A. dendroides*, *A. muscoides*, *A. nayadiformis*, *A. pacifica*, *A. spicifera*, and *A. ramulosa*, is supported. Species delimitation is mainly based on features of spines, either in relation to vegetative or to reproductive structures.

In order to give a detailed picture of the global distribution of *Acanthophora*, distribution patterns of *Acanthophora* species are presented, based on herbarium collections, critical (published) checklists and catalogues. The geographic distribution of the species shows a disjunct pattern, although some species, such as *A. spicifera* and *A. muscoides*, are widely distributed.

Phylogenetic analysis shows *A. aokii* as the most primitive member of *Acanthophora*, suggesting a Pacific origin of this genus. Additionally, the isolated position of *A. dendroides* in the tree suggests this species to belong to the Indo-Pacific algal flora and *A. ramulosa* to be a West African endemic.

Presumably, species of *Acanthophora* once have arisen in the West Pacific and migrated in a westerly direction facilitated by westward circumtropical currents via the Tethys Sea in late Mesozoic times (135–65 Mya). This suggests a primary Tethyan imprint. Due to several geological events, however, these distribution routes became discontinuous. The closure of the Tethys Sea by a relative uplift of the Middle East separated the Indo-Pacific and proto-Atlantic-Mediterranean areas at about the early Cenozoic (Hallam, 1981) and blocked further westward distribution. Apparently *Acanthophora* species never reached the Central (proto) Atlantic-Mediterranean areas or became extinct during Atlantic surface water temperature crises at late Cenozoic times. Geographical segregation and subsequent (allopatric) cladogenesis of *A. aokii* and *A. dendroides* can be reduced to the opening of the Indian Ocean (135 Mya) and the separation of the Indian basin by the rise of the Malaysian Arch (starting 50 Mya).

The presence of *A. ramulosa* in the eastern Atlantic and *A. muscoides* in the East and West Atlantic Ocean is very likely caused by migration from the Indian Ocean via South Africa during the early Cenozoic (65–50 Mya). An introduction and radiation of *A. nayadiformis* is observed in the Mediterranean, with a secondary invasion of

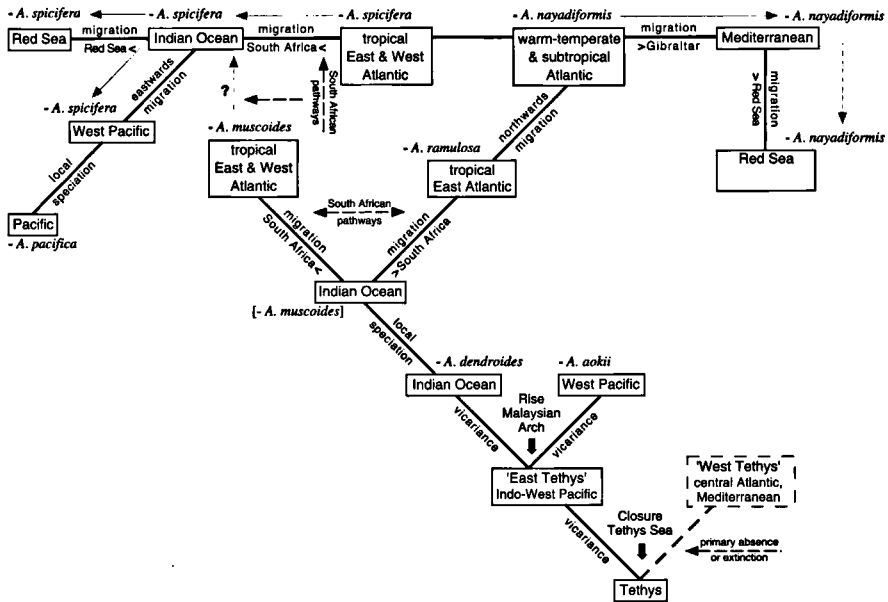


Fig. 49. Schematic representation of postulated biogeographical events affecting the evolution of *Acanthophora*.

this species into the Red Sea and Indian Ocean after the opening of the Suez Canal. Because the first records of *A. nayadiformis* from the Mediterranean are from far before the opening of the Suez Canal (in 1869), a Lessepsian origin of *A. nayadiformis* is excluded. The world-wide distributed species *A. spicifera* is proposed to have re-migrated into the Indo-Pacific region using the South African passageway at its final stage (around 40 Mya), followed by further eastward migration of *A. spicifera* and a local speciation of *A. pacifica* at Hawaii and Tahiti.

The absence of *A. muscooides* and *A. spicifera* in the East Pacific despite their presence in the Caribbean and a gateway through the Isthmus until its closure (3–3.5 Mya) is puzzling and suggests a relatively late invasion of this species into the tropical West Atlantic region (Lüning, 1990).

Acanthophora muscooides is supposed to have reached the Atlantic region shortly after local giving rise to this species in the Indian Ocean (Fig. 49). Alternatively a parallel re-introduction of *A. muscooides* and *A. spicifera* into the Indian Ocean during the middle Cenozoic after speciation into the Atlantic Ocean is conceivable, and supports the belief of Hommersand (1989), who proposed a floral displacement of ancient Indo-Pacific taxa by newly developed and better adapted Atlantic remigrants during the middle to late Cenozoic.

The absence of *Acanthophora* species in the warm-to-temperate Atlantic Ocean except Florida is striking. This can be caused by extinction during the Pleistocene ice-periods, assuming *A. nayadiformis* to have survived in East Mediterranean and Caribbean refugia.

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