

Sponge–seaweed associations in species of *Ptilophora* (Gelidiaceae, Rhodophyta)

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SUMMARY

Sponge–seaweed associations in the seaweed genus *Ptilophora* are poorly understood; therefore, 94 specimens, representing all 17 species of *Ptilophora*, were examined to detail this phenomenon. All but 2 *Ptilophora* species were shown to produce surface proliferations, with 13 species found to have sponge associations. Evidence for facultative sponge epiphytism was found with species–specific interactions being unlikely. Results show that surface proliferations are not induced by sponge epiphytes, as they often occur in the absence of sponge epiphytes, and vice versa. The significant number of proliferate thalli found with sponge epiphytes suggests that there is a likely relationship between the presence of surface proliferations and sponge infestation. Sponge epiphytes and *Ptilophora* species appeared structurally related in that the sponge probably exploits a niche habitat provided by the alga, for which surface proliferations might aid the sponge in bonding to the alga.

Key words: Gelidiaceae, *Ptilophora*, Rhodophyta, South Africa, sponge–seaweed association, surface proliferations.

INTRODUCTION

Sponge–seaweed associations have been reported in detail for several seaweed genera (Vacelet 1981; Price *et al.* 1984; Scott *et al.* 1984; Rützler 1990; Price & Kraft 1991; Grant & Hinde 1999; Trautman 1999; Zea & Weerdt 1999; Trautman *et al.* 2000; Davy *et al.* 2002; Phillips 2002). Some associations form non-structural relationships where the seaweed grows endozoic in the sponge host. It is unlikely that the seaweed plays any structural role in the sponge architecture. Examples are *Audouinella spongicola* (Weber-van Bosse) Stegenga (Acrochaetiaceae) (Woelkerling & Womersley 1994; Stegenga *et al.* 1997) and *Ostreobium* cf. *constrictum* Lucas (Ostreobiaceae) (Rützler

1990). Both are microscopic and filamentous algae that grow embedded in *Mycale laxissima* Duchassaing and Michelotti (Mycalidae). Some sponge–seaweed associations form a structural relationship where the sponge is epiphytic on a seaweed host. In such cases the sponge might determine the overall shape of the association, for example, in the subtropical western Atlantic *Xytopsues osburnensis* George and Wilson (Phoriospongiidae), which reinforces its skeleton with fronds of an articulated coralline alga, *Jania capillacea* Harvey (Corallinaceae) (Rützler 1990). In other cases, the seaweed determines the overall shape of the association (Scott *et al.* 1984; Norris 1991; Womersley & Lewis 1994; Zea & Weerdt 1999; Phillips 2002). An example is the symbiosis between *Ceratodictyon spongiosum* Zanardini (Lomentariaceae) and *Haliclona cymiformis* Esper (Chalinidae) in the tropical Indo-Pacific region (Price *et al.* 1984; Norris 1987a; Price & Kraft 1991; Grant & Hinde 1999; Trautman 1999; Trautman *et al.* 2000; Davy *et al.* 2002). The alga has a stiff, branched thallus, which provides the underlying rigid skeletal structure of the association and determines its shape (Vacelet 1981).

To date, sponge–seaweed associations in the seaweed genus *Ptilophora* Kützling (Gelidiaceae, Rhodophyta) have only been noted (Papenfuss 1940; Norris 1987b, 1991, 1992). *Ptilophora* is a relatively small genus with 17 species currently recognized. It has an Indo-West Pacific distribution and occurs subtidally to more than 100 m. It is characterized by a large frond (generally 10–35 cm tall) with complanate branching and compressed or flattened blades (midribbed and alate in some species), which is attached to the substratum by a fibrous holdfast. Papenfuss (1940) confirmed that the hyaline bristles covering the thalli of 3 *Ptilophora* species, as noted by previous authors (Kützling 1847; Harvey 1855; Agardh 1876; Schmitz

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& Hauptfleisch 1897), were in fact spicules of an encrusting sponge. To date, this association has been reported in 4 *Ptilophora* species (Papenfuss 1940; Norris 1987b, 1991; Huisman 2000), although only the extensiveness of the sponge-coverings on seaweed thalli was described. Norris (1987b) maintains that there was a relationship between the presence of surface proliferations and epiphytic sponges in *Ptilophora*, having observed their co-occurrence in 3 species of the genus. He also speculates that the formation of surface proliferations was likely to be stimulated by the presence of the associated sponges. He further expounded this idea (Norris 1991) in a discussion on proliferations in *Osmundaria prolifera* Lamouroux (Rhodomelaceae), although it is pointed out by Phillips (2002) that this hypothesis has neither been tested experimentally, nor has a mechanism been suggested whereby the alga might be induced by the animal to produce proliferations.

Definition of terms and aims

In this research note, the term ‘sponge–seaweed association’ means the co-occurrence of these organisms where they grow attached to one another. The interaction between the sponge and seaweed is referred to as their ‘relationship’. The term ‘surface proliferations’, or merely ‘proliferations’, is used by Norris (1987b, 1991, 1992) and Phillips (2002) to refer to any short branch issuing from the surface of a flattened or compressed blade, such as that occur on the midribs or alae in *Ptilophora*. In the present study, the term is used in the same way.

The aims of this research note are:

- 1 To illustrate the range of surface-proliferation morphology in *Ptilophora* [the surface proliferations of 7 of the species are described in Tronchin *et al.* (2003), some illustrated, although the complete range in surface proliferation morphology in the genus is not documented, as these structures had not yet been found in the remaining species. A comprehensive understanding of the extent of production of these structures in *Ptilophora* is an essential first step in evaluating the relationship between sponge epiphytes and surface proliferations, and, in turn, furthering our understanding of sponge epiphytism in this genus].
- 2 To critically evaluate the hypothesis that there is a direct causal relationship between the presence of surface proliferations and the presence of sponge in species of *Ptilophora*.
- 3 To improve our understanding of the sponge–seaweed association in *Ptilophora* by determining how widespread the phenomenon is and categorizing the relationship between these organisms, in compari-

son to other reported cases of sponge–seaweed associations.

MATERIALS AND METHODS

In the present study, 94 specimens were examined representing all 17 *Ptilophora* species (Table 1). The extent to which surface proliferations and encrusting sponges occurred on the thalli was determined. Specimens were collected along the KwaZulu-Natal Province coastline (South Africa) between 1999 and 2002. Specimens were also loaned from local and international herbaria. Type specimens of 14 species were examined as well as specimens from several type localities. The majority of specimens studied were dry (pressed), although a few were wet (preserved in 5% formalin in seawater). The number of specimens observed for each species varied because of their availability (some species are only known from type collections).

Specimens were categorized into four classes depending on the presence or absence of surface proliferations and sponge epiphytes. A χ^2 goodness of fit was performed on the data to test the null hypothesis that sponge epiphytes are as likely to occur on proliferate thalli as on non-proliferate thalli. Observations were made using a Wild M400 stereo dissecting photomicroscope and photos were taken with an Olympus Camedia digital camera.

Transverse sections were cut from pressed specimens of *Ptilophora diversifolia* (Suhr) Papenfuss, *Ptilophora spissa* (Suhr) Kützing and *Ptilophora copejansii* Tronchin et De Clerck, stained with 1% aniline blue stain and preserved in a 50% Karo solution. From these, the physical integrity of the interface between sponge epiphyte and seaweed cortex was examined. Photos were taken with an Olympus DP50 digital camera mounted on a Leitz Diaplan compound microscope.

Sponge epiphytes were identified from 4 species of *Ptilophora*. Fragments of sponge containing ectosomes (unicellular surface layer of sponges) and choanosomes (all organic sponge matter bounded by the ectosome) were cut from voucher specimens. Histological sections were prepared according to the protocol set out for sectioning sponges in Hooper (1996).

RESULTS

Almost all *Ptilophora* species were found to produce surface proliferations with a variety of morphologies (Table 2) ranging from simple cylinders (Fig. 1) to ligulate, subcylindrical or flattened proliferations (Fig. 2), often with tripartite apices and occasionally becoming pinnately branched to varying degrees (Fig. 3). *P. diversifolia* and *P. spissa* were similar in producing scale-like proliferations. In *P. diversifolia* these were

Table 1. Details of specimens of 15 species of *Ptilophora* observed in the present study

Species	Total number of specimens observed	Origin of specimens observed	Specimen collection locations
<i>Ptilophora biserrata</i> (Børgesen) Norrist†	4	C	Mauritius
<i>Ptilophora copejansii</i> Tronchin et De Clerck†	4	BOL, GENT	South Africa
<i>Ptilophora diversifolia</i> (Suhr) Papenfuss	9	BOL, F.C., GENT	South Africa
<i>Ptilophora helenae</i> (Dickinson) Norris	6	GRA, BOL	South Africa
<i>Ptilophora hildebrandtii</i> (Hauck) Norrist†	11	BOL, GENT, L	South Africa, Kenya
<i>Ptilophora irregularis</i> (Akatsuka and Masaki) Norrist†	6	TNS	Japan
<i>Ptilophora leliaertii</i> Tronchin et De Clerck†	10	BOL, GENT, GRA	South Africa
<i>Ptilophora mediterranea</i> (H. Huvé) Norrist†	1	P	Greece
<i>Ptilophora pectinata</i> (A. et E. S. Gepp) Norrist†	4	BM, F.C., GRA	Australia
<i>Ptilophora pinnatifida</i> J. Agardh†	11	BOL, F.C., GENT, LD	South Africa
<i>Ptilophora prolifera</i> (Harvey) J. Agardh†	13	F.C., MELU	Australia
<i>Ptilophora pterocladoides</i> Andriamampandry†	2	P	Madagascar
<i>Ptilophora rhodoptera</i> Norrist†	3	F.C., GENT, NU	South Africa
<i>Ptilophora rumpii</i> (Dickinson) Norrist†	2	BM, NU	South Africa
<i>Ptilophora scalaramosa</i> (Kraft) Norrist†	2	MELU, F.C.	Philippines
<i>Ptilophora spissa</i> (Suhr) Kützing†	1	W	South Africa
<i>Ptilophora subcostata</i> (Okamura ex Schmitz) Norris	6	LD, S,	Japan

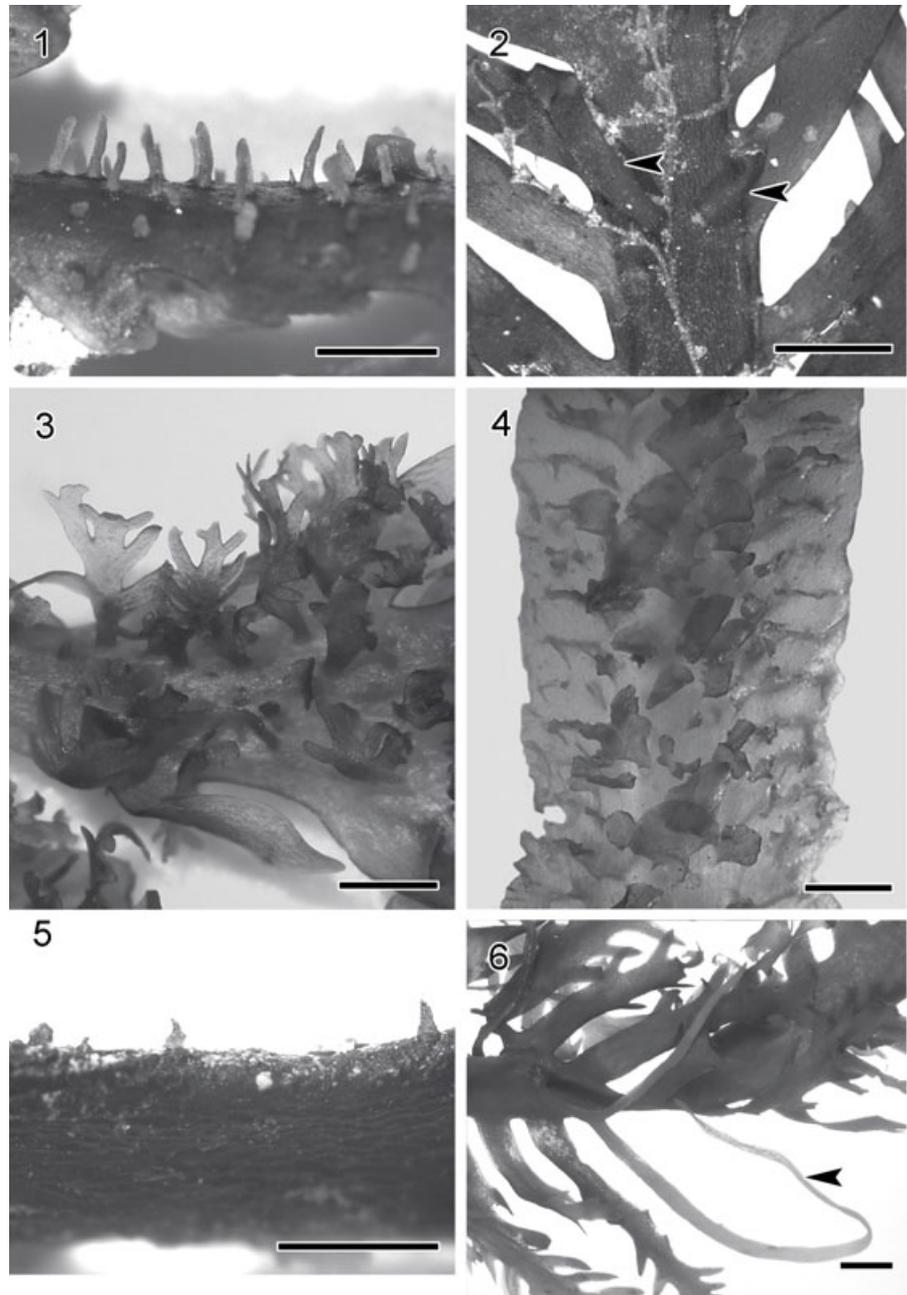
†Type specimens were observed. F.C., personal field collections including specimens collected worldwide by D.W. Freshwater. Herbarium codes: BM, The Natural History Museum, England; BOL, University of Cape Town, South Africa; C, University of Copenhagen, Denmark; GENT, University of Gent, Belgium; GRA, Albany Museum, South Africa; L, Nationaal Herbarium Nederland, Leiden University branch, Netherlands; LD, Botanical Museum (Lund), Sweden; MELU, University of Melbourne, Australia; NU, University of Kwazulu-Natal, South Africa; P, Muséum National d'Histoire Naturelle (Paris), France; S, Swedish Museum of Natural History (Stockholm), Sweden; TNS, National Science Museum (Tokyo), Japan; W, Naturhistorisches Museum Wien, Austria.

Table 2. The extent of surface proliferations (SP) and sponge epiphytes on the surface of fronds of 17 *Ptilophora* species, and the type of SP produced by each species

Species	Produces SP	Figure number illustrating type of SP produced	Number of specimens with both SP and sponges‡	Number of specimens with sponges and no SP	Number of specimens with SP and no sponges	Number of specimens with neither SP nor sponges	Specimens always with <10% sponge epiphyte cover
<i>Ptilophora biserrata</i> (Børgesen) Norris	✓	2	3 (3)	1			✓
<i>Ptilophora diversifolia</i> (Suhr) Papenfuss	✓	1, 2, 4	7 (3)		2		
<i>Ptilophora copejansii</i> Tronchin et De Clerck†	✓	1–3	4 (1)				
<i>Ptilophora helenae</i> (Dickinson) Norris	✓	2, 3	1		5		✓
<i>Ptilophora hildebrandtii</i> (Hauck) Norris	✓	1–3	5 (4)	1	5		
<i>Ptilophora irregularis</i> (Akatsuka and Masaki) Norris	✓	2, 3, 6			3	3	
<i>Ptilophora leliaertii</i> Tronchin et De Clerck†	✓	1–3, 6	4 (3)	6			
<i>Ptilophora mediterranea</i> (H. Huvé) Norris		n/a				1	
<i>Ptilophora pinnatifida</i> J. Agardh	✓	1–3	3 (3)	1	2	5	
<i>Ptilophora prolifera</i> (Harvey) J. Agardh	✓	1–3	10 (9)		1	2	
<i>Ptilophora pterocladoides</i> Andriamampandry	✓	2	1			1	✓
<i>Ptilophora pectinata</i> (A. et E. S. Gepp) Norris		n/a				3	✓
<i>Ptilophora rhodoptera</i> Norris	✓	1,2	3 (1)				
<i>Ptilophora rumpii</i> (Dickinson) Norris	✓	2,3	1 (1)	1			✓
<i>Ptilophora scalaramosa</i> (Kraft) Norris	✓	5, 6			2		
<i>Ptilophora spissa</i> (Suhr) Kützing	✓	1, 2, 4	1 (1)				
<i>Ptilophora subcostata</i> (Okamura ex Schmitz) Norris	✓	3, 6	1	1	1	3	✓
Totals for species	15		13	6	8	7	6

†*Ptilophora copejansii* and *Ptilophora leliaertii* were referred to as *Ptilophora* sp. and *Beckerella* sp., respectively, in Tronchin *et al.* (2003). ‡Numbers in brackets indicate the number of these specimens that produced surface proliferations in regions of the thallus that were not encrusted by sponge.

Figs 1–6. 1. Marginal view of flattened branch of *Ptilophora prolifera* with short cylindrical proliferation issuing from the convex surface. Scale = 1 mm. 2. Ligulate proliferations issuing from the midrib of *Ptilophora hildebrandtii*. Scale = 1 mm. 3. Pinnately branched proliferations borne on the surface of a distal branch of *Ptilophora prolifera*. Scale = 1 mm. 4. Scale-like, flattened surface proliferations issuing from the midrib of *Ptilophora diversifolia*. These develop on the ala as well but are often eroded, leaving a marginal series of parallel ridges as shown here. Scale = 1 mm. 5. Marginal view of the lower axis of *Ptilophora scalaramosa* from which minute spurs are borne, which are probably the primordia of adventitious rhizoids. Scale = 1 mm. 6. Basally branched adventitious rhizoid (arrowhead) issuing from the surface of a major branch of *Ptilophora scalaramosa*. Scale = 1 mm.



sometimes eroded, leaving a series of parallel ridges on the alae adjacent to the blade margins (Fig. 4). In a few species, surface proliferations were rhizoidal in nature, either minute spurs (Fig. 5), probably representing rhizoid primordia, or long, relatively unbranched and lightly pigmented outgrowths (Fig. 6). Surface proliferations are present but have not been previously reported for *Ptilophora biserrata* (Børgesen) Norris, *Ptilophora helenae* (Dickinson) Norris, *Ptilophora irregularis* (Akatsuka and Masaki) Norris, *Ptilophora pterocladoides* Andriamampandry, *Ptilophora rumpii* (Dickinson) Norris and *Ptilophora subcostata* (Okamura ex Schmitz) Norris. The surface proliferations

in *P. irregularis* and *P. subcostata* occurred on the proximal part of the axis and, except for a few adventitious determinate branches, were all rhizoidal in nature. *P. biserrata* and *P. pterocladoides* produced surface proliferations very infrequently (e.g. three on one plant) and only a few surface proliferations were found scattered on major branches in *P. rumpii*. *P. helenae* had a few surface proliferations issuing from the midrib (mostly on the proximal axis) and from sites of injury (circular recesses) on the midrib. Although the surface proliferations of some of the species were similar, the morphology of these structures was not found to be species specific.

Because of the non-standardized number of specimens examined for each species, the numbers scored in Table 2 merely indicate the occurrence of surface proliferations and sponge in those species rather than statistical significances. Thirteen species produced both surface proliferations and sponge associations, some consistently but others occasionally (Table 2). The χ^2 test performed on the data found significantly more sponge epiphytes on proliferate thalli ($P < 0.0001$). Sponge epiphytes were generally bonded to the surface proliferations and the blade surface in the interstices between surface proliferations (Fig. 7). However, surface proliferations sometimes developed in parts of the seaweed thallus without a sponge, and vice versa. The broad-bladed *Ptilophora rhodoptera* Norris was particularly notable in this respect because it bore very few surface proliferations but was almost entirely covered in a thin layer of sponge. Sponges were found to be bonded comparatively weakly in non-proliferating parts of specimens, especially on cylindrical axes, as they could easily be removed whole without damaging the sponge.

Some specimens had sponge epiphytes but completely lacked surface proliferations, and vice versa. All sponge-encrusted specimens had normal pigmentation regardless of the thickness of the sponge cover and surface or lateral proliferations bearing fertile structures were noted to always extend beyond the sponge cover. Six species had only a minor sponge association with never more than 10% of their thalli covered (Table 2). All 6 were similar in producing surface proliferations relatively infrequently on any single thallus and having narrow blades or pinnae.

Two specimens of *P. copejansii* were completely enveloped in a sponge except for some distal branch ends, which served in the identification of the specimens (Fig. 9). The sponge was carefully removed from a basal portion of the frond to reveal the underlying seaweed thallus, which had an aberrant morphology (Fig. 11). Lateral branches were closely spaced and covered in tufts of pinnate or digitate surface proliferations. The branching pattern was irregular and in two planes rather than one. Some lateral branches were fine and subcylindrical rather than flattened, whereas others had abnormally broad, contoured and abruptly terminated apices. Reticulating lateral proliferations were also produced (Fig. 10). A formalin-preserved specimen was bleached and viewed against strong backlighting to see the underlying seaweed thallus through its sponge encrustation. The ends of distal branches were observed to have the normal branch morphology (proliferations absent; pinnae flattened, <3 mm long, <1.3 mm apart) and branching pattern of this species (Fig. 9). A specimen of *Ptilophora Ieliaertii* Tronchin et De Clerck was found with an aberrant morphology similar to that observed in *P. copejansii*, with fine, retic-

ulating lateral proliferations (Fig. 8), but it altogether lacked a sponge epiphyte.

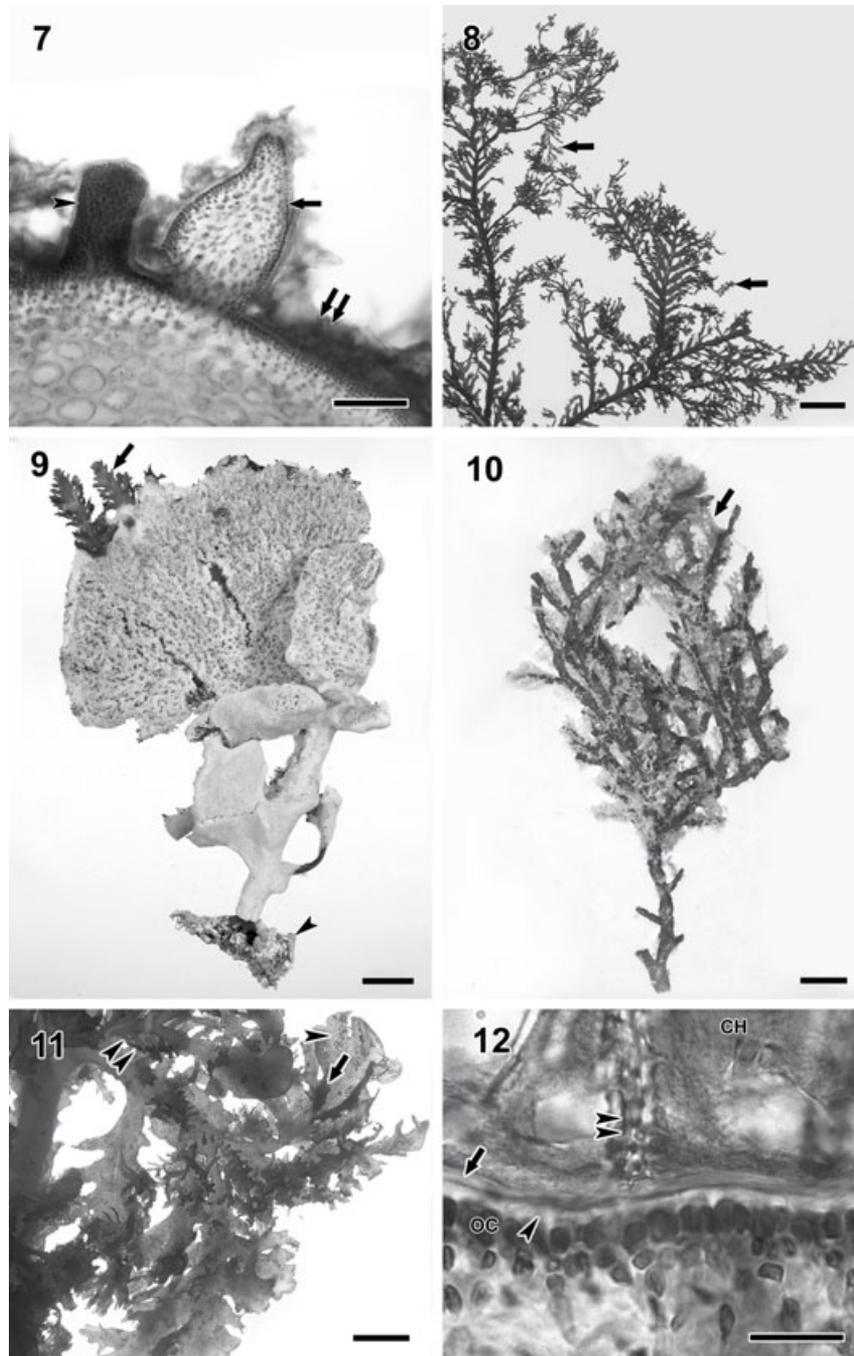
In transverse sections of sponge-encrusted seaweed branches, the interface of the association showed no sign of interpenetration (Fig. 12). The cuticle surrounding the seaweed cortex was always intact and merely covered by sponge.

Eight sponge species in seven genera were identified growing epiphytically on 4 species of *Ptilophora*, with up to 3 sponge species on the same specimen of *P. diversifolia* and 2 species on the same specimen of *P. copejansii* (Table 3). *Halichondria* cf. *panicea* Pallas (Halichondriidae) and *Ophlitaspongia* sp. (Microcioniidae) were found on specimens of *P. diversifolia* and *P. copejansii*.

DISCUSSION

The presence or absence of surface proliferations has had implications for the taxonomy of *Ptilophora* species historically. Eleven species of *Ptilophora* were formerly classified in the genus *Beckerella* Kylin because of the absence of surface proliferations in these species. However, the present study reports the production of surface proliferations in all but two species in the genus. Undoubtedly, these structures in many of the species went unnoticed by previous researchers as they sometimes occur infrequently (as in *Ptilophora hildebrandtii* [Hauck] Norris), are exceedingly small and inconspicuous (such as the spur-like rhizoid primordia in *Ptilophora scalaramosa* [Kraft] Norris), and differ significantly in shape (like the adventitious rhizoids of *P. scalaramosa*) from the obvious and numerous proliferations of *P. diversifolia*, *Ptilophora prolifera* (Harvey) J. Agardh and *P. spissa*. Norris (1987b) merged *Beckerella* and *Ptilophora* after having found these structures concealed beneath a sponge encrustation in a specimen of the type species of *Beckerella* (a decision recently supported on molecular and morphological grounds by Tronchin *et al.* 2003). Considering that all 3 species ascribed to *Ptilophora* at that stage produced numerous, obvious surface proliferations and were commonly associated with sponge epiphytes, it is not surprising that Norris (1987b) hypothesized that proliferations and sponge epiphytes were causally linked. In the present study, surface proliferations produced by *Ptilophora* species were found to retained a structure resembling either a rhizoid or lateral branch, unlike the irregularly contoured excrescences of *Thamnoclonium dichotomum* (J. Agardh) J. Agardh, a species consistently associated with an epiphytic sponge.

The majority of *Ptilophora* species are commonly found with sponge epiphytes. This phenomenon is most noticeable in the species occurring along the east coast of South Africa and south-western Australia. This could



Figs 7–12. 7. Transverse section through the midrib of a lateral branch of *Ptilophora diversifolia* coated in a sponge epiphyte (double arrows). The section cuts longitudinally through a surface proliferation (single arrow) and a second proliferation lies in the background (arrowhead). Scale = 100 μm . 8. Distal branches of *Ptilophora leliaertii* bearing narrow, reticulating lateral proliferations (arrow). Scale = 1 cm. 9. Sponge-encrusted *Ptilophora copepejansii* specimen where sponge epiphyte forms a fan uniting the branches of the underlying seaweed thallus. Un-encrusted distal branch ends have the normal branch morphology (arrow). The holdfast (arrowhead) is encrusted in sand. Scale = 1 cm. 10. Reticulating lateral proliferation of a specimen of *Ptilophora copepejansii* enveloped in sponge. Most of the sponge covering was removed although some still remains between branches (arrow). Scale = 1 mm. 11. Specimen of *Ptilophora copepejansii* with thick sponge cover removed. Sponge spicules remain in places (arrowhead). Surface proliferations issue frequently from branches, and digitate or pinnate proliferations might sometimes occur in tufts (single arrow). Fine, prolific and subcylindrical branches often present (double arrowheads). Scale = 3 mm. 12. Detail of the sponge–seaweed interface in transverse section of a sponge-encrusted branch of *Ptilophora diversifolia*. Spiny spicules called Acanthostyles (double arrowhead) are arranged perpendicularly to the surface of the algae within the choanosome (CH) of the sponge. There is no sign of disruption to or interpenetration of the outer cortex (OC) of the alga, and the cuticle (single arrowhead) is intact. A band of spongin fibres (arrow) bonds the sponge to the seaweed's surface. Scale = 20 μm .

Table 3. List of sponge epiphytes on four species of *Ptilophora*

Species of <i>Ptilophora</i>	Specimen collection location	Sponge epiphyte
<i>Ptilophora diversifolia</i> (Suhr) Papenfuss (specimen 1)	Protea Banks, South Africa	<i>Tedinia</i> (<i>Tedania</i>) sp. (Tedaniidae)
<i>Ptilophora diversifolia</i> (specimen 2)	Protea Banks, South Africa	<i>Halichondria</i> cf. <i>panicea</i> Pallas (Halichondriidae)
		<i>Ophlitaspongia</i> sp. (Microcionidae)
<i>Ptilophora pinnatifida</i> J. Agardh	The Kowie, South Africa	<i>Myxilla</i> (<i>Myxilla</i>) <i>simplex</i> Baer (Myxillidae)
<i>Ptilophora prolifera</i> (Harvey) J. Agardh	Penguin Island, Australia	<i>Tedinia</i> (<i>Tedania</i>) <i>anhelans</i> Lieberkuhn (Tedaniidae)
<i>Ptilophora copejansii</i> Tronchin et De Clerck (specimen 1)	Protea Banks, South Africa	<i>Isodictya</i> cf. <i>multiformis</i> Stephens (Isodictyidae)
<i>Ptilophora copejansii</i> (specimen 2)	Protea Banks, South Africa	<i>Mycale</i> (<i>Mycale</i>) sp. (Mycaliidae)
		<i>Haliclona</i> (<i>Gellius</i>) sp. (Chaliniidae)
<i>Ptilophora copejansii</i> (specimen 2)	Protea Banks, South Africa	<i>Halichondria</i> cf. <i>panicea</i> Pallas (Halichondriidae)
		<i>Ophlitaspongia</i> sp. (Microcionidae).

be related to the distributions of the sponge epiphytes, although they are not known at present.

This sponge–seaweed association does not appear to be species-specific, for either organism, because two sponge species were found growing together on more than one species of *Ptilophora*. This is in contrast to the obligate *Ceratodictyon spongiosum*–*Haliclona cymiformis* association, which has been shown to involve a species-specific chemical interaction in which nutrients are exchanged (Grant & Hinde 1999; Davy *et al.* 2002).

In species of *Ptilophora*, the occurrence of sponge epiphytes in the absence of surface proliferations, and vice versa, strongly suggests that there is no direct causal relationship between surface proliferations and the presence of epiphytic sponges. Phillips (2002) comments on the unlikelihood that proliferations in *Epiglossum smithae* (J. D. Hooker et Harvey) Kützing (Rhodomelaceae), a large frondose seaweed, are induced by sponge epiphytism as basal non-proliferate blades are usually present. Furthermore, in the present study, the sponge–seaweed interface (on or near proliferations) showed no signs of disruption, in keeping with the results of ultrastructural investigations of the interface of similar host–epiphyte associations in *Thamnoclonium* Kützing (Halymeniaceae), *Codiophyllum* Gray (Halymeniaceae) (Scott *et al.* 1984), *E. smithae* and *O. prolifera* (Phillips 2002).

There does appear, however, to be a relationship between the presence of surface proliferations and associated sponges, also noted by Norris (1987b) for a significant number of proliferate thalli in several diverse groups of red seaweed consistently associated with sponge epiphytes. It is likely that sponges exploit a niche habitat provided by the seaweed, surface proliferations enabling them to bond well and to resist removal by water movement. This was suggested as the reason for sponge growth on *Codiophyllum* and *Thamnoclonium* by Scott *et al.* (1984) and could also be true for the associations in *C. spongiosum* (Price & Kraft

1991), *E. smithae* and *O. prolifera* (Phillips 2002). *Codiophyllum* and *C. spongiosum* produce networks of anastomosing filiform laterals and branches, respectively, which create compartments that the sponge fills. *E. smithae* and *O. prolifera* produce dense, morphologically distinct proliferations (Norris 1991; Phillips 2002) analogous to the irregularly contoured excrescences produced by *T. dichotomum*. It appears that sponges bond relatively weakly to cylindrical non-proliferate axes in plants of some *Ptilophora* species, as Scott *et al.* (1984) found in their study on *T. dichotomum*.

In the present study, 2 specimens of *P. copejansii* had very aberrant morphology in parts of the thallus that were totally enveloped by a sponge, whereas the parts of the seaweed thallus that were sponge-free had a normal morphology. However, younger distal regions of these seaweed thalli that were thickly encrusted with sponge appeared normal and lacked surface proliferations. Similarly, in southern Australia, the flattened non-proliferate blades of *Carpopeltis spongeaplexus* Womersley et J. A. Lewis are free from protrusions or excrescence but are almost entirely covered by a thick sponge encrustation (Scott *et al.* 1984; Womersley & Lewis 1994). Taking the above into consideration and the fact that a similar aberrant morphology was found in a drift specimen of *P. leliaertii* devoid of sponge, it seems more likely that the aberrant morphologies were produced by an undetermined environmental factor prior to the development of a sponge encrustation.

Species of *Ptilophora* and epiphytic sponges are structurally related: the seaweed dictates the shape of the association and the sponge develops epiphytically, producing small patchy encrustations to completely envelope the seaweed. Given that sponge encrusted specimens generally retained the usual overall appearance of un-encrusted specimens, disadvantages caused by sponge epiphytism to growth in the seaweed, were not obvious.

Considering the scarcity of surface proliferations and extensive sponge epiphyte cover in the broad-bladed *P. rhodoptera*, as well as the minor sponge associations in several narrow-bladed species, there might also be a relationship between the presence and extensiveness of sponge epiphyte cover and the breadths of the host blades. Species that produce narrow blades (e.g. *P. biserrata*, *P. helenae*, *P. hildebrandtii*, *P. irregularis*, *Ptilophora pectinata* [A. et E. S. Gepp] Norris, *P. pterocladoides*, *P. scalaramosa* and *P. subcostata*) that are generally under 3 mm wide, provide less surface area for sponge establishment than species with blades often between 4 and 7 mm wide (e.g. *P. diversifolia*, *Ptilophora pinnatifida* J. Agardh, *P. prolifera*, and *P. rhodoptera*). *P. leliaertii* is particularly interesting in this respect, because despite the fact that this species has fairly narrow (<2.5 mm) fronds, the concave profiles of the branches appear to provide a protective habitat for sponge epiphytes. Such morphology apparently also favors sponge attachment to the smooth frond of the Western Australian *Curdia irvineae* J. Agardh (Gracilariales) (Womersley 1996).

In the *Haliclona (Haliclona) epiphytica* Zea et Weerdt (Chalinidae)/*Laurencia poiteaui* (Lamouroux) Howe (Rhodomelaceae) association, which is abundant in wave-surge areas (Zea & Weerdt 1999; Littler & Littler 2000), the alga lacks structural modifications likely to aid in sponge bonding, suggesting that other factors might also be responsible for the pairing. In the case of *Ptilophora*, these erect, complanate seaweeds, often growing in turbid and rapidly moving water, would seem to provide an optimal substratum for a filter-feeding organism to occupy by virtue of their location. On Protea Banks, a deep offshore reef on the east coast of South Africa, *Codiophyllum natalense* (Gray), *P. copejansii*, *P. diversifolia*, *P. leliaertii*, *P. pinnatifida*, *P. rhodoptera* and *T. dichotomum*, all readily form sponge associations. Here, these seaweeds grow on open reef flats, their thalli extending upwards into the water column, periodically exposed to a strong prevailing current. The water is often turbid and carries organic particles from the numerous nearby estuaries. It is perhaps not surprising then that these species also have relatively robust and rigid holdfasts and primary axes that can offer some resistance to the flow of current and stand the increased drag conferred by the sponge epiphyte.

The present study seriously questions the suggestion of Norris (1987b) that surface proliferations in many macroalgae are caused by epiphytic sponges. However, in view of the inconsistent production of these structures in *Ptilophora* species, Norris is correct in concluding that the presence or absence of surface proliferations is taxonomically uninformative for distinguishing between otherwise anatomically similar genera in the Gelidiales. Considering the overlap of surface proliferation characteristics between species (Table 2),

these structures are also uninformative for classifying species.

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