

Growth pattern assessment in the genus *Acanthophora* (Rhodophyta, Ceramiales)

CESIRA PERRONE¹, ESTER CECERE^{2*} AND GIOVANNI FURNARI³

¹Department of Plant Biology and Pathology, University of Bari, Via E. Orabona 4, 70126 Bari, Italy

²Institute for Marine Coastal Environment, Talassografico "A. Cerruti"-C.N.R., Via Roma 3, 74100 Taranto, Italy

³Department of Botany of the University of Catania, Via A. Longo 19, 95125 Catania, Italy

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The results of a morphological study, mainly based on the growth pattern and shape of both apical zone and branch primordia of all the terete species of *Acanthophora*, are presented here. This study shows that species are mainly distinguished on the basis of developmental features such as monopodial vs sympodial growth pattern and not by characters such as the presence or absence of spines on the main axes and the morphology of the stichidial ramuli previously generally used to distinguish the species of this genus, and which have proved to be of no diagnostic value. A key to the species of *Acanthophora* based on both the results of the present research and easily detectable characters is also proposed.

KEY WORDS: *Acanthophora*, *Acanthophora aokii*, *Acanthophora dendroides*, *Acanthophora muscooides*, *Acanthophora nayadiformis*, *Acanthophora ramulosa*, *Acanthophora spicifera*, taxonomy

INTRODUCTION

The genus *Acanthophora* J.V. Lamouroux (1813) consists of seven species: *A. ramulosa* Lindenberg ex Kützing, *A. dendroides* Harvey, *A. muscooides* (Linnaeus) Bory De Saint-Vincent, *A. spicifera* (Vahl) Børgesen, *A. aokii* Okamura, *A. nayadiformis* (Delile) Papenfuss, all with terete thalli, and *A. pacifica* (Setchell) Kraft with a flattened thallus. Traditionally, these species were distinguished on the basis of the following features: (1) species with main axes spineless (only *A. spicifera*) and (2) species with spines also on main axes (*A. nayadiformis*, *A. dendroides*, *A. muscooides*, *A. ramulosa* and *A. pacifica*) (Falkenberg 1901; Kraft 1979; de Jong *et al.* 1999).

Cecere & Perrone (2002) carried out a detailed study on the morphology of *A. nayadiformis* and observed that a ramisymphodial growth pattern can cause such deep changes at any thallus level and especially in the apical zones, that very often the gross morphology of the species is quite different from the common descriptions reported in the literature. Furthermore, they recognized: (1) the occurrence of four kinds of morphologically distinct primordia developing into four distinct kinds of indeterminate branches; (2) that the presence vs absence of spines on main axes depends on both the kind of primordium from which first order branches arise and the monopodial vs sympodial growth pattern; and (3) that tetrasporangial branches can be either spinous or spineless owing to the nature of their parent primordia. These results are summarised in Table 1.

Based on the above observations, we examined all the other species of *Acanthophora* with terete thalli in a different light, especially studying the growth pattern and the morphology of both the apical zone and branch primordia, which proved to be of fundamental importance in the taxonomy of the genus.

MATERIAL AND METHODS

The observations were carried out on both dried and liquid-preserved herbarium specimens. Herbarium abbreviations follow Holmgren *et al.* (1990). Our comments are reported in square brackets.

SPECIMENS EXAMINED: *Acanthophora aokii*: Yonakuni Island, Ryukyu, 15 April 1985, NY 7220.

Acanthophora muscooides – as *Chondria muscooides* C. Agardh, LD 94068.9765 NEOTYPE [the specimen chosen as neotype by de Jong *et al.* (1999) is that numbered 38011 and in our opinion it belongs to *A. spicifera*; the sheet also contains another specimen numbered 38012, belonging to *Acanthophora ramulosa*]; *A. muscooides* (Linnaeus) Bory, Antilles, Herb. Lugd. Bat. held in L 938.92. . .102 [tetrasporic (in our opinion it probably belongs to *A. spicifera*)]; *A. muscooides* (L.) Bory, St Thomas, 1895–96, C 69 [three specimens belonging to *Acanthophora spicifera*]; *A. muscooides* (L.) Bory, Angola, C 1376 [containing two specimens belonging to *Acanthophora ramulosa*]; as *A. muscooides* (L.) Bory, Angola, C 1378 [belonging to *Acanthophora ramulosa*]; *A. muscooides* Bory, Algues de la Barbade, 1903, LD 99030-0856 [belonging to *Acanthophora ramulosa*]; *A. muscooides*, Mafia Island, Chole Bay, Tanzania, 3 September 1967, Herb. Lugd. Bat. held in L 162589 [belonging to *Acanthophora spicifera*]; *A. muscooides* (Linnaeus) Bory, Lae-Lae Island, Sulawesi, Indonesia, 2 June 1989, – 1 m, cystocarpic, Herb. Lugd. Bat. held in L 992.274. . .357 [belonging to *Acanthophora spicifera*]; *A. muscooides* (Linnaeus) Bory, Cuyo Islands, Palawan, Philippines, 22 May 1978, – 1.5–3 m, Herb. Lugd. Bat. held in L 986.324. . .086 [belonging to *Acanthophora spicifera*].

Acanthophora spicifera – dried specimens: as *Fucus spiciferus* Vahl, St Croix, Virgin Islands, C 1044, HOLOTYPE [consisting of two dried specimens (one tetrasporic, the other

* Corresponding author (ester.cecere@iamc.cnr.it).

Table 1. Characters described in *Acanthophora nayadiformis* and used in the descriptions of the other species (cf. Cecere & Perrone 2002).

Type of primordium	Origin (from)	Position	Growth pattern	Development (into)
Rounded with slightly constricted base and sunken apex	haptere of germling; rhizomatous base stipe	terminal lateral	monopodial	main axis (spineless in the basal part) first order branches (spineless at their bases)
Spiny with three to five spines overarching the tip	youngest spine mature spine	'terminal' lateral	sympodial	ramisymphodial main axis (spineless) first, second, third order ramisymphodia; 'spiny' tetrasporic branches
Conical with exerted apex	axilla of the spine	lateral	monopodial	first, second, third order branches; 'ovate' tetrasporic branches
Terete with obtuse apex	stipe; branches of any order	lateral	monopodial	stolons (spineless); 'terete' tetrasporic branches

cystocarpic) and two slides]; *A. spicifera*, Mokuleia Beach, Waialua, O'ahu, August 1965, FI 4064/7; as *A. thierii* J.V. Lamouroux, Ceylon, Herb. Hort. Bot. Reg. Kew held in BM, unnumbered sheet containing four specimens (a–d), [specimen a, cystocarpic; specimens c–d, sterile]; as *A. thierii* Lamouroux, Guadeloupe, BM, unnumbered sheet [containing two specimens both tetrasporic]; Rio de Janeiro, Brazil, 24 April 1988 [cystocarpic], BM, unnumbered sheet; Little Cayman, Cayman Islands, 4 June 1938 [containing two specimens a (tetrasporic), b (sterile)], BM, unnumbered sheet; as *A. thierii* Lamouroux, Guadeloupe [tetrasporic], Herb. Hort. Bot. Reg. Kew held in BM, unnumbered sheet; *A. spicifera* (Forsskål) Børgesen, South Bais Bay, Negros Oriental, Philippines, 15 May 1978 [cystocarpic], Herb. Lugd. Bat. held in L 514685. Liquid-preserved specimen: Punaluu, Hawaii Islands, April 1988 (I. Abbott, BISH) [tetrasporic].

Acanthophora ramulosa – as *Chondria ramulosa* Lindenberg, Angola, 1839, Herb. Kützing in Herb. Lugd. Bat. held in L 939.6. .124, HOLOTYPE [tetrasporic; on the same sheet there is a smaller cystocarpic specimen on the left with no annotations]; *A. ramulosa* Lindenberg, Angola, FI 4064/6; *A. ramulosa* (Lindenberg mscr.) Kützing emend. Steentoft, HBG 41–45/1842 [the sheet contains the following four specimens: no. 41, Angola, tetrasporic; no. 43, Angola, September 1842, cystocarpic; no. 44, tetrasporic; no. 45, cystocarpic]; HBG no. 51/1842 [cystocarpic].

Acanthophora dendroides – as *Acanthophora*, Rottneest, BM unnumbered sheet, specimen c (numbered 224), HOLOTYPE [the sheet, labelled as *Acanthophora dendroides* Harvey, contains three more specimens of *A. dendroides* (a,b,d) from Western Australia]; *A. dendroides*, Australia, [tetrasporic], Harvey's Austr. Alg. exsicc. 139 a, held in MICH 1319 [de Jong *et al.* (1999) report this sample as 'Type', but the collection place was not annotated on the sheet; conversely, in the protologue Harvey (1855) reported that the collection place was Rottneest and referred to a sample numbered 224; therefore, the sample kept in the British Museum as *Acanthophora*, numbered 224 and collected at Rottneest, as annotated on the sheet, has to be considered the holotype of *A. dendroides*]; Ceylon, May 1867, FI 4064/3; Fremantle, May 1867 [tetrasporic], FI unnumbered sheet; as *Acanthochondria falkenbergii* Weber van Bosse, Bonthain, male gametophyte, Herb. Weber van Bosse in Herb. Lugd. Bat. held in L 938.303. .84, SYNTYPE; as *Acanthochondria falkenbergii* Weber van Bosse, Bonthain (Celebes), October 1888, Herb. Weber van Bosse in Herb. Lugd. Bat. held in L 938.303. .85, SYNTYPES [containing four specimens inside an envelope,

one of them is annotated as tetrasporic]; Herb. Lugd. Bat. held in L 941. 98. .165 [containing two specimens inside an envelope]; *A. dendroides* Harvey, Dwarka, 19 January 1928, C 5315 [containing two specimens].

Acanthophora nayadiformis – as *Fucus nayadiformis* Delile, Alexandria, Egypt, BM unnumbered sheet, HOLOTYPE [with propagules; Cecere & Perrone (2002) were unable to examine the type of this species because de Jong *et al.* (1999), probably due to a misprint, wrote that the specimen was held in 'LD' instead of BM].

RESULTS

Acanthophora aokii

Because the Type specimen, collected in Taiwan and deposited in the Okamura's Herbarium (SAP) could not be borrowed, we could only observe the specimens collected at Yonakuni Island, Ryukyu, and deposited in the New York Botanical Garden (NY). They have the same features shown in the type and reported by de Jong *et al.* (1999).

This species has a very distinct gross morphology that makes it very easy to identify. Uprights are fastigiate and bear long naked stipes. Sometimes, three to seven first order branches sprout almost at the same level (Fig. 1).

In accordance with Okamura's (1934) description, we have observed that the apical zone of the vegetative branches is *Asparagus*-like (Fig. 1, frame). Both terminal and lateral primordia are of the rounded type; the seemingly naked axes are covered by minute, spirally arranged, widely spaced primordia (about 50 µm in diameter), located in small longitudinal furrows. No signs of ramisymphodial growth have been detected.

Acanthophora muscoides

From the observations of the neotype, a very young and small vegetative plant, main axis apical zones are spadix-like; main apex consists of a terminal very small rounded primordium (approximately 130–180 µm in diameter) which produces crowded lateral primordia of the same kind, not subtended by spines (Fig. 2, frame). The main axis growth is usually monopodial but occasionally can shift into a ramisymphodial pattern and in this case rosette-like apical zones can be observed. First order branches grow as ramisymphodia and rarely develop monopodially. Some adventitious rounded primordia can secondarily arise near the base of the first order branches (Fig. 2).

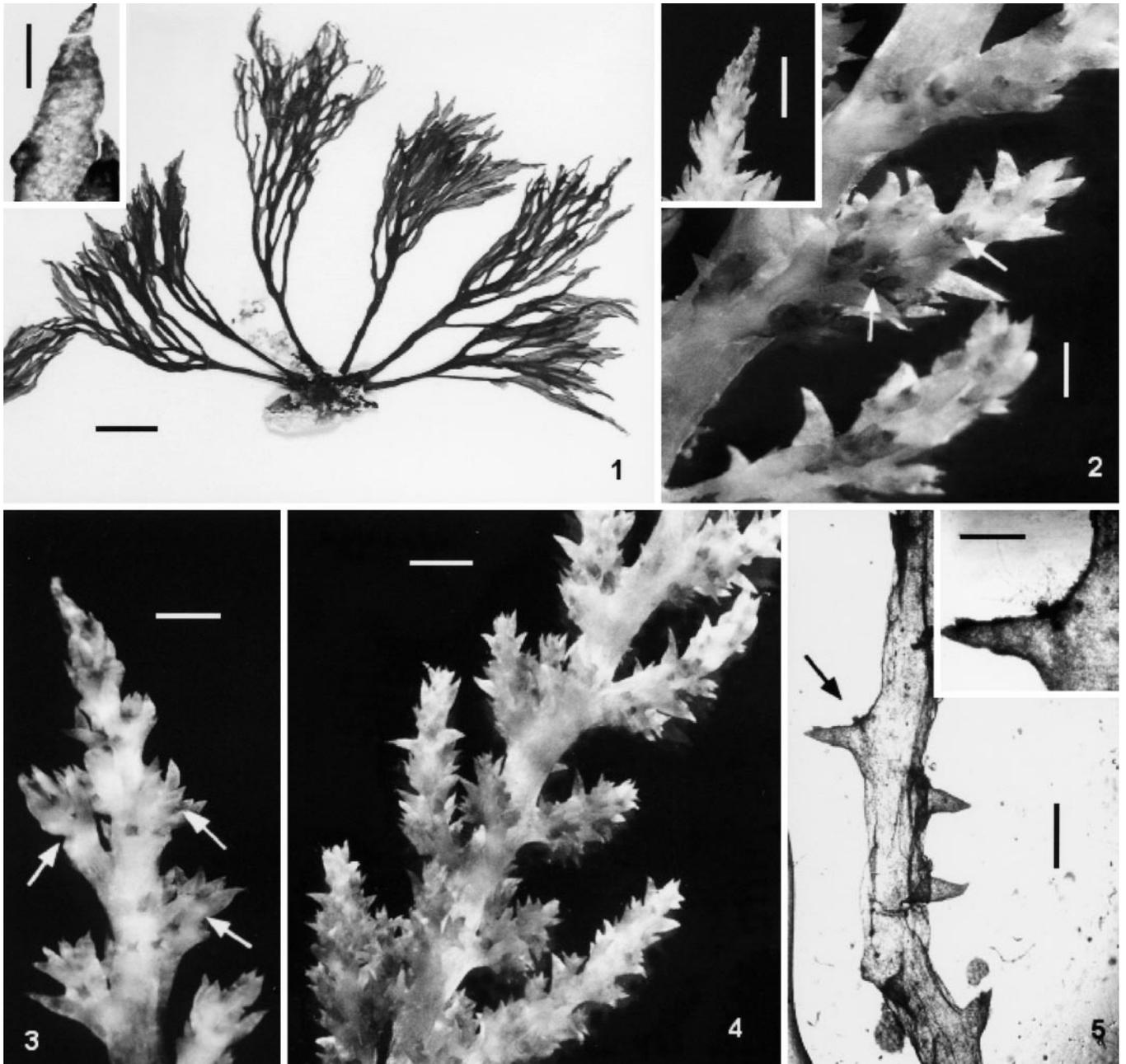


Fig. 1. *Acanthophora aokii* (NY 7220). Habit. Scale bar = 5 mm. In the frame (top left) *Asparagus*-like apical zone. Scale bar = 250 μ m.

Fig. 2. *Acanthophora muscoides* (as *Chondria muscoides*); LD 94068.9765 NEOTYPE [chosen by de Jong *et al.* (1999), but in our opinion belonging to *A. spicifera*]. Main axis with first order branches growing as ramisymphodia. Scale bar = 500 μ m. In the frame spadix-like apical zone. Scale bar = 1 mm.

Figs 3–5. *Acanthophora spicifera* (as *Fucus spiciferus*); C 1044, HOLOTYPE.

Fig. 3. Distal part of a main axis. Arrows indicate young first order laterals (from rounded primordia) early developing into ramisymphodia. Scale bar = 1 mm.

Fig. 4. First order branches (brachiblasts in the literature). Note the 'terminal' and lateral spiny primordia. Scale bar = 1 mm.

Fig. 5. Spinous axis monopodially growing. Note a conical primordium (arrow) arising in the axil of a spine. Scale bar = 340 μ m. In the frame the enlargement of the conical primordium. Scale bar = 700 μ m.

The holdfast consists of a rhizomatous prostrate system of entangled conspicuously corticated stolons.

Other observed herbarium samples should be assigned to different species of *Acanthophora*, especially *A. ramulosa* and *A. spicifera*, but also *A. dendroides* and *A. nayadiformis*. Moreover, also the herbarium tetrasporic specimen labelled *A.*

muscoides, held in L 938.92. . .102, probably belongs to another species (*A. spicifera*) because tetrasporangial sori are ovate when derived from conical primordia and spinous when derived from ramisymphodial spiny primordia (Table 1).

Therefore, because both the neotype and other herbarium specimens of *A. muscoides* belong to different species, *A.*

muscooides requires a reinvestigation to better define its distinctiveness from other species. At the moment it is, in our opinion, a taxon *inquirendum*. Finally, it should be noted also that the specimen LD 94/068.9763 (no. 38005) illustrated in the fig. 15 of the paper by de Jong *et al.* (1999) as *A. muscooides*, in our opinion belongs to *A. ramulosa*.

Acanthophora spicifera

The holotype shows spadix-like apical zones. First order laterals (referred to as brachiblasts in the literature) have proved to be indeterminate branches. As a rule, they develop into ramisymphodia (Figs 3, 4), but rarely into monopodial axes with spirally arranged spines (Fig. 5), in the axilla of which conical primordia can be present (Fig. 5, frame). Adventitious primordia can also form on main axes out of the spiral arrangement.

Tetrasporic branches can be ovate, terete and spiny (Table 1); in the holotype spiny tetrasporic branches can be observed. The attachment structure is stoloniferous and rhizomatous.

It should be noted that the general developmental trend corresponds to that of most herbarium specimens labelled as *A. muscooides*.

Acanthophora ramulosa

In the type as well as in all other studied specimens of *A. ramulosa*, the apical zone of both main and lateral axes appears rod-like, with a few small spines at most (Figs 6, 7). The terminal primordium is a rounded *Coelochondria*-like bud (about 500 μm in diameter), with the apical cell sunken in a shallow pit (Fig. 6, frame). The apex produces both widely arranged spines and widely spaced lateral rounded primordia giving rise to the first order branches; primordia of higher order branches are all of the same kind. Lateral branches are slightly tapered at their bases (Figs 6, 7). Usually, mature plants bear four orders of indeterminate branches.

All the axes exhibit a monopodial growth pattern only. Due to the spaced first order laterals and the small diameter of higher order branches (the ultimate branchlets in particular), plants assume a slender habit.

Tetrasporic branchlets originate from lateral rounded primordia. They bear one or two spines at most.

The holdfast consists of stolons and rhizomes, as observed, for example, in *A. ramulosa* Lindenberg, Angola, FI 4064/6.

Acanthophora dendroides

From the observations on both the holotype and other specimens of *A. dendroides*, the thallus organization is analogous to that of *A. ramulosa*.

The apical zone of both main and lateral axes is rod-like with a large *Coelochondria*-like bud (1–1.5 mm in diameter) as terminal primordium (Fig. 8). The apical zone bears closely arranged spines, very broad at their bases.

On main axes, the rounded primordia are less spaced than in *A. ramulosa* and, therefore, give rise to closely arranged first order laterals. Lateral branches are constricted at their bases (Fig. 8). The enlarged apical zone, the dense arrangement of the branches of all the orders as well as the large dimensions of both main axes and any order branches lead plants to assume a typical bushy habit (Fig. 9).

The base is rhizomatous. Tetrasporic branchlets are similar to those observed in *A. ramulosa*.

Acanthophora nayadiformis

The type specimen, which had not been previously observed, shows all the characteristics reported for *A. nayadiformis* from the Gulf of Taranto by Cecere & Perrone (2002) and summarised in Table 1.

Plants grow in both a monopodial and a sympodial pattern. Most plants grow especially as ramisymphodia, and in this case the main axis apical zone appears rosette-like; this very often happens in vegetative thalli, female gametophytes and tetrasporophytes. A few plants, on the contrary, show a prevalent monopodial growth pattern, such as most male gametophytes.

Because during summer *A. nayadiformis* produces typical vegetative propagules, summer–autumn plants bear almost all the apices transformed into spiked cones, that is, the shape peculiar to the propagules (cf. figs in Cecere & Perrone 2002).

DISCUSSION

Based on the above results, the terete species of *Acanthophora* (the taxon *inquirendum* *A. muscooides*, requiring a reinvestigation also supported by molecular analysis, excepted) can be divided into two groups as follows: (1) species with only monopodial growth (*A. aokii*, *A. ramulosa* and *A. dendroides*) and (2) species with both monopodial and sympodial growth patterns (*A. spicifera* and *A. nayadiformis*).

A monopodial growth pattern governs main axis development in all the species of *Acanthophora* starting from a rounded primordium. Such a type of primordium usually delays the production of the determinate branches typical of the genus, trichoblasts and spines, the latter originating adaxially from the basal cell of the trichoblasts. Therefore, the basal parts of both main axes and laterals arising from rounded primordia are usually spineless.

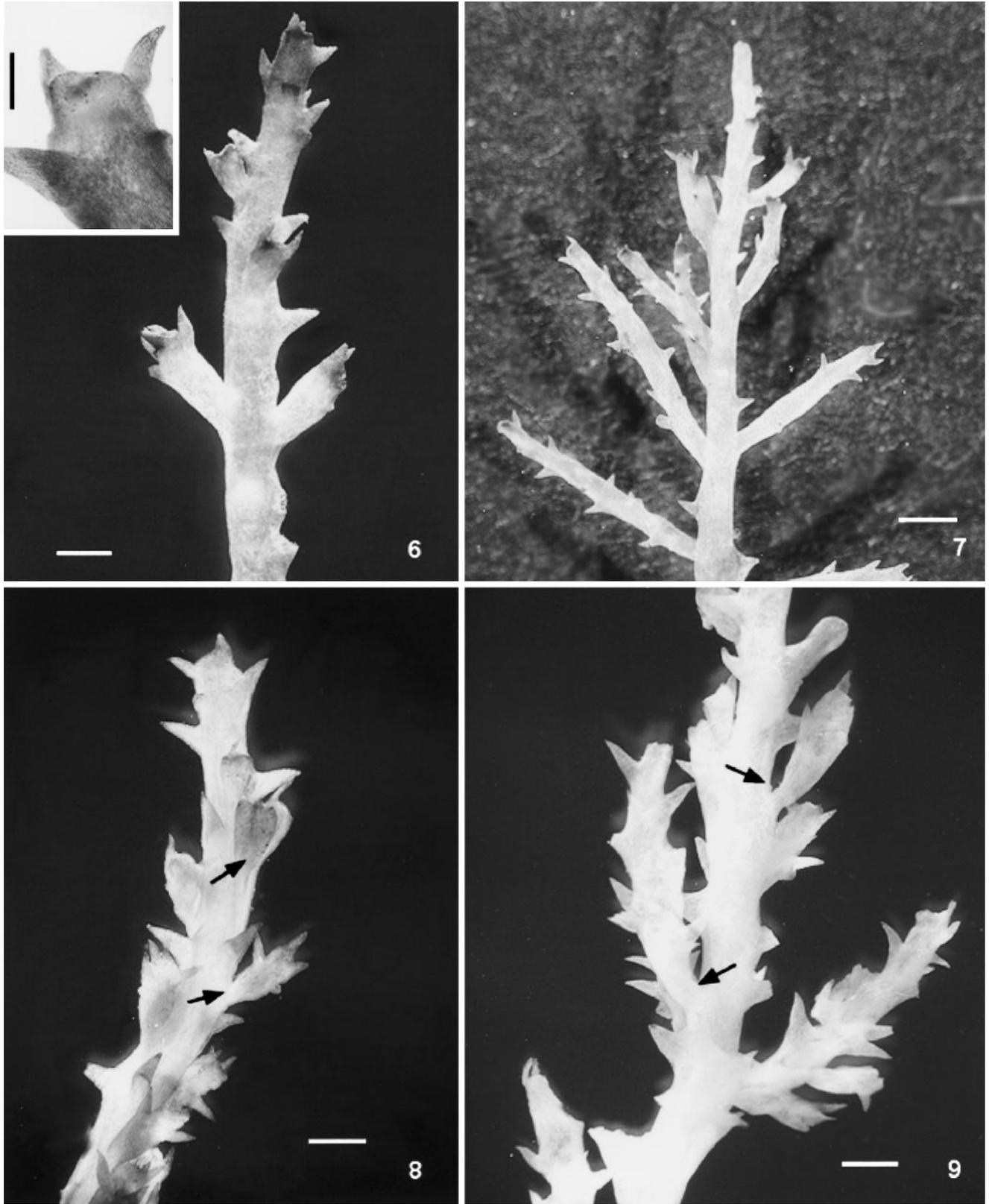
In particular, in *A. aoki* and *A. spicifera* (the latter generally considered as having spineless main axes) spines form very late and infrequently so that they occur only in the distal parts of well developed thalli.

Indeterminate laterals can grow according to either a monopodial or a sympodial pattern depending on the kind of primordium from which they are derived.

In all the species, first order laterals sprout as rounded primordia, not subtended by spines and growing as main axes do. Depending on the species, on the other hand, higher order laterals can originate from either rounded primordia, as in *A. dendroides*, *A. ramulosa* and *A. aokii*, or conical axillary primordia subtended by spines, as usually occurs in *A. nayadiformis* and also rarely in *A. spicifera*.

In *A. dendroides*, *A. ramulosa* and *A. aokii*, in which only the monopodial growth pattern and rounded primordia are present, main axes appear almost regularly spinous in their distal parts.

In contrast, in the other species where the growth pattern early shifts to the sympodial one (which can happen at any thallus level), both main axis and any order laterals arise from spiny primordia and therefore develop into ramisymphodia. In such cases, when ramisymphodia are well developed, the spines



Figs 6, 7. *Acanthophora ramulosa* (as *Chondria ramulosa*); L 939.6. . .124, HOLOTYPE.

Fig. 6. Distal part of a main axis. Note the rod-like apical zone. Scale bar = 600 μ m. In the frame (top left) the rounded terminal primordium. Scale bar = 250 μ m.

Fig. 7. Distal part of a plant with spaced first order laterals. Scale bar = 1.3 mm.

Figs 8, 9. *Acanthophora dendroides* (as *Acanthophora*); BM unnumbered sheet, specimen c, HOLOTYPE.

Fig. 8. Distal part of a main axis. Note the rod-like apical zone and the crowded arrangement of both spines and first order branches. Lateral branches are constricted at their bases (arrows). Scale bar = 2 mm.

Fig. 9. Branches of higher order: arrows indicate the constrictions at their bases. Scale bar = 2 mm.

bearing spiny primordia are far from the axes so that the main axes appear spineless, as usually occurs in *A. nayadiformis*, a species considered as having a spinous main axis (Cecere & Perrone 2002). Such a phenomenon can also be observed in some specimens of *A. spicifera*.

Our observations have also shown that in *Acanthophora* the gross morphology of the apical region of both main and lateral axes does not have the same characteristics in all the species. Usually, in *A. aokii* the apical zone looks like a turion, so that Okamura (1934) defined it as *Asparagus*-like. *Acanthophora spicifera* shows spadix-like apices; in contrast, *A. dendroides* and *A. ramulosa* have rod-like apical zones. In most plants of *A. nayadiformis* we observed rosette-like apices with numerous well developed pointed spines hiding the tip (apex of a ramisymphodium) (Cecere & Perrone 2002). Rarely, also *A. spicifera* bears rosette-like apical zones when the main axes grow as ramisymphodia.

As for the attachment system morphology, the observation of the type specimens of the *Acanthophora* species here studied led us to ascertain that in all of them it consists of stolons, which undergo extensive cortication becoming perennial rhizomes, as already described in *A. dendroides* (Jaasund 1976), *A. spicifera* and *A. pacifica* (Kraft 1979) and *A. nayadiformis* (Cecere & Perrone 2002). Hence, we can state that all the species of the genus are 'hémicryptophycées', according to the terminology proposed by Feldmann (1951) or decidueiphytes, according to V.J. Chapman & D.J. Chapman (1976).

On the basis of the above reported observations, we propose amending the genus *Acanthophora* as follows.

***Acanthophora* J.V. Lamouroux gen. emend.**

Thallus terete or flattened, cartilaginous in texture, attached to the substrate by means of clusters of multicellular branched rhizoids issuing from perennial creeping axes. Aged holdfasts consisting of thick rhizomatous bases resulting from stolon overcortication. Uprights more or less covered by spine-like branchlets arranged in a spiral pattern; main axis and first order branches monopodially growing from rounded primordia. Monopodially growing axes at first producing deciduous determinate monosiphonous branches (trichoblasts), then both determinate (spines) and indeterminate polysiphonous branches. Higher order branches either growing monopodially or sympodially, spines being able to produce ramisymphodia. In some species, the growth pattern of both main axis and laterals can shift from monopodial to sympodial at any level. On mature axes, stolons can be produced as adventitious branches from distinct primordia.

Dome-shaped apical cell either sunken in a pit or projecting in the primordia of monopodia. In the primordia of ramisymphodia the apical cell is hidden by overlapped spines. Polysiphonous axes with five pericentrals; outer cortex of axially elongated polygonal cells, inner cortex parenchymatous giving origin to two kinds of secondary multicellular rhizoidal filaments.

Diocious plants. Urceolate cystocarps, developed on the ventral side of the spines; club-shaped carpospores from gonimoblast filaments at first monopodially then sympodially branched. Flattened leaflet-like spermatangial sori developed from modified trichoblasts. Tetrahedrally divided tetrasporangia in whorls, in the apical parts of indeterminate laterals;

spinous or spineless tetrasporangial sori depending on the kind of primordium from which they arise.

The following considerations aim to draw up a key to the identification of the species of *Acanthophora* based on the results of the present study.

Because in some species both monopodial and sympodial growth can be observed on the same axis, the character 'presence vs absence of spines on the main axes', on which both the ancient and the recent distinction of the *Acanthophora* species were based, cannot any longer be considered as diagnostic.

In addition, another character, namely the morphology of the stichidial ramuli, historically used for distinguishing the species of *Acanthophora*, has no diagnostic significance in *A. nayadiformis*. In fact, in that species, a noticeable morphological variation of the so-called stichidia was described by Saracino *et al.* (1996). Later, Cecere & Perrone (2002) demonstrated that tetrasporic branches were indeterminate (so that they should not be considered stichidia), and that their morphology reflected both the origin and the development of the primordia from which they derived. Moreover, the present study showed that in *A. aokii*, *A. dendroides* and *A. ramulosa*, where only rounded primordia are present, tetrasporic branchlets are spineless or with few spines; in *A. spicifera* they are rarely spineless, usually spinous or very spinous, due to their origin from either terete, conical or spiny primordia, respectively. Therefore, because there is not a morphological type of tetrasporangial branchlet characteristic of each species of *Acanthophora*, tetrasporic ramuli cannot have a diagnostic value.

In conclusion, species identification should be mainly based on developmental features (monopodial vs sympodial growth pattern). Nevertheless, because such a character could be too complicated and thus leading to misinterpretations, in the following key other more easily detectable diacritic characters are added.

Key to the ascertained terete species of *Acanthophora*

1. Thallus with monopodial growth pattern only 2
1. Thallus growth shifting from monopodial to ramisymphodial pattern 4
2. *Asparagus*-like apical zone of both main axes and laterals, with widely spaced, minute lateral primordia; thallus fastigiate *A. aokii*
2. Rod-like apical zone with the apical cell in a sunken pit 3
3. Apical zone of both main axes and laterals with small, spaced spines; lateral branches slightly tapered at their base *A. ramulosa*
3. Apical zone of both main axes and laterals with a very large terminal primordium and closely arranged spines, very broad at their bases; branches constricted at their base *A. dendroides*
4. Spadix-like apical zone of main axes, with crowded lateral primordia; in lateral ramisymphodia (the so-called brachiblasts) the apical zones are rosette-like
. *A. spicifera*
4. Rosette-like apical zone of both main axes and laterals sympodially growing; apices attenuate in the few monopodially growing axes; summer–autumn plants bearing

apices of laterals transformed into typical spiked cone-shaped vegetative propagules *A. nayadiformis*

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