Cnidogenesis in the jewel anemone *Corynactis californica* (Carlgren, 1936) and *C. viridis* (Allman, 1846) (Anthozoa: Corallimorpharia)

E.A. Robson

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E.A. Robson, School of Animal & Microbial Sciences, The University of Reading, P.O. Box 228, Reading RG6 6AJ, UK (e-mail: e.a.robson@reading.ac.uk).

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Precursor stages of large holotrichs in the mesenterial filaments of *Corynactis californica* and *C.viridis* have been visualised by simple methods using stained whole-mount preparations. Samples were taken from mesenterial filaments emitted during aggressive behaviour (which is reported for the first time in *C. viridis*). Results suggest that in natural conditions localised stimuli may provoke discharge along short stretches of mesenterial filament, followed by localised recruitment within these depleted areas.

Introduction

Stinging capsules or cnidae (Gosse, 1860) are a hallmark of the phylum Cnidaria. They play an important role in behaviour such as prey capture, aggression and locomotion. Control of their discharge by the cnidocyte and associated cellular elements is the subject of active research (Hessinger & Lenhoff, 1988; Watson & Mire-Thibodeaux, 1994; Watson & Mire, 2004; Holtmann & Thurm, 2001a, b; Thurm et al., 2004; Ozakmak et al., 2001; Westfall et al., 2002; Westfall, 2004; Kass-Simon & Scappaticci, 2002; 2004).

Each nematocyst is secreted by a nematoblast which matures into an epithelial nematocyte. The capsule contains a tubule, usually barbed, which everts on discharge, and capsular fluid. New research on *Hydra* spp. is revealing the molecular composition of these functional components as well as their role during the complex process of differentiation within the cell (Koch et al., 1998; Engel et al., 2001; Szepanek et al., 2002; Engel et al., 2002; Özbek et al., 2004). Current work on other Cnidaria (Engel et al., 2002) suggests a common molecular basis for nematocyst structure and this will furnish further clues about the genetic determination of cnidae.

This short contribution considers the supply and replacement of nematocysts in the tissues of anemones and corals (cf. Robson, 1988). Although the cellular pathways involved in cnidogenesis have not yet been clarified in Anthozoa it is assumed here that they are probably similar in different groups of anemones and corals. K.A. Möbius (1866: 3) described the situation succinctly: "A few figures may show that exhaustion of the supply of stinging capsules is not in the least to be imagined. The common North Sea red anemone (= *Actinia equina*) has in one tentacle of average size more than 4 million mature stinging capsules and in all its tentacles together at least 500 million. One tentacle of the splendid velvet-green anemone (= *Anemonia viridis*) contains over 43 million stinging capsules: thus an animal with 150 tentacles possesses the huge stock of 6450 million. And underneath the mature (ones) situated ready on the tentacles, a

younger generation is everywhere at hand, which can quickly replace the capsules used up". The question to be addressed is how this happens in anemones and corals.

Möbius' research (1866) "On the Structure, Mechanism and Development of the Stinging Capsules of some Polyps and Jellyfish" includes remarkably accurate observations. From details given the numerical aperture of his immersion objective was probably 1.0 or higher (Bradbury, 1967). Tardent (1988) drew attention to this fine paper, which depicts eversion of the tubule and shaft in discharging and discharged nematocysts of the solitary coral *Caryophyllia smithii,* and of the anemones *Corynactis viridis* and *Sagartia elegans.* Cnidoblasts from the tentacles of these species and others are illustrated. A section through tentacle ectoderm of *S. elegans* (Taf. 1 (1)) shows the serial development of cnidoblasts in the basal zone of the ectoderm, where they fill the space beneath closely packed distal cnidae.

Möbius (1866) examined material from a wide range of live aquarium specimens. He cites the following Anthozoa: corals *C. smithii* and *Balanophyllia regia;* the corallimorpharian *C. viridis*; the actiniarians *S. elegans, A. equina, A. viridis, Urticina felina, Calliactis parasitica, Sagartiogeton undata, Anthopleura ballii* and probably *Halcampa duodecimcirrata* (nomenclature updated as in Stephenson (1935) and Manuel (1981)), also *Cerianthus lloydii;* and these Hydrozoa: *Hydra vulgaris, Hydractinia* sp., and *Sarsia tubulosa;* and among the Scyphozoa, polyps of *Cyanea capillata, Lucernaria quadricornis* and *Haliclystus auricula.* He sampled tentacles, mesenterial filaments and acontia, probably using scissors, and with a needle and lancet transferred tissues from seawater to glass slides. Little is said about his methods of preparation but some of the nematoblasts and nematocytes he observed live (Möbius, 1866: Taf. 2 (10-52)) are shown after fixation (Taf. 2 (7-9)). Most of Möbius' observations are still accurate and useful.

Electron microscopy of young *Metridium senile* tentacles (Actiniaria) (Westfall, 1960) supports Möbius' suggestion (1866) that cnidoblasts differentiate beneath the mature cnidocytes (i.e., not at the surface of the epithelium). Research on *Haliplanella luciae* has confirmed this in acontia (Yanagita & Wada, 1959); in tentacles (Watson & Mariscal, 1983b); and in tentacles, mesenterial filaments and acontia (L. Minasian in Fautin & Mariscal, 1991). Changes in the cnidom of anthozoans which develop specialised tentacles as a result of aggressive interactions are well documented (*Rhodactis sanctithomae*, *Montastrea cavernata* (den Hartog, 1977); *H. luciae* (Watson & Mariscal, 1983a); *Galaxea fascicularis* (Hidaka et al., 1987); *Antipathes fjordensis* (Goldberg et al., 1990); *Rhodactis rhodostoma* (Langmead & Chadwick-Furman, 1999a, b)). As yet, however, the dynamics of cnidoblast populations *in situ* have been considered only by Yanagita & Wada (1959: preliminary experiments) and by Watson & Mariscal (1983a, b).

Factors which control the size of cnidae in Anthozoa are not well understood. The large nematocysts of the cup coral *C. smithii* and the jewel anemone *C. viridis* (in Allman, 1846) were described by Gosse (1853, 1860) and his observations led Möbius to examine the same material. Among Anthozoa the largest cnidae (100-300 µm) occur in mesenterial filaments or tentacles of Corallimorpharia (Weill, 1934; den Hartog, 1980; Dunn & Hamner, 1980; den Hartog et al., 1993) and of some Scleractinia (Weill, 1934; Thomason & Brown, 1986; Pires, 1997). Large nematocysts discharge more slowly than small ones (Gotknecht & Tardent, 1988; Tardent et al., 1990; Thomason, 1991; also Weill, 1961). In natural habitats they are associated with pronounced toxic effects.

Corallimorpharian anemones resemble scleractinians in many respects (Gosse, 1853; den Hartog, 1980; Pires & Castro, 1997; Fautin et al., 2002; Daly et al., 2003). Their

mesenterial filaments perform similar functions and are broadly similar in structure, having a median cnidoglandular tract (Duerden, 1900, 1902). All such filaments are specialised tissues of some complexity (Goldberg, 2002a, b). In reef corals they effect digestion both inside and outside the coelenteron, being extruded from the mouth and other apertures and later withdrawn (Lang & Chornesky, 1990; Ferriz-Dominguez & Horta-Puga, 2001; cf. Goldberg, 2002a). In some corals they also are agents of interspecific aggression, the discharge of cnidae and of digestive enzymes being evoked by contact with foreign tissues. Corallimorpharians similarly may extrude mesenterial filaments in feeding (*Corynactis californica* (Chadwick, 1987), *Rhodactis howesii* (Hamner & Dunn, 1980)). Feeding activators which cause mouth opening and extrusion of filaments in corals elicit the same behaviour in *Discosoma* (= *Rhodactis*) *sanctithomae* (Mariscal & Lenhoff, 1968; Elliott & Cook, 1989). Mesenterial filaments are emitted by *C. californica* (Chadwick, 1987), *D. sanctithomae* (Miles, 1991) and *Rhodactis rhodostoma* (B.L. Kuguru, cited in Muhando et al., 2002) in response to aggressors.

In natural habitats corallimorpharians usually hold their own, competing successfully for space (Chadwick, 1987; 1991; Chadwick & Adams, 1991; Rossi & Snyder, 1991). *Corynactis spp*. are avoided by mobile predators (*C. californica* (Waters, 1973; Wolfson et al., 1979; Annett & Pierotti, 1984; Patton et al., 1991), *C. viridis* (Edmunds et al., 1974, 1976; but see den Hartog et al., 1993)).

Actiniarian anemones do not extrude their mesenterial filaments. In the Acontiaria they are prolonged aborally into long "stinging threads" or acontia (Gosse, 1860) which are emitted as weapons of aggression (*M. senile* (Brodrick, 1859)) or defence (*C. parasitica, Adamsia palliata* (Ross, 1971, 1984)). Acontia offer a ready source of cnidocytes and cnidae for experimental purposes (e.g. Yanagita & Wada, 1959; Yanagita, 1973; Salleo et al., 1996; Hidaka & Mariscal, 1988; Greenwood et al., 2003) and might also permit quantitative aspects of cnidogenesis to be investigated.

The present study traces developing stages of large nematocysts (holotrichous isorhizas or holotrichs) in the mesenterial filaments of *Corynactis spp*., the size of these cnidae facilitating simple microscopical observations. Filaments were sampled from anemones which extruded them in the course of an aggressive response (Chadwick, 1987) and examined as stained whole mounts.

Materials and methods

Corynactis californica Carlgren, 1936, was studied at the Bodega Marine Laboratory (September 1998) and *Corynactis viridis* Allman, 1846, at the Plymouth Marine Laboratory (April and June 1999). At these laboratories all specimens were held in running seawater. Mesenterial filament samples were obtained as follows.

A specimen of *C. californica* from the aquarium was placed in contact with an *Anthopleura elegantissima* Brandt, 1835, collected from the shore. As described by Chadwick (1987), loops of mesenterial filaments were usually emitted from the mouth, a response lasting some hours. Under a binocular microscope filament loops were excised with fine scissors and transferred to anaesthetic solution by means of a fine plastic pipette. The size range of *C. californica* is 5-15 mm basal disc diameter (Chadwick, 1987). Samples were obtained from three individuals.

At Plymouth specimens were collected intertidally or subtidally. *C. viridis* has a

basal diameter of 5-10 mm (den Hartog et al., 1993). *C. viridis* placed in contact with *Metridium senile* Linnaeus, 1761, responded by shortening and then opening the mouth and extruding mesenterial filaments. This moderate response was of relatively short duration (0.5-1 hr) but sufficient to allow samples of filaments to be excised. Samples were obtained from 15 anemones.

Corynactis annulata Verrill, 1868 (Carlgren, 1938), was examined at a field laboratory near Cape Town (January 2003). A group of anemones was collected from a long-standing submerged site which was fairly isolated from other hard substrates. Samples of mesenterial filaments were obtained from one of these specimens by dissection.

Histological preparations of filaments were made using the maceration method of Hertwig & Hertwig (1879; cf. Gatenby & Painter (1937)). The Hertwig method applied to these samples yields stained whole mounts which can be viewed intact or else dissociated fairly easily. Excised pieces of filament were transferred to a 1:1 mixture of seawater and 7½% $MgC1_2.6H_20$ in a small waxed Petri dish, to relax the mesenterial muscles. After 10-20 minutes they were transferred to a larger Petri dish containing the same medium, having a square of Parafilm over the wax, and a lid. The samples were pinned out carefully, and the dish placed over ice in a fume cupboard. The anaesthetising medium was removed and the tissues fixed briefly (5-10 mins) with cold 0.2% acetic acid in seawater containing 0.04% osmium tetroxide. The fixative solution was replaced with one or two changes of cold 0.2% acetic acid in seawater, after which the preparations were removed with care into stoppered vials with new medium and left in a refrigerator for 48 hrs.

The preparations were transferred to a pool of fluid on a Parafilm surface, and trimmed as necessary with a fine blade before staining with picrocarmine. A fine pipette was used to transfer the preparations to cleaned slides and then remove excess fluid before adding a large drop of stain. Slides were left in Petri dishes with damp filter paper to prevent evaporation of the stain. After ½-1h the preparations were inspected and thin (No 0) coverslips were added to make whole mounts later sealed with Vaseline. These macerated samples remained intact but could be dissociated by tapping the coverslip before removing excess fluid.

Commercial picrocarmine (vintage Grübler) was used in aqueous 0.1-0.2% solution. Ranvier described its preparation (1875: 100-101; see also Gatenby & Painter, 1937; Baker, 1958; and Lillie, 1969). Distilled water was added to the dry stain followed by drops of 10% ammonia solution until a residue of undissolved carmine had cleared. The picrocarmine solution remained stable and was stored at 4°C.

Olympus and Zeiss microscopes were used for light microscopy and micro-photographs were taken using Ektochrome or Kodachrome film.

Results

Aggressive behaviour of *Corynactis spp*.

Corynactis californica at Bodega emitted mesenterial filaments as described by Chadwick (1987: fig.1), who found that after contact with *A. elegantissima* or *M. senile* for at least half an hour, filaments were extruded from the mouth and other apertures, for a period which might last 1-12 hours. During the present work extruded loops of

mesenterial filaments were excised from three different jewel anemones, 1-4 hrs after they were placed in contact with *A. elegantissima*; one of them furnished samples readily on three different days. Anemones were sampled only if they showed an aggressive response within 4-5 hrs (some did not).

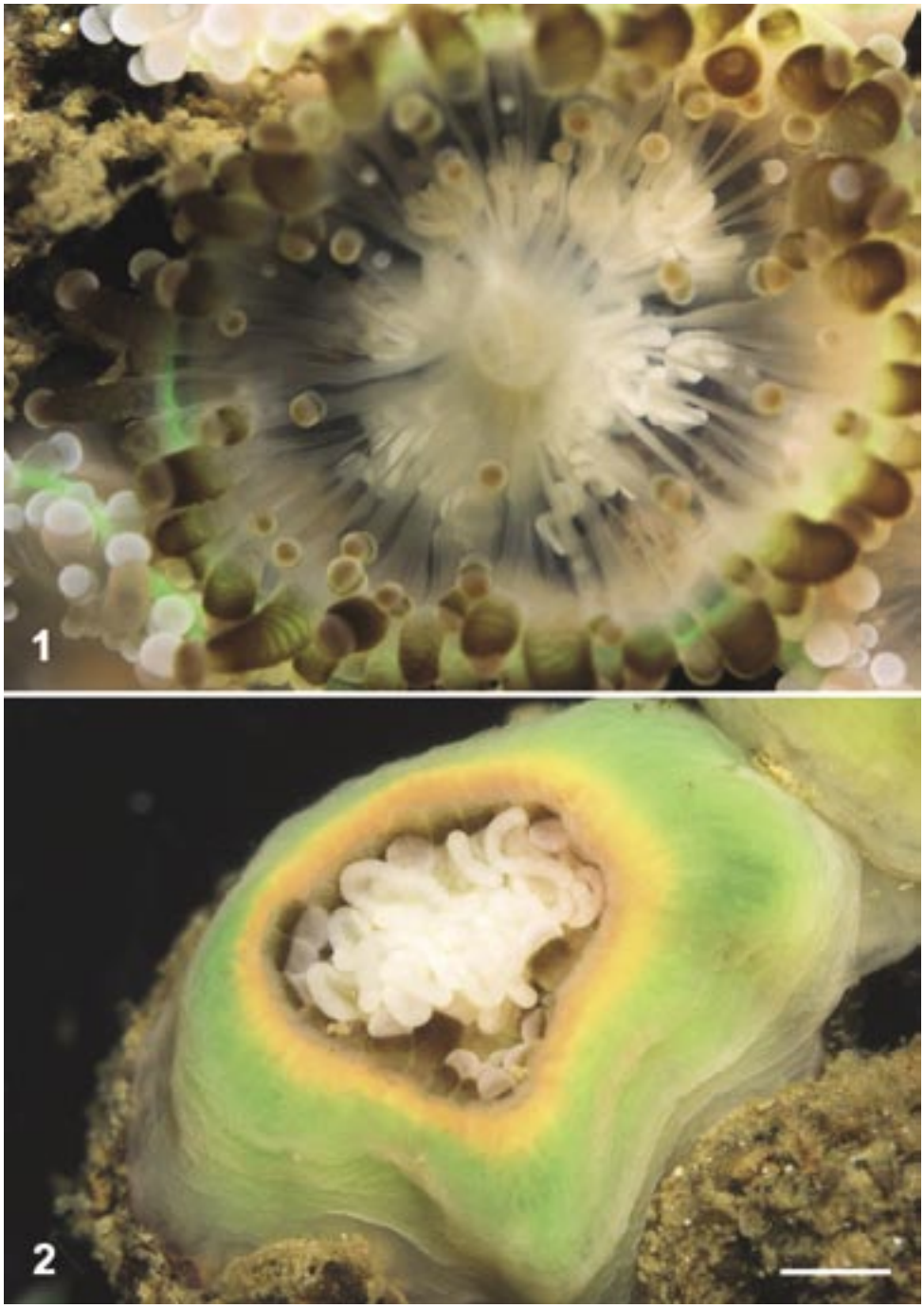
Corynactis viridis is a well known species (den Hartog et al., 1993) but its aggressive behaviour has not been reported previously. The response to contact with *M. senile* is relatively modest and is illustrated in figs 1, 2. As shown in fig. 2, the mouth opens and one or more mesenterial filaments are extruded. A large bundle may be emitted (later withdrawn) but individual loops migrate outwards only for short distances (up to 2 mm from the mouth). The response is seen soon after contact with the crown (i.e., tentacles) of the *M. senile,* and it occurs whether the *C. viridis* polyp is initially expanded or retracted. Expanded jewel anemones retracted and closed up before re-expanding and slowly emitting filaments. Retracted ones stayed closed and dome-shaped but extruded filaments nevertheless, hence the marginal sphincter and mouth had opened sufficiently to permit this. A response to *M. senile* appeared within 1-5 mins and lasted at most an hour, by then all filaments having been withdrawn and the mouth closed. The specimens of *C. viridis* available included both solitary individuals and clones. For the record, tests of *C. viridis* with *Anemonia viridis* Forskål, 1775, were negative, but *Actinia equina* Linnaeus, 1758, caused a weak response.

Recently-collected cup corals *Caryophyllia smithii* Stokes & Broderip, 1828, did not extrude filaments when placed in contact with *M. senile, A. equina* or *C. viridis.* The role of the heavily-armed filaments in *C. smithii* may possibly be in defence against predators or in digestion of prey rather than aggression (cf. Hiscock & Howlett, 1976).

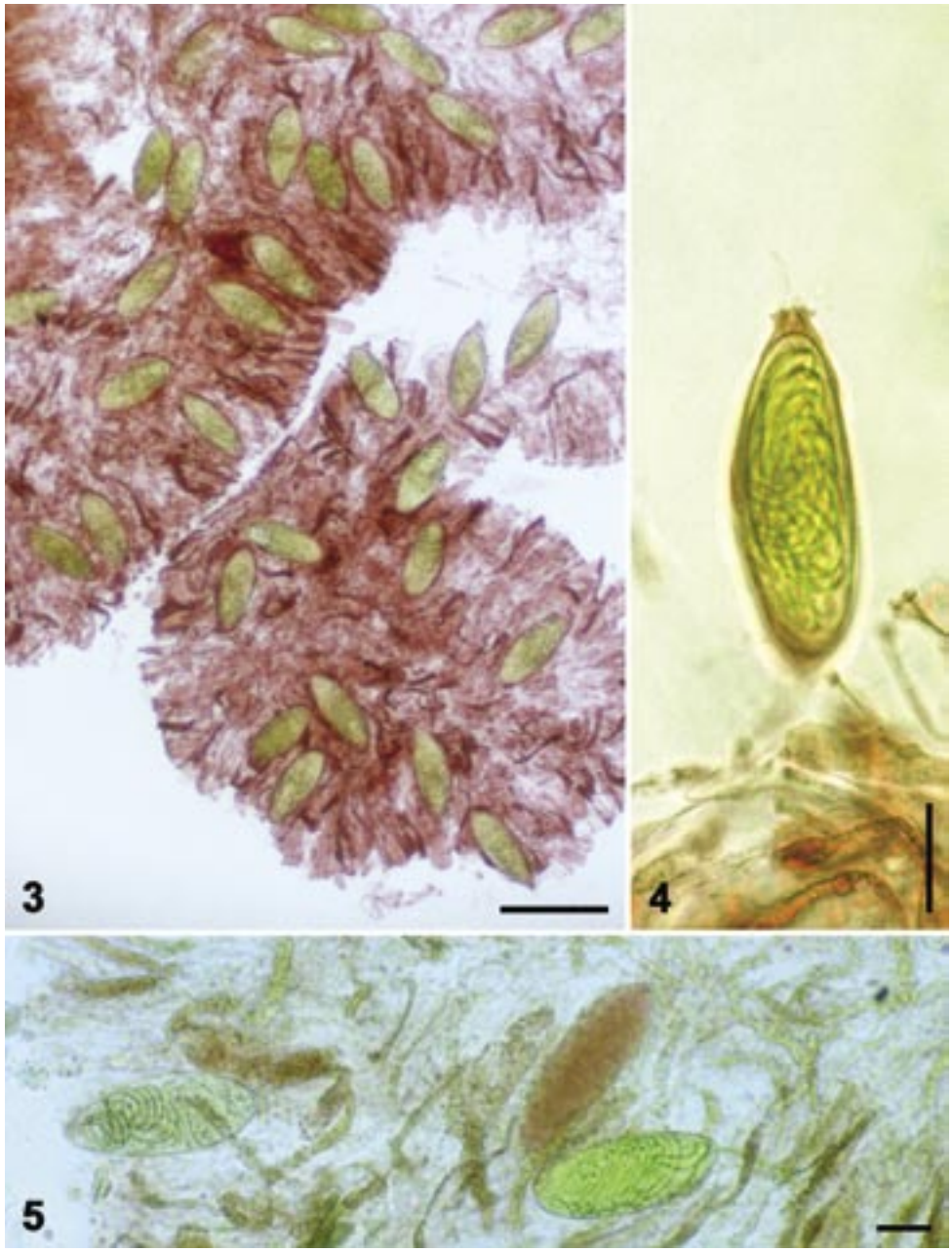
Mesenterial filaments: microscopical observations

The cnidoms of *C. californica* and *C. viridis* have been recorded by Carlgren (1936) and Hand (1954), and by den Hartog et al. (1993). Mesenterial filaments lack spirocysts and the most common nematocysts are microbasic p-mastigophores (medium and small size classes) and holotrichs (large and medium size classes). These capsules were easily identified in stained whole mounts and their dimensions were within the range expected for each species. Microbasic p-mastigophores are seen in fig. 9 (e.g. near mid-point of the right border, two of medium size) and in fig. 5 (one to the right of digit 5, small size). There are a large and a medium sized holotrich near the upper right border in fig. 9. The present account refers mainly to large holotrichs (capsules 70-90 µm in length) because their size facilitates simple observations. In preparations from *C. viridis* their density per mm of filament was at most 40 (commonly 20-35), compared to perhaps 75 in a piece of unfixed, somewhat contracted filament in seawater (Robson, 1973: fig. 1). Transverse sections of the cnidoglandular tract suggest that it may accommodate three or four large holotrichs in staggered packing.

Picrocarmine is a differential stain. Mature nematocysts are coloured yellow by picric acid, which also stains the cytoplasm of sensory and nerve cells. Immature nematocysts and their developing stages, however, are clear red, as are nuclei and muscle fibres, against a background of light red cytoplasm. Spirocysts always stain red but are not present in filaments. Mucus cell contents and mesogloea remain colourless. Differentiating nematoblasts are identified by their relatively large round or oval nuclei,



Figs 1, 2. *Corynactis viridis.* Scale bar 1 mm. Photos: Mr D. Nicholson. Fig. 1. An expanded polyp showing white mesenterial filaments within the coelenteron. Fig. 2. Another polyp extruding mesenterial filaments about 10 mins after contact with *Metridium senile.*



Figs 3-5. *C. californica.* Fig. 3. A mesenterial filament showing large nematocysts (mature holotrichs) in moderate density. The tissue has been spread out and flattened. Capsules are within nematocyts and apical cones and basal nuclei are present. Scale bar 100 µm. Fig. 4. Dissociated filament: a nematocyte showing the apical cone and cilium; the proximal stalk and nucleus are out of focus. Scale bar 25 µm. Fig. 5. Dissociated filament. Mature capsules stain yellow (e.g. two large holotrichs), whereas immature nematocysts and their nematoblasts are red (e.g. to right of centre). Scale bar 25 µm.

in the case of large holotrichs perhaps 10 µm in diameter together with a crimson-stained nucleolus at least 2 µm in size, and by a cytoplasmic vacuole or later stage of the developing nematocyst. The nematoblasts of microbasic p-mastigophores are smaller but with similar features: late stages are identifiable by their size, capsular shape and shaft. Maturation of a nematocyst is indicated by changes in its staining properties, when first the capsule wall and later the tubule and spines are coloured by picric acid instead of carmine.

Figs 3-9 represent whole mounts of mesenterial filament samples and illustrate the distribution of large holotrichs. Mature capsules are situated within epithelial nematocytes (figs 4, 5) whose forerunners are large nematoblasts present singly or in groups (figs 5, 9).

Some preparations show large holotrichs mainly as mature capsules, with few or none of their developing stages present (fig. 3), or else these were at a stage too small to be recognized distinctly. In others, several large nematoblasts occupy an area of filament without mature capsules (fig. 7). More commonly, however, these differentiating nematoblasts are observed amongst fully-formed capsules (figs 5, 6, 8). They are situated either near the filament surface or lower down in the epithelium.

Within preparations from the same anemone the relative proportions of large holotrichs and of their nematoblasts could vary unevenly from one area of filament to the next. This variability might depend on the collection site or history of the particular specimen but it did not seem to depend on the species. Similar results were obtained from *C. californica* (3 anemones) and *C. viridis* (15 anemones).

In samples taken from one specimen of *C. annulata*, the mesenterial filaments had abundant large holotrichs and very few large nematoblasts.

To summarise: in areas dense with holotrichs, large nematoblasts may be sparse or absent; or nematoblasts may be found in an area which does not show any mature capsules; or else capsules and nematoblasts may occur together, each in variable density.

It is concluded that large holotrichs are formed by differentiation of the correspondingly large nematoblasts which are situated among and below them in the epithelium. The density of such nematoblasts along short stretches of filament is variable. This suggests that within a depleted area, discharged holotrichs are replaced by local recruitment.

Discussion

After a nematocyst has differentiated the nematoblast becomes a nematocyte, which acquires epithelial polarity and is anchored between neighbouring cells at the apical circumference and base (cf. fig. 4). The nematocyte becomes competent to control discharge as its functional attributes develop e.g., synapses and other intercellular junctions, multicellular complexes, and not least receptor elements (Westfall, 2004; Watson & Mire, 2004; Thurm et al., 2004; Kass-Simon & Scappaticci, 2004).

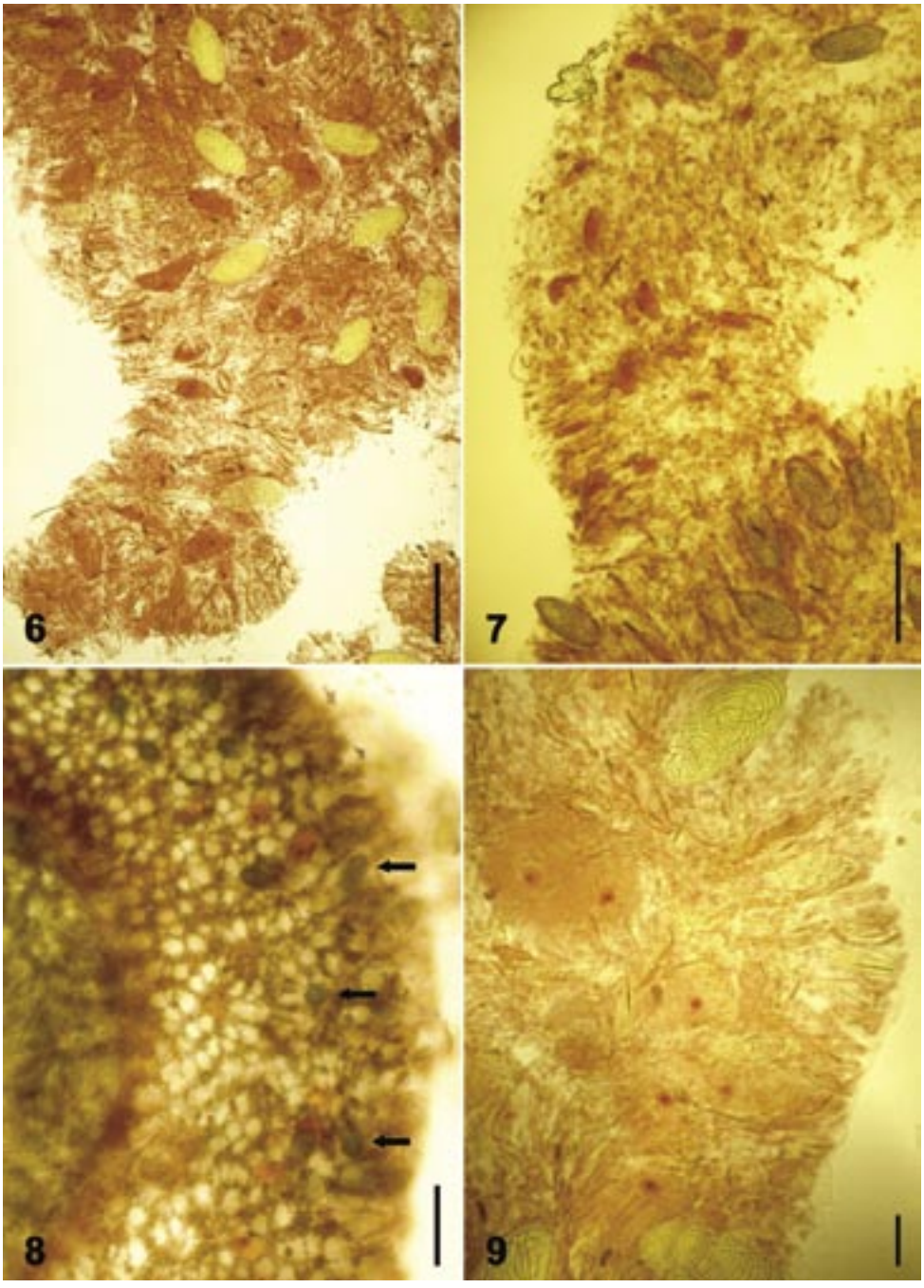
Present observations suggest that large holotrichs in the mesenterial filaments of *C. californica* and *C. viridis* (and probably *C. annulata*) are discharged in localised areas or patches in a non-propagated manner. It appears that discharged holotrichs are then replaced locally. These conclusions would be consistent with the role of extruded

mesenterial filaments in aggressive behaviour if holotrichs were discharged mainly at restricted contacts between filaments and foreign tissues: i.e., where mature holotrichs were reduced to a low density, the development of a batch of new holotrichs would be entrained (cf. Bode's review (1996) of cell lineages in hydra). Samples of filaments showing differences from one polyp to another might be expected to reflect the incidence of recent deployment in aggressive or defensive behaviour.

An almost full complement of holotrichs in preparations from a *C. annulata* polyp suggests the lack of recent disturbance, for example by mobile invertebrates on the same substrate (nudibranchs, urchins etc.). The collection site was fairly isolated although not immune from potential predators. The anemone sampled was one of a group of at least 30 *C. annulata.* Had the filaments of several individuals been sampled and similarly found to have a full complement of holotrichs, this group could have been used for depletion experiments to test the effects of contact with potential predators, competitors or prey. It would be simpler, however, to design such experiments using *C. californica* or *C. viridis* as these species are easier to maintain in the laboratory.

As the distribution of holotrichs in mesenterial filaments was examined in a limited number of samples, there may be other explanations for the observed diversity. Anatomical differences exist between cycles of mesenteries, but these are unlikely to have influenced the present results. In *C. californica* and *C. viridis* (Hand, 1954; den Hartog et al., 1993) the first two cycles of mesenteries possess filaments but not the third. All first cycle mesenteries and some of the second join the pharynx (i.e. they are perfect or complete) so it is most probably their filaments which are emitted from the mouth in an aggressive response; reasonably consistent samples would then be obtained. Significant diversity, however, might result from differential growth or development along the oral-aboral axis of the filament. Cnidoglandular tracts were examined only in short samples taken from loops of extruded filament, not in their entirety along the whole border of a mesentery. In *Corynactis spp*. large holotrichs probably do not occupy the whole length of a filament. There may be a process of axial differentiation or zonation which has not yet been examined (see details in Duerden, 1900, and den Hartog et al., 1993). Growth experiments with corallimorpharians would clarify this possibility (den Hartog, 1980: 55).

In actiniarian sea anemones the upper and lower parts of mesenterial filaments differ morphologically. Stephenson (1928) and Van Praët (1978, 1985) give clear descriptions of the characteristic uppermost (oral) portion which is trilobed in section. In the convoluted lower (aboral) part of the filament only the median lobe, which is the cnidoglandular tract, is present. The cnidoglandular tract furnishes nematocysts which immobilize ingested prey, and secretory cells responsible for extracellular digestion (Van Praët, 1985). In contrast, the mesenterial filaments of corals and corallimorpharians have no trilobed portion and are single-lobed throughout. In corals there are functional distinctions between the straight upper (oral) part of the filament, the adjacent convoluted portion, and sometimes also its most aboral part (Wilson, 1988; many examples in Duerden, 1902; Dr D.O. Pires, personal communication). In *Lophelia prolifera* and *Caryophyllia smithii,* Carlgren (1940, 1945) found large holotrichs and large microbasic p-mastigophores only in the convoluted portion. Thomason & Brown (1986), and Dr J.C. Thomason (unpublished data) provide evidence for a zoned distribution of nematocysts in filaments of corals, for example, in *Galaxea fascicularis* where holotrichs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(mean size 24.25 µm) are far more abundant in the aboral third of the filament, and in *Lobophyllia hemprichii.* Among corals it is thus the convoluted portion of mesenterial filaments which would be the most effective if used in aggressive behaviour or to dispatch prey.

The large nematoblasts of *Corynactis spp*. seen here are attributable to large holotrichs by their size. Duerden (1900: 153; 1902: 563) recognized stages in development of large holotrichs in filaments of *Discosoma* (= *Actinotryx*) *sanctithomae* and *Cladocora arbuscula* from sections, noting that the earliest stained with carmine. To trace the early development of holotrichs and microbasic p-mastigophores from less well differentiated precursors or undifferentiated "interstitial cells", more sophisticated methods are needed (see Bode, 1996; Engel et al., 2002). In the mesenterial filaments of *Corynactis* spp. early precursor cells would be found near the base of the epithelium within or near the cnidoglandular tract. Supporting evidence from actiniarian tissues (p. 3) includes studies of acontia in *H. luciae* (Yanagita & Wada, 1959) and of acrorhagi in *Anthopleura krebsii* (Bigger, 1982). A supply of precursors or of "interstitial cells" would be maintained by mitoses within the tissue, since little if any cell migration has yet been detected (see results obtained by Minasian (1980) after exposing *H. luciae* to tritiated thymidine).

The replacement of cnidae takes several days. Schmidt (1982) found that in tentacles of *Anemonia viridis* which were depleted of their cnidae, initial numbers were regained after five or six days. In a comparable study of tentacles of *Corynactis viridis* undertaken by O. Langmead (1994: Honours project, The University of Reading; personal communication), cnidae of the acrospheres were replaced within six to eight days. It may be supposed that in the mesenterial filaments of *Corynactis spp*. the time needed to replace nematocysts is also about a week. Bigger (1982), however, concluded that when acrorhagial ectoderm regenerated after peeling in *Anthopleura krebsii*, all cellular components including holotrichs were present after 48 hrs.

In many marine landscapes anthozoans feature prominently. Their competitive edge and survival, as in all Cnidaria, has been influenced by the possession of cnidae. In respect of Anthozoa, the cellular processes and dynamics of cnidogenesis are still poorly known, and jewel anemones provide simple but effective models for their further study.

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Figs 6-7. *C. viridis.* Scale bars 100 µm. Fig. 6. A mesenterial filament partly dissociated, showing several large nematoblasts (red). In the area shown they outnumber mature capsules (yellow) suggesting recruitment in progress. Compare to figs 3 and 8. Fig. 7. Mesenterial filament with several large nematoblasts (red) in an area which lacks mature holotrichs. Fig. 8. *C. californica.* Mesenterial filament in oblique side view. Stained large holotrichs (arrows) are seen end-on in the epithelium. These mature capsules (greenish-yellow) can be distinguished from developing capsules (red) in large nematoblasts. Clear spaces represent mucus cells, and the crescentic band to the left is longitudinal muscle. Scale bar 100 µm. Fig. 9. *C. viridis.* Nematoblasts of large holotrichs in a partly dissociated filament. The prominent nucleoli, cytoplasm and cytoplasmic vacuoles of differentiating nematoblasts stain red. The vacuoles represent early stages of cnidogenesis. Scale bar 25 µm.

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