# Redescription of *Oulactis concinnata* (Drayton in Dana, 1846) (Cnidaria: Anthozoa: Actiniidae), an actiniid sea anemone from Chile and Perú with special fighting tentacles; with a preliminary revision of the genera with a "frond-like" marginal ruff

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Häussermann, V. Redescription of *Oulactis concinnata* (Drayton in Dana, 1846) (Cnidaria: Anthozoa: Actiniidae), an actiniid sea anemone from Chile and Perú with special fighting tentacles; with a preliminary revision of the genera with a "frond-like" marginal ruff.
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Key words: Actiniaria; Actiniidae; *Oulactis concinnata*; *Isoulactis chilensis*; *Isocradactis magna*; *Saccactis coliumensis*; *Oulactis muscosa*; *Actinostella*; *Phyllactis*; Chile; Perú; benthos; catch or fighting tentacles; marginal "frond-like" ruff.
Two species of sea anemones with a conspicuous marginal ruff of frond-like structures encompassing the tentacular crown occur on the Chilean coast. *Oulactis concinnata* (= *Isoulactis chilensis*) (Drayton in Dana, 1846) is re-described in detail and further information is provided for *Oulactis coliumensis* (Riemann-Zürneck & Gallardo, 1990) (= *Saccactis coliumensis*) (both Actiniidae). The distribution of *O. concinnata* from Playa Las Salinas, Perú (9°19′10′′S, 78°26′30′′W), to the region of Valdivia, Chile (39°47′S, 73°21′W), lies within a zoogeographical unit known as the Peruvian Province. Re-description of *O. concinnata* is based on examination of 10 specimens collected between 1975 and 2003, and on observations of about 50 living anemones in their habitat and in aquaria. Specimens of this species occur in the intertidal zone and to depths of 15 m in crevices filled with sand, broken shells or pebbles. The most distinctive and conspicuous features of *O. concinnata* are its large size, the lobed and often colourful oral disc and the column with adhesive verrucae. Towards the margin these become smaller and compound and, on the upper margin, form the ruff of frond-like papillae. The structure of the marginal ruff is described in detail and its possible function is considered. The hypothesis is presented that the frond-like structures of the ruff are derived from verrucae. *Oulactis concinnata* is unusual in possessing special fighting tentacles with batteries of large basitrichs but lacking holotrichs. The genera *Isoulactis* Carlgren, 1959, *Isocradactis* Carlgren, 1924, and *Saccactis* Lager, 1911, are synonymized with the genus *Oulactis* Milne Edwards & Haime, 1851. The diagnoses of two other genera with a marginal ruff, *Actinostella* Duchassaing, 1850, and *Onubactis* López-González, den Hartog & García-Gómez, 1995, are provided. The diagnoses of the genera *Oulactis* and *Actinostella* are amended, their distinguishing features and cnidae compared and the described species listed.

A lo largo de la costa chilena se distribuyen dos especies de anémonas de mar con un collar vistoso de estructuras papilosas que rodean a la corona de tentáculos. *Oulactis concinnata* (= *Isoulactis chilensis*) (Drayton in Dana, 1846) (Actiniidae) es re-descrita en detalle. Además se aporta información adicional sobre la especie *Oulactis coliumensis* (Riemann-Zürneck & Gallardo, 1990) (= *Saccactis coliumensis*). *Oulactis concinnata* se distribuye desde Playa Las Salinas, Perú (9°19′10′′S, 78°26′30′′W) hasta la región de Valdivia, Chile (39°47′S, 73°21′W), y se encuentra integrada a la región zoogeográfica conocida como la provincia peruana. La re-descripción de *O. concinnata* está basada en el examen de 10 especimenes recolectados entre 1975 y 2003, y en observaciones de unas 50 anémonas vivas en su hábitat y en acuario. Los ejemplares de esta especie se distribuyen desde la zona intermareal hasta una profundidad de 15 m, y generalmente se encuentran en grietas llenadas de arena, conchas quebradas y cascajo. Los caracteres más distintivos y vistosos de *O. concinnata* son: su gran tamaño; su disco oral lobado, el cuál presenta frecuentemente un color intenso; y por último su columna con verrucas adhesivas. Hacia el margen del disco las verrucas se hacen más pequeñas y compuestas y, en el margen superior, forman un collar de papilas llamativas. La estructura del collar marginal esta descrito en detalle y su posible función es discutida. Asimismo también se discute la relación de parentesco evolutivo entre las papilas y las verrugas. *Oulactis concinnata* se diferencia de otras especies del mismo género por presentar "catch tentacles" que poseen grandes basitricos pero no holotricos. Los géneros *Isoulactis* Carlgren, 1959, *Isocradactis* Carlgren, 1924 y *Saccactis* Lager, 1911 son sinonimizadas con el género *Oulactis* Milne Edwards & Haime, 1851. Se presenta la diagnosis de dos otros géneros con collar, *Actinostella* Duchassaing, 1850 y *Onubactis* López-González, den Hartog & García-Gómez. Se rectifica las diagnosis de los géneros *Oulactis* y *Actinostella* y se comparan sus caracteres distintivos ofreciendo además una lista de las especies descritas.

## Introduction

Worldwide sixteen species of six genera in the family Actiniidae that exhibit a conspicuous marginal ruff are described. Two of those, *Oulactis concinnata* (Drayton in Dana, 1846) and *Oulactis coliumensis* (Riemann-Zürneck & Gallardo, 1990), can be found along the Chilean coast. Although there is no proof for a monophyletic relationship of these six genera, morphological similarities and possibly functional ones justify joint discussion. Most of the literature on these genera is very old and confusing and conclusions are often contradictory (c.f. Carlgren, 1924; Carlgren, 1949b; Carlgren, 1951). Stephenson (1922) made an attempt to revise them, but he noted that "these genera present a good deal of difficulty" and "it may need carrying a good deal further in the light of new knowledge". Now, 80 years later, most species with a marginal ruff are still very poorly known and a revision is needed more than ever (López-González, den Hartog & García-Gómez, 1995). Recent detailed descriptions of *Oulactis coliumensis* (Riemann-Zürneck & Gallardo, 1990), *Actinostella correae* (Schlenz & Belèm, 1988 (92)), *Actinostella flosculifera* (Ocaña, 1994) and *Onubactis rocioi* (López-González, den Hartog & García-Gómez, 1995) provide a good base for this revision.

Modern techniques like SCUBA diving deliver samples in optimal conditions and enable sampling on substrates and at sites where sampling by boat is not possible. Especially in animals with few preservable structures, like sea anemones, observations on specimens *in vivo* or better *in situ* can provide important information on morphology and biology that cannot be obtained from preserved material. Photographs of living animals help to illustrate written descriptions and reduce subjective interpretation. Sea anemones with a marginal ruff of frond-like vesicles encompassing the tentacular crown are excellent subjects for *in situ* observations. The examination of living anemones has yielded new information about these marginal structures and reveals important characteristics usually lost during preservation but possibly essential for the delimitation of species.

The present paper provides a detailed redescription of *Oulactis concinnata*, which is herein synonymized with *Isoulactis chilensis*. A list of all described species with a marginal ruff is provided and the division into the existing genera is discussed and preliminarily revised. The genera *Isoulactis*, *Isocradactis* and *Saccactis* are synonymized with the genus *Oulactis*. For a complete revision of this group a detailed examination of the species of the genus *Oulactis* from New Zealand and Australia and of the species of the genus *Actinostella* (= *Phyllactis*) is necessary.

## Material and methods

Between 1994 and 2003, Günter Försterra and I observed and examined about 50 specimens of *Oulactis concinnata* along the Chilean coast from Arica (18°30'S, 70°19'W) to Los Molinos/Valdivia (39°50'S, 73°24'W) (fig. 1; app. 1). Lists of all study sites up to S44 can be recalled in the online appendix of Häussermann & Försterra (2001) at http://www.senckenberg.uni-frankfurt.de/odes/. The studies were carried out in the intertidal zone during low tide and also by means of SCUBA-diving. Some specimens were kept in aquaria for several days for detailed examination. Five specimens were preserved, three of which were examined histologically. I also examined five specimens collected by K.P. Sebens and R.T. Paine in 1975 (fig. 1; app. 2), one specimen from Perú collected by S. Austermühle in 2002 (fig. 2; app. 3) and two specimens of *Oulactis coliumensis* dredged by the research vessel Kaikai of the Universidad de Concepción in November 1998 from ~ 20 m depth. This study also utilizes information gathered by S. Austermühle in 2002, who collected and observed several specimens in Perú (fig. 2; app. 3).

Photographs were taken both in situ and in the aquarium. For preservation, the specimens were relaxed with menthol crystals for 30–120 min and fixed in 10-15% seawater formaldehyde. Specimens were kept in this formaldehyde solution for at least 4 months before being transferred to 70% alcohol. For histological examination parts of three specimens of *O. concinnata* and of one specimen of *O. coliumensis* were embedded in paraffin, sectioned at 8 – 9 µm and stained with Azocarmin triple staining.

For cnidae examination, squash preparations of small amounts of tissue from two living and four preserved specimens of *Oulactis concinnata* and one living and one preserved specimen of *Oulactis coliumensis* were examined with a light microscope (1000× oil immersion), drawn or photographed, and measured. The discharge of fresh cnidae was provoked with distilled water or 4% acetic acid solution. Permanent slides of discharged cnidae were prepared with the technique of Yanagi (1999): a small amount of tissue is put into a drop of 4% acetic acid or HCl solution on a microscopic slide. After some minutes the liquid is suck off carefully with a Kleenex. Then a solution of 1:1 sea water:glycerin with very few phenol and formalin (a few drops on 100 ml solution) is added. A cover slide is sealed several times with nail coating. If the coating is repeated regularly, the permanent slides stay in good condition for at least seven years (Yanagi, in litt., 2003).

Nematocyst terminology follows England (1991). According to Acuña et al. (2003), data on nematocyst size ranges of different specimens should not be grouped to determine statistical descriptive parameters. Thus the size ranges of table 1 are values taken from a single preserved specimen.

## Results

### Diagnosis of the genera with a marginal ruff

Family Actiniidae Rafinesque, 1815.

a) Genus *Oulactis* Milne Edwards & Haime, 1851.

Amended diagnosis, with changes in bold: Actiniidae with well-developed pedal disc; **oral disc wide, round to lobed.** Column smooth in its lowest part, otherwise

Table 1: Size and distribution of preserved cnidae of a single specimen *Oulactis concinnata* (letters A-P refer to fig. 9), in each tissue in order of abundance: $^{s}$: sporadic, $^{f}$: few, $^{c}$: common and $^{v}$: very common. “$m_l$“ and “$m_w$” are the means, “$d_l$” and “$d_w$” are the standard deviations (all in µm), “t” are the number of turns on the proximal part of the tube, “#” is the number of capsules measured, “p” is the proportion of animals examined with respective type of cnida present. Exceptional sizes in parenthesis.

| Tissue/Cnidae type, abundance | Capsule length (µm) | $m_l$ | $d_l$ | Capsule width (µm) | $m_w$ | $d_w$ | t | # | p |
|---|---|---|---|---|---|---|---|---|---|
| TENTACLES | | | | | | | | | |
| spirocysts$^{v}$ (D) | (14.4) 16.2 – 27.0 | 20.2 | 2.62 | 1.8 – 2.7 | 2.0 | 0.36 | | 46 | 4/4 |
| basitrichs$^{v}$ (E) | (15.3) 19.8 – 28.8 | 22.6 | 2.44 | 1.8 – 3.2 | 2.6 | 0.29 | 3-4 | 45 | 4/4 |
| FIGHTING TENTACLES | | | | | | | | | |
| microbasic b-mastigophors$^{v}$ (F) | 22.5 – 31.5 | 26.9 | 2.03 | 3.2 – 5.0 | 4.0 | 0.55 | ~5 | 47 | 4/4 |
| ACRORHAGI | | | | | | | | | |
| holotrichs I$^{v}$ (J) | 39.6 – 53.1 | 44.9 | 3.36 | 2.3 – 3.2 | 2.8 | 0.26 | | 42 | 2/2 |
| holotrichs II$^{c}$ (K) | (36.0) 43.2 – 54.9 (60.3) | 49.9 | 4.44 | 4.5 – 8.1 | 6.0 | 0.68 | | 46 | 2/2 |
| COLUMN | | | | | | | | | |
| basitrichs$^{c}$ (C) | (13.5) 15.3 – 21.6 (24.3) | 17.0 | 1.78 | 1.4 – 2.7 | 2.0 | 0.30 | 3-4 | 45 | 4/4 |
| holotrichs$^{f-c}$ (A) | 25.2 – 35.1 | 29.2 | 2.30 | 4.5 – 6.3 | 5.4 | 0.37 | | 47 | 4/4 |
| rod-like basitrichs$^{f}$ (B) | (22.5) 27.0 – 33.3 | 29.3 | 2.83 | 1.4 – 1.8 | 1.5 | 0.22 | | 20 | 4/4 |
| MARGINAL RUFF (PAPILLAE) | | | | | | | | | |
| basitrichs$^{f}$ (I) | 11.7 – 15.3 (21.6) | 14.2 | 2.39 | 1.4 – 1.8 | 1.5 | 0.22 | 3-4 | 25 | 4/4 |
| ACTINOPHARYNX | | | | | | | | | |
| basitrichs$^{c}$ (G) | 17.1 – 27.0 (30.6) | 23.1 | 3.55 | 1.8 – 3.2 (3.6) | 2.6 | 0.48 | 4-5 | 43 | 4/4 |
| microbasic - amastigophors A$^{s}$ | 21.7 | | | 4.1 | | | | 1 | 1/4 |
| MESENTERIAL FILAMENTS | | | | | | | | | |
| microbasic - b-mastigophors$^{c}$ (L) | 38.7 – 57.6 (62.1) | 49.9 | 4.76 | 5.4 – 9.9 | 8.3 | 1.17 | ~10? | 40 | 4/6 |
| microbasic p-mastigophors B$^{c}$ (O) | 22.5 – 28.8 (34.2) | 25.9 | 2.31 | 2.7 – 4.1 (5.4) | 3.2 | 0.69 | | 44 | 4/6 |
| basitrichs$^{f-c}$ (N) | 13.5 – 19.8 | 16.1 | 1.40 | 1.4 – 1.8 (2.3) | 1.7 | 0.18 | 3-4 | 41 | 4/6 |
| microbasic amastigophors A$^{f}$ (P) | 18.0 – 22.5 | 20.8 | 1.16 | (3.6) 4.1 – 5.4 | 4.6 | 0.40 | ~5 | 40 | 4/6 |
| rod-like basitrichs$^{s}$ (M) | 33.0 – 36.0 | 34.1 | 1.42 | 1.5 – 2.0 | 1.78 | 0.21 | | 4 | 1/6 |
| PEDAL DISC | | | | | | | | | |
| basitrichs$^{f-c}$ (H) | (10.8) 15.3 – 21.6 | 17.6 | 1.72 | 2.3 – 2.7 | 2.6 | 0.29 | 3-4 | 40 | 4/4 |

**covered with** longitudinal rows of **adhesive** verrucae **except in its most proximal part; verrucae becoming smaller towards the margin, compound and** set on small lobes. **Thin-walled marginal region carrying delicate frond-like papillae set on lobes and forming a ruff below the tentacles; one frond in each exo- and endo-coel. No distinct fosse. Acrorhagi present or not, when present they are placed on the oral side of the fronds**. **Arrangement of tentacles and mesenteries** hexamerous, longitudinal muscles of tentacles ectodermal. Most of the mesenteries perfect, **reproductive tissue may appear on all mesenteries except youngest cycles (in some species** directives may be sterile). Two well-developed siphonoglyphs and two pairs of directives. **Endodermal** sphincter diffuse, **weak to well developed.** Retractors **diffuse to restricted, moderately strong to strong. Parietobasilar muscles and basilar muscles strong. No zooxanthellae present.**

Cnidom: spirocysts **(in tentacles, may also be found in pedal disc, acrorhagi and oral disc)**, basitrichs **(in all body parts except acrorhagi and fighting tentacles), microbasic b-mastigophors (in filaments and fighting tentacles), microbasic p-mastigophors B (may be found in filaments), microbasic amastigophors A (in filaments, may also be found in pharynx), holotrichs (in acrorhagi, may also be found in column), in some species rod-like basitrichs (in filaments and column).**

b) Genus *Actinostella* Duchassaing, 1850.

Diagnosis after Carlgren, 1949b and amended by Schlenz & Belèm, 1988(1992) (italics), amended with changes in bold: Actiniidae with well-developed pedal disc. **Oral disc round;** column more or less elongate, usually with verrucae in its **upper** part. Above the verrucae and below the margin lies a **ruff or collar** which may be quite wide, and which is formed by a number of shorter or longer series of small frond-like **papillae** containing basitrichs. Above the vesicles a more or less distinct fosse. **Generally 48 tentacles.** No acrorhagi. *All mesenteries perfect or perfect and imperfect, hexamerously and regularly disposed.* Sphincter strong to very weak, circumscribed. Longitudinal muscles of tentacles ectodermal. As a rule two siphonoglyphs. Retractors typically strong, diffuse to restricted. Parietobasilar muscles well developed. Same number of mesenteries proximally and distally. **Zooxanthellae may be present.** Cnidom: spirocysts **(in tentacles)**, basitrichs **(in all body parts), microbasic b-mastigophors (in filaments), microbasic amastigophors A (in spherulae, pharynx and filaments); holotrichs (may be found in column).**

c) Genus *Onubactis* López-González, den Hartog & García-Gómez, 1995.

Diagnosis after López-González, den Hartog & García-Gómez (1995): Actiniidae with well developed pedal disc. Column differentiated into a relatively firm scapus and a thin-walled scapulus with a ruff of hollow papilla-like outgrowths. Scapus smooth to slightly corrugate. Acrorhagi absent. Arrangement of tentacles and mesenteries hexamerous. More mesenteries distally than proximally. Mesenteries 48, arranged in four cycles: those of cycles I-III fertile, those of cycle IV microcnemic, without filaments and gonads, and only present in the distalmost part of the body. Stomadaeum with two siphonoglyphs supported by 2 pairs of directives. Sphincter weak, diffuse to restricted diffuse. Retractors of the mesenteries very strong and diffuse. Zooxanthellae absent.

Cnidom (for a comparison of cnidocyst nomenclature see England, 1991): spirocysts (numerous in tentacles and base), spirulae[1] (in all body parts), penicilli A[2] (in filaments only) and penicilli B1[3] (present in sparse numbers in filaments).

The distinguishing features of the genera *Oulactis*, *Actinostella* and *Onubactis* and

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[1] Also called basitrichs or microbasic b-mastigophors (see England, 1991)

[2] Also called microbasic amastigophors A (see England, 1991)

[3] Also called microbasic p-mastigophors B1 (see England, 1991)

Table 2: Diagnostic characters of the genera *Oulactis* Edwards & Haime, 1851, *Actinostella* Duchassaing, 1850 and *Onubactis* López-González, den Hartog & García-Gómez, 1995.

| characters | *Oulactis* M. Edwards & Haime, 1851 | *Actinostella* Duchassaing, 1850 | *Onubactis* López-González, den Hartog & García-Gómez, 1995 |
|---|---|---|---|
| Synonymized genera | *Isocradactis* Carlgren, 1924 nov, syn., *Isoulactis* Carlgren, 1959 nov. syn., *Saccactis* Lager, 1911, *Cradactis* Stuckey, 1909; ?*Tealidium* Stuckey, 1909 | *Phyllactis* M. Edwards & Haime, 1851; *Cradactis* McMurrich, 1893; *Asteractis* Verrill, 1869; *Metridium* p. p. Dana, 1846; *Oulactis* p. p. M. Edwards & Haime, 1851; *Lophactis* Verrill, 1869 | none |
| Species | Genotype: *O. (Metridium) muscosa* (Drayton in Dana, 1846) = *O. plicata* Hutton, 1878 =?*O. (Tealidium) cinctum* (Stuckey, 1909) (O. Ocaña, in litt., 2003): Australia, New Zealand: intertidal, sand-filled crevices.<br>O. *(Metridium) concinnata* (Drayton in Dana, 1846) = *Isoulactis chilensis* Carlgren, 1959: Chile, intertidal to 15 m, sand-filled crevices.<br>*O. (Cradactis) magna* (Stuckey, 1909) = ?*O. (Tealidium) cinctum* (Stuckey, 1909) (O. Ocaña, in litt., 2003): New Zealand, intertidal, sand-filled crevices.<br>*O. (Saccactis) mcmurrichi* (Lager, 1911) = ?*S. australis** Lager, 1911 = ?*S. muscolosa** Lager, 1911: SW Australia, low water. *: species inquirendae *sensu* Riemann-Zürneck & Gallardo (1990).<br>*O. (Saccactis) coliumensis* Riemann-Zürneck & Gallardo (1990): Central Chile, 20-50 m, soft bottom. | Genotype: *A. (Actinia) flosculifera* (Le Sueur, 1817) = *Oulactis fasciculata* McMurrich, 1889 = *Metridium praetexla* Couthouy in Dana, 1846= *A. conchi lega* McMurrich, 1905 (*sensu* Carlgren, 1949, Schlenz & Belèm, 1988 (92)): both sides of the tropical and subtropical Atlantic, Carribean Sea; *sensu* Ocaña (1994) also: = *Oulactis conquilega* Duchassaing & Michelotti, 1860 = *Oulactis foliosa* Andres, 1884 = *Asteractis* n. sp. Duerden, 1898 = *Asteractis expansa* Duerden, 1902: all Carribean Sea; = A. *formosa* (Duchaissing, 1850): Guadeloupe<br>A. *(Oulactis) radiata* Duchassaing & Michelotti, 1860: West India<br>*A. (Cradactis) digitata* McMurrich, 1893: Southern Atlantic Ocean close to Argentina<br>*A. (Asteractis) bradleyi* Verrill, 1869: California to Panama, Gulf of California; (=?*Oulactis californica* McMurrich, 1893)<br>*A. (Oulactis) californica* McMurrich, 1893: Gulf of California | *Onubactis rocioi* López-González, den Hartog & García-Gómez, 1995 |

| | | | |
|---|---|---|---|
| | | A. (Phyllactis) *correae* Schlenz & Belèm, 1988 (92): Brasil, intertidal<br>A. *(Lophactis) ornata* (Verrill, 1869): Pearl Island<br>*A. cichoracea* M. Edwards in Haeckel, 1876: Red Sea<br>?A. *(Cradactis) excelsa* (Wassilieff, 1908): Japan (most probably belongs to another genus)<br>?A. *striata* Wassilieff, 1908: Japan (most probably belongs to another genus)<br>?A. (Cradactis) variabilis Hargitt, 1911 | |
| Distribution | Southern hemisphere: Australia, New Zealand, Chile | Tropical and subtropical oceans | Province of Huelva, Atlantic coast of the southern Iberian Peninsula |
| Habitat | Intertidal and shallow water, in crevices, under stones or borrowed in sand | Intertidal to shallow water | Probably sandy and muddy bottoms in deeper water |
| Shape of oral disc | Round to wide, lobed | Round | Round |
| Shape of column | Cup-like to elongate | +/- elongate | Cylindrical |
| Marginal ruff | Thin-walled marginal region carries delicate frond-like structures | Compound vesicles below the tentacles form a ruff; in *A. flosulifera* expanded during the day whereas the tentacles are expanded during the night | Hollow, papilla-like outgrowths arranged in parallel rows on the scapulus |
| Verrucae | Present (except in most proximal region); compound and set on small lobes in uppermost part | Present (only in distal region - see discussion) | No; column divided into smooth scapus and thin-walled scapulus |
| Acrorhagi | Present or may be present | No | No (not found in 9 specimens) |
| Endodermal sphincter | Diffuse, weak to well developed | +/- circumscript, very weak to well - developed | Diffuse |
| Tentacles | 96 to more than 400 | Up to 48 | Up to 96 |
| Zooxanthellae | No | Yes (in A. *flosculifera*, A. *californica* and *A. correae*-other species have to be re-examined to confirm this) | No |
| Rod-like basitrichs | May be present in column and filaments | No | No |

their described species are listed (table 2). Cnidae of the species *Oulactis concinnata, O. magna, O. coliumensis, O. muscosa, Actinostella flosculifera* and *Onubactis rocioi* are listed and compared (table 3).

## *Oulactis concinnata* (Drayton in Dana, 1846)

*Metridium concinnatum* Drayton in Dana, 1846: 152 (San Lorenzo Island, Callao, Perú); Dana, 1859: 3, 11.

*Oulactis concinnata;* Milne Edwards, 1857: 292 (Peruvian coast); Verrill, 1869: 463; Andres, 1884: 290 (505); Verrill, 1907: 268 (footnote).

Non *Asteractis concinnata*; Pax, 1912: 12 (Paita, Perú, six specimens).

*Phyllactis concinnata*; Stephenson, 1922: 283; Carlgren, 1949b: 67; Carter, 1965: 146 (Valparaíso, Chile)

Non *Phyllactis concinnata*; Carlgren; 1951: 424 (California, seven specimens); Brusca, 1980 (Gulf of California).

Non *Oulactis californica* McMurrich, 1893: 196 (Pichilingue, California, two specimens);

Carlgren, 1896: 175;

Non *Phyllactis californica*; Stephenson, 1922: 284; Carlgren, 1949b: 67; Pickens, 1988 (California).

*Isoulactis chilensis* Carlgren, 1959: 20 (Iquique and Lota/S of Concepción, Chile); Sebens & Paine, 1979: 223 (Chile, Iquique to Valdivia); Riemann-Zürneck & Gallardo, 1990: 451; López-González, den Hartog & García-Gómez, 1995: Häussermann, 1998: 63; 382; Häussermann & Försterra, 2001: 221 (Chile, Arica to Valdivia).

Examined material.— **Chile:** *Oulactis concinnata*. One specimen from Arica/Playa Corazones (S2), collected 31.xi.1997 by G. Försterra (GF) and V. Häussermann (VH), 4 m depth (Ex. 41=ZSM 20020265); one specimen from Iquique (P1) collected 30.ix.1975 by K. Sebens (KS) and R. Paine (RP), intertidal (RMNH Coel. 32160), very firm as dried up and rehydrated; two specimens from Antofagasta (P8) collected 6.x.75 by KS and RP,

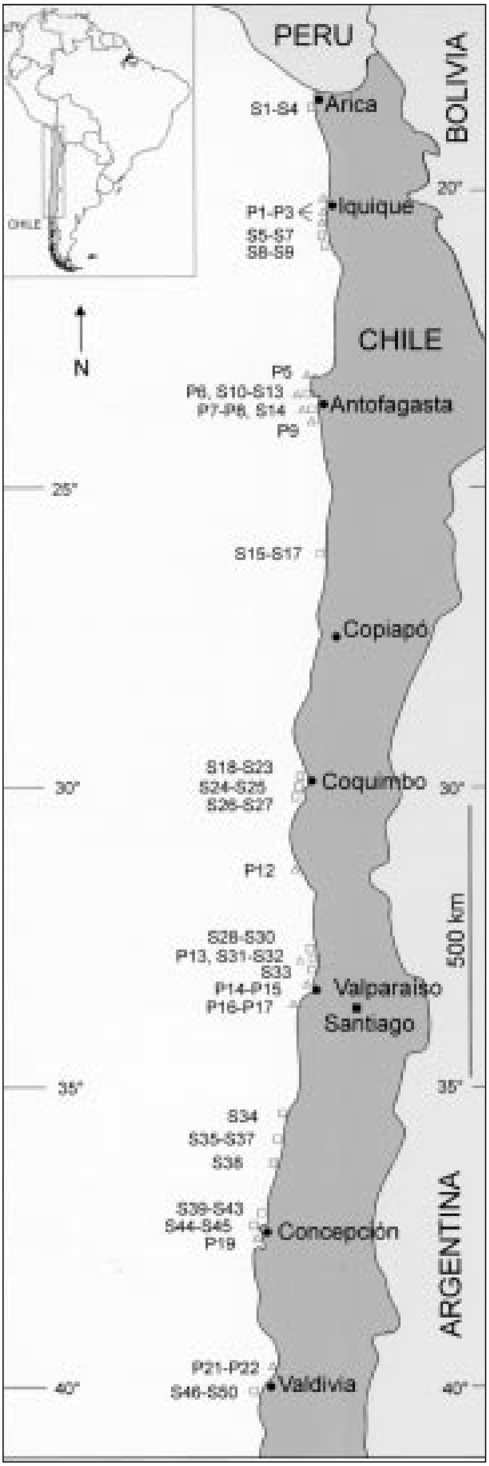

Fig. 1: Sites studied by VH and GF (S1-S50) and K.P. Sebens and R.T. Paine (P1-P22) in Chile. For precise localities and short description of sites see app. 1-2.

intertidal (RMNH Coel. 32161), the identification of the small one is not sure; two specimens from Pingueral (S41), collected 31.x.1997 (Ex.8=ZSM 20020264) and 5.iv.1998 (Ex. 329=ZSM 20020266) by GF and VH, 7 m depth; one specimen from Pingueral (S41), collected 1.iv.1995 (Museo de la Universidad de Concepción, MZUC 23166) by GF and VH, 6 m depth; two specimens from Playa Misión (S46a), collected 31.xi.02 by A. Bravo, intertidal (IZUA-CNI-0032); three specimens from Mehuín (P21), collected 2.xi.75 by KS and RP, intertidal (RMNH Coel. 32162), very firm as dried up and rehydrated (P 1–P 22: numbers used as in Sebens & Paine, 1979).

*Oulactis (Saccactis) coliumensis.* Two specimens from the Bahía de Coliumo (S42). collected by the research vessel Kaikai at the beginning of November 1997, ~ 20 m depth (Ex. 25 = ZSM 20020267, Ex. 41= ZSM 20020268 ).— **Perú:** *Oulactis concinnata*. One specimen from Pucusana (R15), collected xii.2002 by S. Austermühle, 2-3 m depth (ZSM 20030294).

Fig. 2: Sites studied by other scientists in Perú (R1-R16). For precise localities and additional information see app. 3.

For detailed description and location of sampling sites see app. 1-3 and figs. 1-2.

Holotypes.— *Oulactis (Metridium) concinnata* (Drayton in Dana, 1846), San Lorenzo Island, Callao, Perú (12°05'S, 77°12'W). No type material. For original drawings of animal in the habitat see Fautin (2003: *Metridium concinnatum*).

— *Isoulactis chilensis* Carlgren, 1959, Iquique, southern part of the town, Chile, intertidal (20°13'10''S, 70°10'19''W). Swedish Museum of Natural History SMNH 3021 (examined); three paratypes: Museum of Zoology, Lund University L949/3594; Bahía de Lota, SE of Punta Fuerte Viejo, Golfo de Arauco, intertidal (37°06'17''S; 73°09'15''W). For original drawings of histological sections see Fautin (2003: *Isoulactis chilensis*).

— *Saccactis coliumensis* Riemann-Zürneck & Gallardo, 1990. Holotype 11538, paratypes 11539-11542; deposited in the Zoological Museum of the University of Hamburg. For figures of original description see Fautin (2003: *Saccactis coliumensis*).

Information on the type material of the other *Oulactis* species.

— *Oulactis mucosa* (type species of the genus *Oulactis*): No type material. For drawings of the living specimens see Fautin (2003: *Saccactis coliumensis*).

— *Oulactis magna* (Stuckey, 1909) (type species of the genus *Isocradactis*): No type material. *O. magna sensu* Carlgren, 1924: one specimen on which Carlgren based his re-description, Zoological Museum of the University of Copenhagen. *Sensu* Riemann-Zürneck & Gallardo (1990) it is not at all sure whether this animal is Stuckey´s species. For information about the species see Fautin (2003: *Cradactis magna*).

— *Oulactis mcmurrichi* (Lager, 1911) (type species of the genus *Saccactis*): Type material: several syntypes, see Fautin (2003: *Saccactis mcmurrichi*), also for figures of original description.

Differential diagnosis of *Oulactis concinnata.*— Large-sized anemone, which lives in sand-filled crevices in the intertidal and down to depths of 15 m in north and central Chile and southern Perú. Numerous, short, thick tentacles and thread-like elon-

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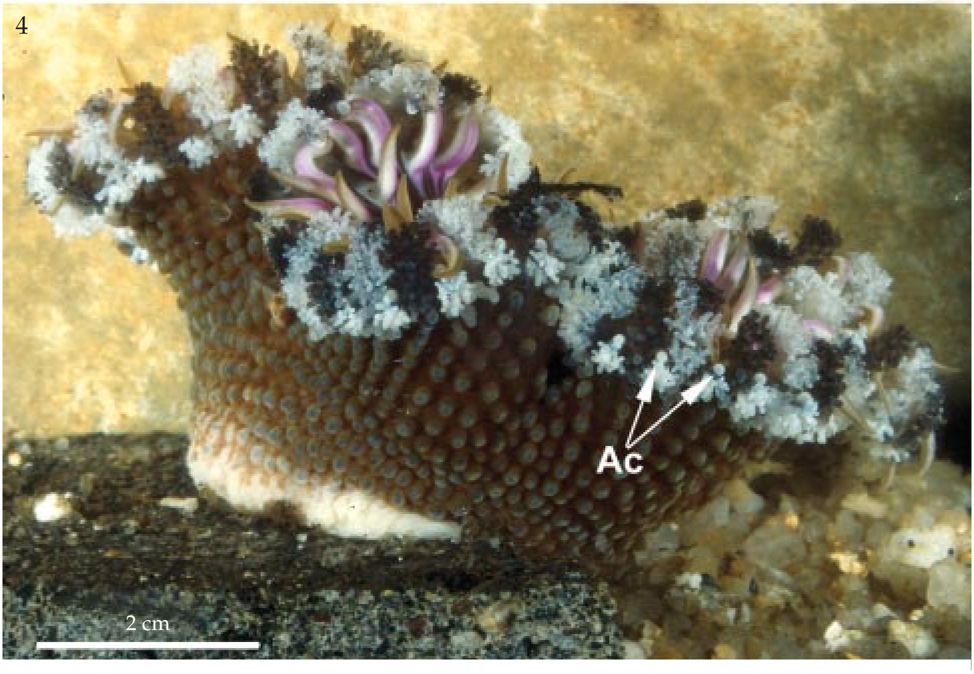


Fig. 3-4: *Oulactis concinnata*. Fig. 3. Lobed oral disc and tentacles of an individual in its typical habitat; note elongated mouth opening. Fig. 4. Lateral view of specimen ZSM 20020264; note the rows of adhesive verrucae visible in the upper part of the column and the marginal ruff consisting of large brown fronds alternating here with a large white and two small ones; the most proximal region of the column is white and lacks verrucae. Acrorhagi (Ac).

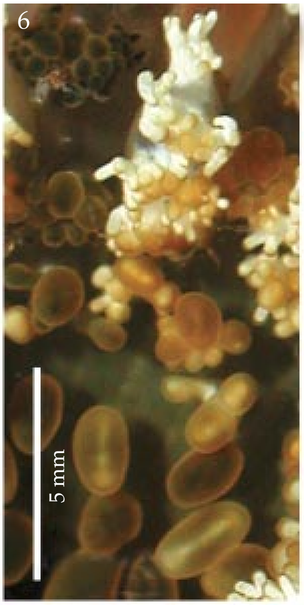
gated fighting tentacles. Lobed oral disc strongly and/or brightly uni- to bi-coloured, rarely tri-coloured; mouth opening round or lengthened, lips thick. Column with adhesive verrucae in 96 or more longitudinal rows; verrucae compound and set on small lobes in the most distal region. Thin-walled marginal region with delicate ruff consisting of papillae bundled to approx. 192 fronds; dark ones alternating with white ones or, more rarely, all white. Acrorhagi may be present. Two strong siphonoglyphs; sphincter diffuse and very weak; parietobasilar and basilar muscles strong.

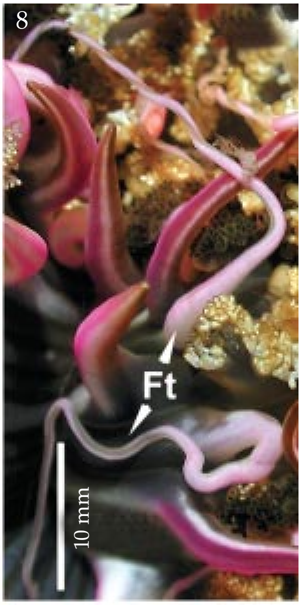
In the field, this species can be distinguished from *Oulactis coliumensis* by the following characters: *O. coliumensis* is uniformly brown to green coloured, has 96 tentacles and lives on soft substrata. *Oulactis magna* from New Zealand differs by the colour of its tentacles (proximal purple to orange and distal yellow to claret), the well-developed sphincter and the microbasic amastigophors A (also called p-mastigophors) in the pharynx. *Oulactis muscosa* from New Zealand posses 96 pale-brown tentacles with circular patterns, microbasic amastigophors A (also called p-mastigophors) in the pharynx and only one type of holotrichs in the acrorhagi.

General morphology.— Large-sized and robust species with only the oral disc being exposed above the sand (fig. 3). Specimens usually much broader than high, column of uniform diameter or broader distally than proximally (fig. 4); young individuals cylindrical, larger specimen oval to irregular. Oral disc lobed (fig. 3). Preserved animals whitish to grey or brownish, marginal ruff white and grey to bluish; oral disc never completely covered by the column in state of contraction. Size and arrangement of tentacles and mesenteries regular and hexamerous in all examined animals.

Colour.— Very variable and often striking: oral disc often brightly uni- or bi-, sometimes tri-coloured, often with a 5-20 mm wide ring around the pharynx in one colour and the rest of the oral disc in another, typical colours of the oral disc are violet and bluish, bright blue and black, brown and grey, uni-coloured specimens often are bright red or green-brown, different shades of brown or grey, or rarely white (for additional phenotypes see Häussermann, 1998); pharynx generally white, rarely dark. Insertions of mesenteries visible on oral disc as light or dark lines beginning at the base of the tentacles and becoming thinner and less obvious towards the pharynx. Tentacles white, frequently with broad longitudinal stripes of two different colours, orally pink and aborally grey or brown, or tentacles longitudinally precisely divided into two of these colours, rarely transparent. Column pale brownish to strongly red-brown, brown or green, lowest part without verrucae generally white (Fig. 4); pedal disc white. Endoderm of ruff, verrucae, mesenteries and pharynx may contain dark brownish granules.

Column.— Low; never higher than broad; in life up to 70 mm high and more than 180 mm diameter; covered with adhesive verrucae apart from a small rim at the limbus. Verrucae arranged in up to 96 or more vertical rows; rows distinct in the distal part of the column of living expanded specimens (fig. 4) but more indistinct in contracted or preserved animals. Each verruca lighter than the column, may be lengthened and end in a small cup if attached to foreign material (fig. 5). Column may be covered with many small stones, fragments of shells, algae, glass, wood, plastic etc. Distal column with additional, often doubled number of verrucae, becoming broader and lower, with higher proportion of white; upper column with composed verrucae set on small lobes, towards the margin transforming into non-adhesive more or less delicate dendritic papillae (figs 6-7); transition zone more or less broad; papillae are





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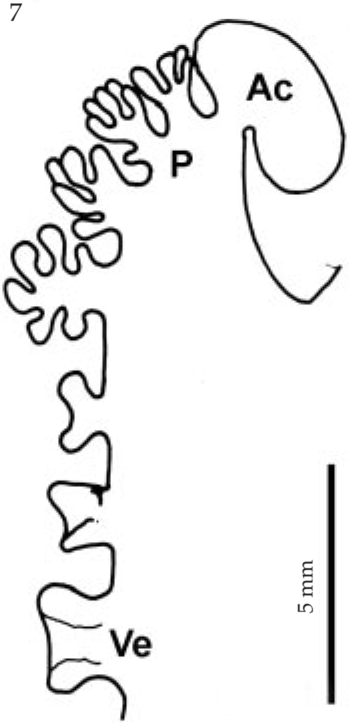

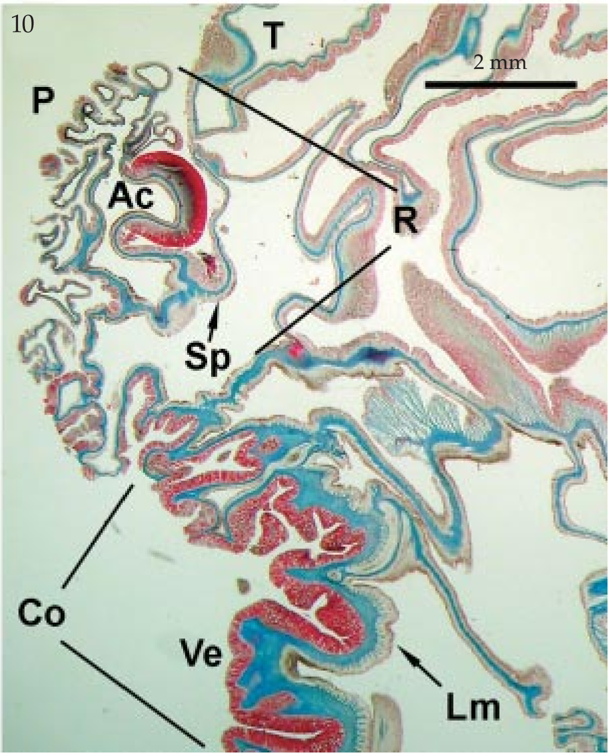

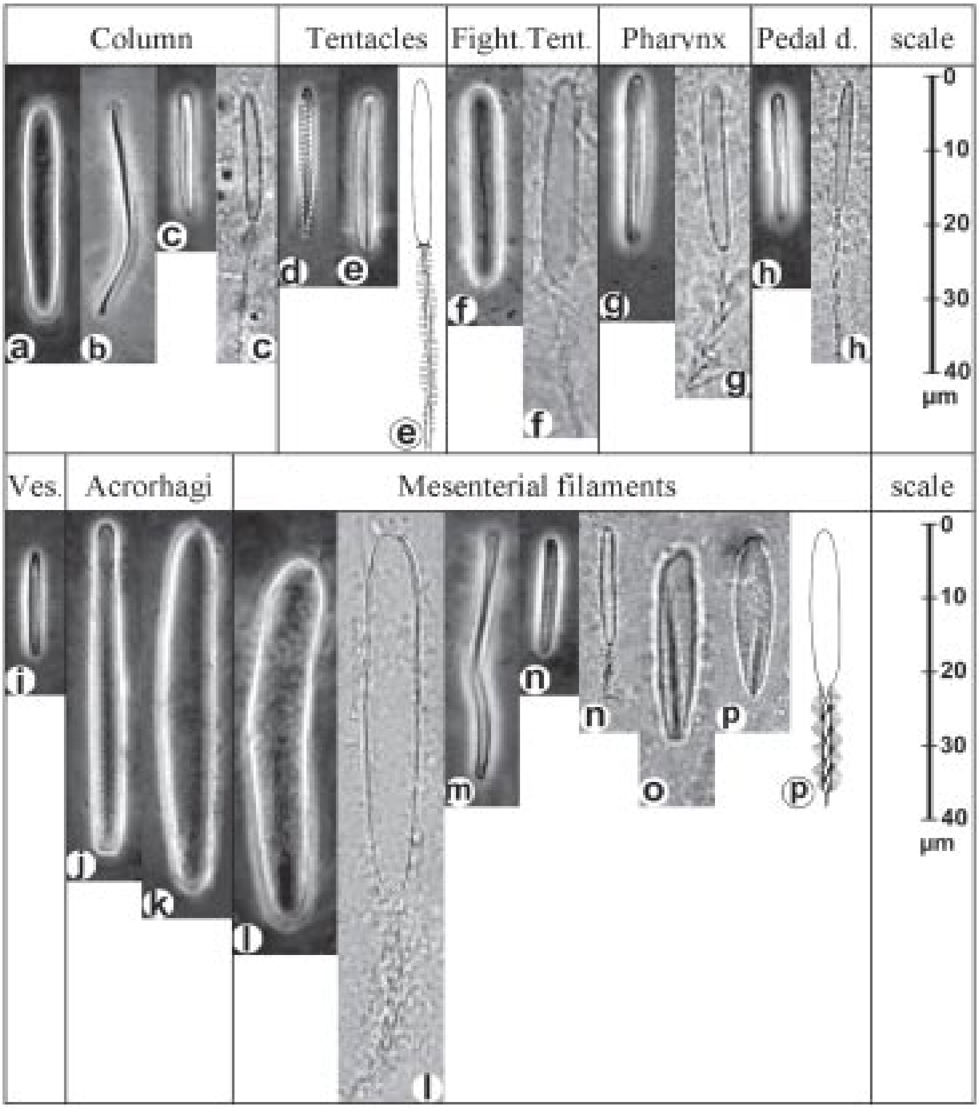

Fig. 9: Cnidae of *Oulactis concinnata*. Letters A–P correspond to cnidae types listed in Table 1.

◀ Fig. 5-8, Fig. 10. *Oulactis concinnata*. Fig. 5. Adhesive verrucae of the column and frond-like structures of the none-adhesive marginal ruff; note how several enlarged verrucae attach to a broken shell or stone. Fig. 6. Marginal ruff: transition sequence from simple verrucae to composed verrucae set on small lobes, towards the margin transforming into non-adhesive more or less delicate dendritic vesicles. Fig. 7. Drawing of transition sequence from verrucae to the marginal ruff of living specimen shown in Fig. 6. Fig. 8. Special fighting tentacles up to three times longer than feeding tentacles, with a paler colour and a different complement of cnidae. Fig. 10. Histological longitudinal section of upper column and marginal ruff (azocarmin triple staining); Mesogloea blue, ectoderm and endoderm red. Acrorhagus (Ac), column (Co), fighting tentacles (Ft), endodermal longitudinal muscle (Lm), papilla (P), marginal ruff (R), endodermal sphincter (Sp), tentacles (Te), verruca (Ve).

situated on thin-walled marginal region; ruff encompassing the tentacular crown; papillae bundled on approx. 192 fronds from which they branch towards the aboral side in a dendritic manner (figs 5-7). Tips of branches rounded; fronds of older cycles lengthened, usually a large brownish, greenish or blackish frond, corresponding to the first cycle, alternating with whitish fronds of different sizes (in many animals one large white and two small white ones), corresponding to subsequent cycles. Small white fronds correspond to the distally inserted rows of verrucae, large white fronds may have a blackish painting on their tips and vice versa, on some specimens all fronds white; acrorhagi present in two of ten examined specimens, generally large, round and light-coloured, placed on the smooth oral side of some of the fronds (74 acrorhagi on approx. 190 fronds counted in one animal). No distinct fosse. Insertions of mesenteries visible on proximal end of the column.

Oral disc and tentacles.— Oral disc wider than pedal disc, up to more than 220 mm × 120 mm diameter, round in small specimens and oval, irregular, and lobed in larger specimens, usually intensely coloured. Mouth central, strongly lengthened in large specimens, lips thick, pharynx longitudinally furrowed. Insertions of the mesenteries usually set off against the oral disc in colour, in some living animals directives visible as white lines. Feeding tentacles numerous, short, thick and conical, poorly retractile: up to more than 400, all of similar size, up to 20 mm long, located at the margin of the oral disc in three to four cycles. Tentacles with small subterminal slit. Four of 10 specimens with special fighting tentacles; fighting tentacles thread-like, up to 50 mm long, paler than feeding tentacles and with a different set of cnidae (fig. 8, 9f). Fighting tentacles seem to originate from the outer rows of tentacles, often restricted to one section of the tentacular crown.

Pedal disc.— Up to more than 20 cm × 10 cm diameter; firm, round in small specimens to oval in larger specimens, white, in living animals insertions of mesenteries visible; limbus weakly notched.

Internal anatomy.— Two medium-sized individuals had approx. 180 and 340 pairs of mesenteries, 50% or more perfect, the youngest ones connected to the pharynx with a small lappet, two pairs of directives. Mesenteries regularly arranged in six to seven cycles. Six of eight examined specimens fertile, only two small specimens sterile: all three sectioned specimens male, thus, sexes probably separate. Eggs of different sizes present on cnidae preparations of the filaments of specimen ZSM 20030294 from Perú. Reproductive tissue mainly on medium-sized mesenteries. All cycles of mesenteries except directives and mesenteries of youngest cycle may be fertile. Approximately same number of mesenteries distally and proximally; mesenteries seem to grow from distal to proximal.

Small marginal and oral stomata, round to slightly oval, oral stomata at about double diameter of marginal stomata.

Actinopharynx long, nearly reaching the pedal disc, with fine, deep longitudinal furrows and two siphonoglyphs, which are more or less aborally prolonged. Strongest mesenteries meet at the centre of the pedal disc.

Cnidom.— Comprises spirocysts (in tentacles), basitrichs (in all tissues except acrorhagi and fighting tentacles), microbasic b-mastigophors (in filaments and fighting tentacles), microbasic p-mastigophors B (in filaments), microbasic amastigophors A (in filaments), holotrichs (in acrorhagi and proximal region of column), rod-like

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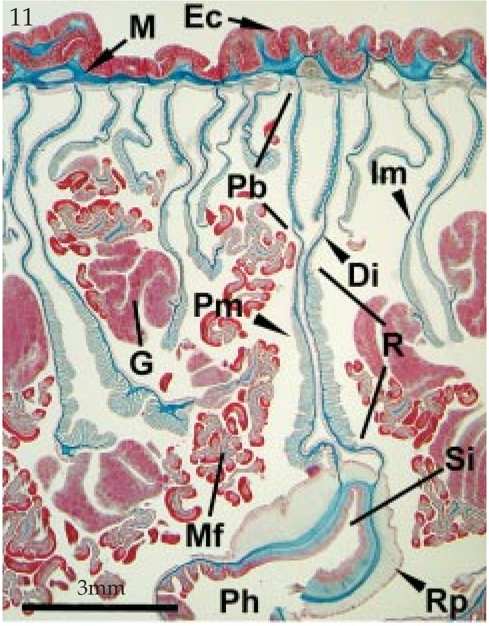

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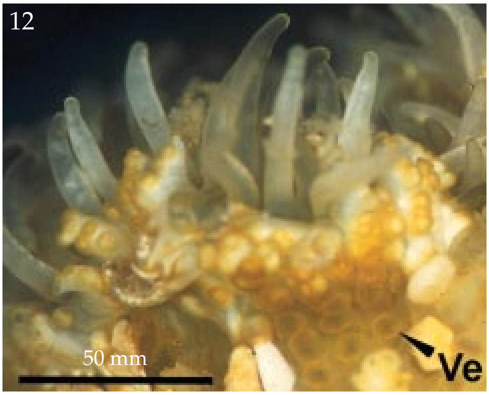

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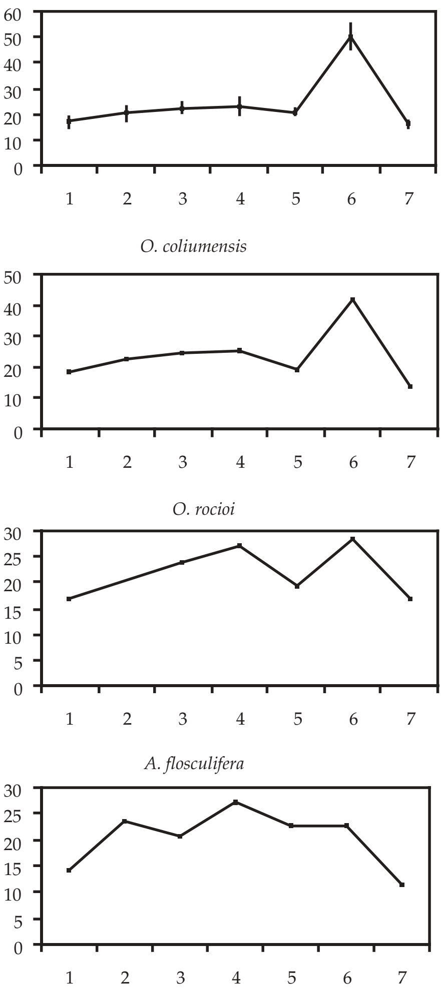
*O. concinnata*

*O. coliumensis*

*O. rocioi*

*A. flosculifera*

Fig. 11-13. Fig. 11. Transverse section of mid column of *Oulactis concinata* (azocarmin triple staining). Ectoderm (Ec), male gonads (G); pair of imperfect mesenteries (Im), mesogloea (M), trilobated mesenterial filament (Mf), lumen of actinopharynx (Ph), parietobasilar muscle (Pb), pair of perfect mesenteries (Pm), directives (Di), retractor muscle (R), reticulated pad (Rp), siphonoglyph (Si). Fig. 12. *Parantheopsis ocellata:* enlarged verrucae (ve) at the margin. Fig. 13. Cnidocyst diagrams of *Oulactis concinnata*, *Oulactis coliumensis*, *Onubactis rocioi* and *Actinostella flosculifera* modified after Schmidt (1972). Mean values were taken from fig. 9, Häussermann (1998), Ocaña (1994) and López-Gónzalez, den Hartog & García-Gómez (1995). x-axis: tissue, y-axis: mean value of cnidocysts in µm, vertical line (for *O. concinnata*): standard deviation; 1: basitrichs (column), 2: spirocysts (tentacles), 3: basitrichs (tentacles), 4: basitrichs (pharynx), 5 : microbasic amastigophors A (filaments), 6 : large basitrichs respectively microbasic b-mastigophors (filaments), 7: small basitrichs (filaments).

basitrichs (sporadic in column, rarely in filaments) (fig. 9).

The cnidom of *Oulactis concinnata* contains several characteristic elements: (1) Acrorhagi armed with two types of holotrichs (fig. 9J-K). (2) Column ectoderm with holotrichs and a few rod-like basitrichs in addition to basitrichs (fig. 9A-C). (3) Filaments with large microbasic b-mastigophors and microbasic p-mastigophors, rarely some rod-like basitrichs (fig. 9L-P). (4) Fighting tentacles with batteries of microbasic b-mastigophors (fig. 9F).

Table 1 provides data on cnidae size of the specimen ZSM 20020264 (Ex. 8), pedal disc diameter 35 mm in preserved state. Types and sizes of cnidae of five additional specimens were checked (ZSM 20020265, ZSM 20020266, IZUA-CNI-0032, MZUC 23166, ZSM 20030294), which lay within the ranges of the first specimen. The shaft of the microbasic p-mastigophors B in average was shorter than the one shown in fig. 9D, but always longer than half the length of the capsule; spines were often not clearly visible. One large microbasic p-mastigophor B 70 × 3.5 µm with a very long shaft and one large basitrich 40 × 2.7 µm were found in the column of specimens ZSM 20020265 resp. ZSM 20020266. The holotrichs of the column were mainly found in the proximal region.

Histology.— Musculature: Sphincter endodermal, diffuse, very weak and hardly recognizable (fig. 10). Mesenterial retractors diffuse, broad, restricted, starting in the middle of the mesentery, thickening and then abruptly ending close to the pharynx (fig. 11). Basilar muscles strong. Parietobasilar muscles strong (fig. 11), narrow in the distal part and broad in the proximal region, with short free pennon. Circular endodermal musculature of the body wall strong, absent in thin-walled marginal region and verrucae. Longitudinal musculature of the tentacles ectodermal. Circular musculature of the oral disc ectodermal. Male gonads strongly developed, may appear on all mesenteries except directives and youngest mesentries, mostly on medium-sized mesenteries, arranged in long strings (fig. 11).

Epithelia: Major part of the column covered with adhesive verrucae, hollow evaginations of the body wall formed by all three tissue layers (fig. 10). Towards the distal margin, verrucae smaller, compound and set on small lobes (fig. 7). All layers of the verrucae show some modifications: central part of the ectoderm with fewer cnidae, endodermal circular musculature of the column weak or absent (fig. 10), endoderm with dark granules and mesogloea thinner towards the centre of the verrucae (15 µm compared to up to 90 µm in the middle of the column). Thin-walled marginal region with a ruff of delicate dendritic papillae encompassing the tentacular crown, no musculature and all layers very thin (fig. 10), few cnidae present; in some regions with dark granules. Most proximal part of the column palisade-like, without verrucae. Pharynx with many fine longitudinal furrows; siphonoglyphs very distinct with strongly developed reticulated pads (fig. 11). Mesogloea of column, tentacles and oral disc spongy-like reticulated; oral disc mesogloea with endodermal protrusions.

Distribution and Zoogeography.— *Oulactis concinnata* is distributed between Playa Las Salinas, central Perú (9°19′10″S, 78°26′30″W), and Valdivia, southern Chile (39°48′31.3″S, 73°23′50.8″W) (see figs 1-2, App. 1-3). It was found regularly, but rarely abundant in north and central Chile from Arica to Valdivia (S2–S48: fig. 1). It was not found between Faro Corona (41°47′02.0″S; 73°52′58.8″W) at the north west tip of Chiloé Island and Punta Arenas (Strait of Magellan) (53°30′S; 70°56′W) (for detailed description and location of sampling sites south of Valdivia see Försterra & Häussermann, 2003).

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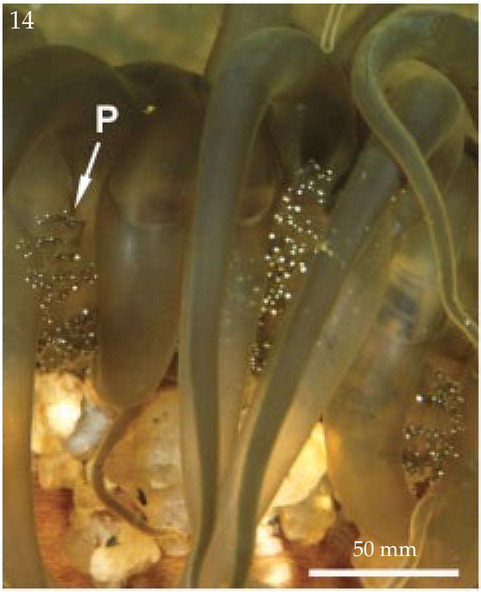

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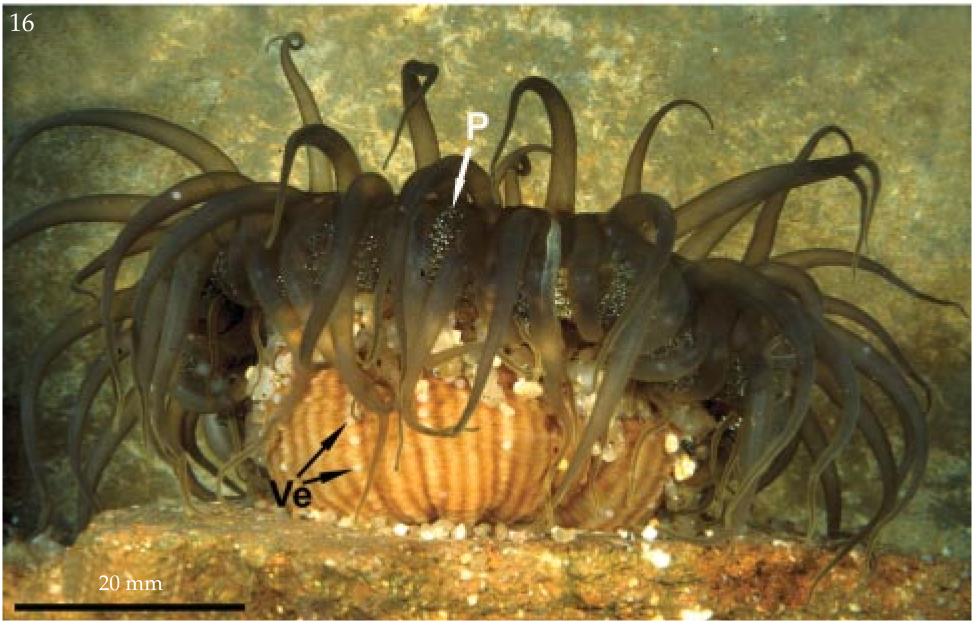

Fig. 14-16: *Oulactis coliumensis*. Fig. 14. Marginal ruff of *O. coliumensis* consisting of non-adhesive papillae (P). Fig. 15. Column and oral disc of *O. coliumensis* ZSM 20020267; note pale adhesive verrucae and lines of mesenterial insertions on the column and flat mouth opening. Fig. 16. Lateral view of *O. coliumensis* ZSM 20020268; note rows of pale, adhesive verrucae (ve) on the column.

*Oulactis concinnata* occurs in high abundance at the southern end of its confirmed distribution, along the exposed coast of Valdivia. Most probably the actual distribution extends further south but does not reach as far as the northern tip of Chiloé Island. From the pattern of presence in Peru (App. 3), it can be inferred that the northern distribution limit lies between Playa Las Salinas (09°19′10-15′′S; 78°26′30′′W) and the Peninsula Bayovar (05°48′15′′S, 81°04′99′′W). This distribution lies within the zoogeographical unit known as the Peruvian Province (Olsson, 1961) or the warm-temperate Southeast Pacific Province (Sullivan & Bustamante, 1999), which extends from the Peninsula Bayovar (5°40′S), Perú, to Chacao Channel north of Chiloé Island (40°30′S). Nevertheless, a recent paper negates the classical hypothesis of a faunal break-up at 42°S (Lancellotti & Vasquez, 1999) and proposes a transitional-temperate region between 35°S and 48°S. The region around Paita is considered by Olsson (1961) to be a transition zone, called the Paita Buffer Zone, where species of both the Peruvian and the Panamaic-Pacific province can be found.

Natural history of *Oulactis concinnata*.— Specimens of *Oulactis concinnata* regularly occur in crevices filled with coarse sand, broken shells or pebble in the intertidal and shallow water down to depths of 8 m (fig. 3). At one place (S37) a specimen was found at 15 m depth. Water temperature in the habitat during sampling ranged from 12 to 23°C, and salinity from 30.5 – 36‰. At two sites this species was so abundant that we found more than 30 specimens in 30 minutes search time (S41, S46a). In the intertidal zone, individuals of this species are generally found in moderately protected tidepools below mean tide level, which are not subject to prolonged water stagnation. At one station (S35), some individuals of *O. concinnata* were found emerged at low tide. Tides at Antofagasta, north Chile, are 0.8 m on average and 1.6 m at spring tide, and show little variation in the study region (Guiler, 1959). Below low tide level specimens of *O. concinnata* generally occur at illuminated sites, with moderate to strong water movement but protected from direct surge, where sedimentation is high (sand pools).

Individuals of *Oulactis concinnata* are fixed on horizontal substratum with the oral disc always directed upward and spread out. Its robust pedal disc is firmly attached to the rocks. Individuals of this species were never observed to touch each other. The inner tentacles are in a vertical position, the outer ones as well as the fighting tentacles are directed sideward or slightly hanging down. *Oulactis concinnata* was generally observed with its entire column buried in the substratum or hidden in a crevice (fig. 3). Where this was not possible, the upper half of the column is densely covered with foreign matter such as small stones, fragments of shells, glass, wood, plastic or whatever had the right size. Heavier or larger particles are attached to several verrucae (fig. 5). The process of attaching these artifacts appears to be quite fast as even living crabs or snails were observed to be attached to the column. The buried or sediment-covered column, together with the marginal ruff, provide *O. concinnata* with a very effective camouflage although its tentacles are always expanded.

With its weak sphincter and poorly movable oral disc and tentacles, *O. concinnata* swallows food by moving its thick lips towards the prey. None of the animals collected had foreign material in the gastrocoel that could be interpreted as food. In some animals, small stones were found in the gastrocoel and between the mesenteries. I found one individual trying to swallow an entire specimen of the crab *Taliepus dentatus* (Molina, 1782) with a carapace length of 60 to 70 mm, which was too large to fit completely into the gastrocoel and thus protruded out of the pharynx.

A small complete polyp was connected to the pedal disc of one specimen. It had about 1/20 of the size of the mother animal. No further specimens showed signs of asexual reproduction.

In the intertidal *Oulactis concinnata* is commonly associated with the sea anemone *Parantheopsis ocellata* (Drayton in Dana, 1846), which occurs in narrower crevices with finer substratum. In tide-pools it can also be found together with the anemones *Phymanthea pluvia* (Drayton in Dana, 1846) and *Anemonia alicemartinae* Häussermann & Försterra, 2001, which extend to more exposed rocky sites. In central Chile, specimens of this species are regularly found together with the ascidian *Pyura chilensis* (Molina, 1782). In the subtidal, it can also be found associated with the anemones *Parantheopsis ocellata, Paranthus niveus* (Lesson, 1830) or *Cereus herpetodes* (McMurrich, 1904). At Pingueral (S41), one specimen of *Oulactis concinnata* was observed with a specimen of the porcellanid crab *Allopetrolisthes spinifrons* (Milne Edwards, 1837) sitting on the column. The crustacean was reported by Baeza & Stotz (1995, 2001) to be a commensal on the sea anemones *Phymactis papillosa* (Lesson, 1830) (= *P. clematis*) and *Phymanthea pluvia*, and on the sea star *Heliaster helianthus* (Lamarck, 1816). Häussermann & Försterra (2001) also observed this crab on the sea anemones *Antholoba achates* (Drayton in Dana, 1846) and *Anemonia alicemartinae.*

The same individuals of *Oulactis concinnata* have been observed during seven years at S41 at exactly the same places. Therefore *O. concinnata* shows an interesting longevity and may become at least seven years old.

As the adhesion of the pedal disc of *O. concinnata* to the substratum is very strong, it is quite difficult to remove specimens without damaging the pedal disc. Thus it is recommendable to collect individuals attached to removable stones. During sampling, individuals of *O. concinnata* hardly contract; they seem unable of fully covering the tentacles with the column. In the sampling jar, they re-expand completely within a few minutes. During low tide, intertidal specimens are slightly retracted. In the aquarium they reattach quite fast and, once attached, do not change position. Fighting tentacles of two specimens in the aquarium were observed making searching movements, which is typical for this type of tentacles. Specimens of *Oulactis concinnata* that are transferred to formalin without previous relaxation react with an extreme expansion of the actinopharynx.

The tentacles stick to human skin when touched.

## Discussion

### Morphology of the marginal ruff

Neither Carlgren (1959) nor Riemann-Zürneck & Gallardo (1990) could find a thin-walled marginal region with delicate frond-like papillae in Carlgren's type specimens of *Isoulactis chilensis.* Examinations of recently collected specimens of *Oulactis concinnata* have shown that this thin-walled marginal ruff first described for *Oulactis coliumensis* (Riemann-Zürneck & Gallardo, 1990) is difficult to observe. These fronds are clearly visible on living animals and on histological sections of well preserved specimens (fig. 6, fig. 10), but not recognizable on badly preserved or old material. This might be due to strong contraction of the marginal region or decomposition of the delicate tissue. The specimens I examined clearly present typical actiniid verrucae on the column which, towards the margin, become smaller, compound and set on lobes. In the uppermost region, there is a distinct thin-walled region, where the verrucae transform more or less abruptly into delicate frond-like, non-adhesive papillae (figs 6-7, see histology section). Each frond of papillae is corresponding to one exo- respectively endocoel. Acrorhagi, when present, are placed at the oral side of the terminal lobes (fig. 7). This can easily be observed on living animals, especially in the aquarium, and was confirmed by the histological sections (fig. 7, fig. 10).

*Oulactis magna* (Stuckey, 1909) and *Oulactis muscosa* (Drayton in Dana, 1846) from New Zealand and Australia are described by Carlgren (1949a) and Riemann-Zürneck & Gallardo (1990) as possessing the same marginal structures consisting of adhesive verrucae formerly described for *O. concinnata*. Original type material of these two species is not available any more. However, it is most probable that the delicate frond-like papillae have been overlooked. Oscar Ocaña (in litt., 2002) confirmed that specimens of these species from New Zealand that he examined present a thin-walled region with delicate frond-like, non-adhesive papillae.

## Function of the marginal ruff

The function of the marginal ruff within the genus *Oulactis* is still unclear. In *Actinostella flosculifera* (Le Sueur, 1817), the marginal ruff is expanded while tentacles are retracted during the day. During the night, the situation is vice versa (Ocaña, 1994). *Actinostella flosculifera* lives buried in sand or soft substratum with only the ruff and oral disc protruding into the water column. As this species is richly supplied with zooxanthellae, this behaviour guarantees a maximum light exposure during the day and maximum feeding success during the night. The abundant presence of nematocysts in the collar indicate that the collar can also be used to catch prey, which is e.g. walking over the oral disc (Ocaña, 1994).

The examined species of the genus *Oulactis* and *Onubactis rocioi* (López-González, den Hartog & García-Gómez, 1995) neither present zooxanthellae nor abundant nematocysts in the marginal ruff. A hypothesis about the marginal ruff of the other genera is that the ruff considerably increases the surface and thus represents an adaptation to a life style in bottoms with low concentrations of dissolved oxygen and high organic matter levels (Sassamann & Mangum, 1972; Riemann-Zürneck & Gallardo, 1990; López-González, den Hartog & García-Gómez, 1995). Both *Oulactis coliumensis* and *Onubactis rocioi* live on sandy and muddy bottoms. Sometimes both *Oulactis muscosa* and *Oulactis magna* from New Zealand can be found in polluted areas or with their pedal discs buried in anoxic substrate (O. Ocaña, in litt., 2003). In contrast to these species, *Oulactis concinnata* lives in intertidal and shallow water crevices, where oxygen supply is no problem. Thus, for this species, the ruff is not necessary for a quick recovery after a time with oxygen deficiency. Specimens of *O. coliumensis* seem to be tolerant of oxygen depletion, as they survived several days in an unventilated aquarium with stagnating water. In comparison, however, specimens of *O. concinnata* are very sensitive to unventilated water: after two hours in an aquarium without air supply, two specimens were in bad condition, with their pharynxes strongly protruded.

A final possible function of a strongly branched marginal ruff in a habitat with strong currents and waves could be to slow down the water current passing by the oral disc as it is known from the tentacles (Koehl, 1982). Lower current speed increases the probability of food particles to get caught by the tentacles. As far as it is known, all species with marginal ruff live buried with only the oral disc protruding out of the substrate. In habitats with strong water movement, sediment particles are transported horizontally on the substrate surface. The ruff might have a sieve function allowing water to pass by the oral disc while sediment particles are kept off. In *O. concinnata*, which is not able to fully contract its oral disc, it additionally improves camouflage.

## Origin of the marginal ruff

The classification of most actiniid genera depends on the definition and taxonomic evaluation of the different wart-, blister- and frond-like structures that may occur in the upper part of the column (Riemann-Zürneck & Gallardo, 1990). Therefore, these structures deserve detailed assessment. The dendritic marginal structures of *Oulactis* have been called vesicles by Riemann-Zürneck & Gallardo (1990). To avoid confusion with the columnar vesicles of species of the genera *Phymactis*, *Phymanthea* and *Bunodosoma* (see Häussermann, in preparation). I will call these structures papillae in the following. Stephenson (1922) interpreted the frond-like papillae as complicated and extended acrorhagi. However, Carlgren (1949a) presumed, at least for the genus *Saccactis,* that the papillae were expanded verrucae. Like Carlgren (1924), I disagree with Stephenson. Acrorhagi are not necessarily present on the marginal fronds of all specimens of these species and thus the papillae cannot be extended acrorhagi. Although I agree with Carlgren that the ruff is derived from distal verrucae, to me, the morphological, histological, and functional differences between the distal fronds and verrucae are sufficient that the fronds should be considered separate from typical columnar verrucae. I see a clear transition series from simple, adhesive verrucae to compound verrucae to non-adhesive papillae in *Oulactis concinnata* (figs 6-7). Even though the transition zone in most examined specimens was smaller than that shown in Fig. 6 it was always present; the distal region with non-adhesive papillae was generally broader. Structures that are similar to transition stages of verrucae in *O. concinnata* were also observed in specimens of other actiniid species such as *Parantheopsis ocellata* (Häussermann 1998) (fig. 12) and *Anthopleura* spp. from Japan (Kensuke Yanagi, in litt., 2002). If the enlarged verrucae as well as the frond-like papillae of the marginal ruff were sequences of variations of the same structure and derived from verrucae, the structures would be homologous. But this phenomenon could also be reversible or could have evolved several times. In this case the group of sea anemones with a marginal ruff might not be monophyletic. Further studies are needed to reveal whether these structures are homologous, which would underline a close relationship of these genera. For further discussion of the terms verrucae, vesicles and acrorhagi see Riemann-Zürneck & Gallardo (1990), den Hartog (1987) and Daly (2003).

## Cnidae

In Table 3, the cnidae of four species of the genus *Oulactis* and one species of each of the further genera with a marginal ruff; *Actinostella* and *Onubactis* are listed. The most striking similarity of the four *Oulactis* species in comparison to the two further species are the large microbasic b-mastigophors in the filaments.

A comparison of cnidae sizes is only of minor usefulness without statistics (Williams, 1996). Thus size ranges of cnidae were not used as a diagnostic feature for the compared anemones. Modified cnidocyst diagrams (after Schmidt, 1972) use mean values and ideally standard deviation to compare relative sizes of the most common types of cnidae. All values of one diagram should be taken from the same specimen. Such diagrams are given for *Oulactis concinnata, Oulactis coliumensis, Actinostella flosculifera* and *Onubactis rocioi* (fig. 13). The cnidocyst diagrams of *O. concinnata* and *O. coliumensis* show striking similarities and differ from these of *A. flosculifera* and *O. rocioi* (fig. 13).

Many of the differences among the compared species (table 3) with respect to the cnidom may be attributed to the patchy distribution and low numbers of certain types of cnidae. For instance, I found the rod-like basitrichs in the column and the filaments of *Oulactis concinnata* only sporadically; these cnidae have been reported for *Oulactis magna*, but not for *Oulactis coliumensis* and *Oulactis muscosa*. Microbasic amastigophors A are mentioned for the pharynx of *O. magna, O. muscosa, O. concinnata* and *Actinostella flosculifera* (table 3). Like Carlgren (1959), I found only one of this type of cnidae in the pharynx of *O. concinnata*. Riemann-Zürneck & Gallardo (1990) found additional p-mastigophors in the filaments of *O. coliumensis;* this type of cnidae is also present in *O. concinnata* (fig. 9O). I did not find these cnidocysts in the specimen of *O. coliumensis* I examined. These small p-mastigophors are already known from some other actiniid species (den Hartog, 1987). A second type of small basitrichs has been reported from the column of *O. muscosa* (Carlgren, 1949a) and from the pharynx of *O. magna* (Riemann-Zürneck & Gallardo, 1990). I found one small basitrich of approx. 15 µm in the tentacles of *O. concinnata* and small basitrichs approx. 20 µm in the pharynx of *O. coliumensis*. These small basitrichs, compared to the larger basitrichs with which they co-occur, are generally very sparse, and might be difficult to observe as they originate from the endoderm. The presence of acrorhagi is facultative, and thus the absence of holotrichs is not informative. These cnidae have not been reported in the column of *O. a)magna sensu* Carlgren (1924) and *O. coliumensis*. However, I found very sporadic holotrichs in the column of the specimen of *O. coliumensis* I examined (Häussermann, 1998). It is not known whether holotrichs of the column are induced as are those of the acrorhagi.

Differences in search technique, intensity or focus may also account for the differences. *Oulactis coliumensis* seems to be the only species with abundant spirocysts in the pedal disc. In the past, scientists generally did not examine the cnidae of the pedal disc, so comparing species is complicated. Furthermore, as Riemann-Zürneck & Gallardo (1990) mention, spirocysts may be difficult to observe on smears, but are obvious on histological sections. Nevertheless, I only found few spirocysts on the sections of the specimens of *O. concinnata* and *O. coliumensis*.

Actiniid sea anemones generally present a rather simple cnidom with few cnidae types, dominated by basitrichs. Thus, more uncommon cnidae like holotrichs and rod-like basitrichs can be helpful to distinguish between species or genera. Diagnostic cnidae must be present and rather abundant in all specimens of a species to be useful as a character for identification. Fired cnidae additionally reveal many structures that can be characteristic of the species; e.g. the relative length of the shaft and the number of windings on the shaft. Thus, if possible, photos or drawings of fired nematocysts should be included in species descriptions. Permanent slides of fired cnidae can easily be prepared even in the field applying the technique of Yanagi (1999). Future detailed examinations, including fired cnidae, of several specimens of the species compared in Table 3 are necessary to decide which cnidae are convenient as a diagnostic feature at the species or genus level.

## Taxonomy

### a) Synonymization of the genera *Saccactis*, *Isocradactis* and *Isoulactis* with the genus *Oulactis*

In the taxonomic literature, there has been a lot of confusion about the validity of the genera *Oulactis* M. Edwards & Haime, 1851, *Saccactis* Lager, 1911, *Isocradactis* Carlgren, 1924, and *Isoulactis* Carlgren, 1959 (Stephenson, 1922; Carlgren, 1959). Carlgren (1949b; 1950; 1954) synonymized the genus *Saccactis* with the genus *Oulactis*. In 1990, Riemann-Zürneck & Gallardo (1990) reintroduced the genus *Saccactis*. They described for the first time a marginal ruff composed of tiny, dendritic papillae, which they thought to be unique for the genus *Saccactis* (fig. 14). The genera *Oulactis*, *Isoulactis* and *Isocradactis* were thought to possess adhesive verrucae at the margin and lack this thin-walled distal region of the scapus (López-Gónzalez, den Hartog & García-Gómez, 1995). *Oulactis* was supposed to possess acrorhagi whereas *Isoulactis* and *Isocradactis* were not thought to exhibit these structures (Riemann-Zürneck & Gallardo, 1990).

In 1924, Carlgren introduced the genus *Isocradactis* for the species *Cradactis magna* because the ruff of the specimens he examined did not contain batteries of nematocysts but could act as “sucking warts” – his specimens did not possess acrorhagi. *Sensu* Carlgren (1924) the fronds of the imperfectly described type species of the genus *Cradactis* are probably “batteries of nematocysts and no sucking warts”. In 1959, Carlgren (1959) doubtfully erected the new and still monotypic genus *Isoulactis* with only minor differences to the equally monotypic genus *Isocradactis*. According to Carlgren (1959), the marginal ruff of *Isoulactis chilensis* is identical to that of *Oulactis*. He also stated that, if Parry’s (1951) observation of acrorhagi in *O. magna* were correct, it undoubtedly would belong to the genus *Oulactis*. As he was not sure whether to believe Parry’s observation, Carlgren (1959) left this species from New Zealand within the genus *Isocradactis*. There is no reason for not believing Parry (1951); in addition Oscar Ocaña (in litt., 2002) regularly observed acrorhagi in *O. magna* from New Zealand.

There are several arguments for the synonymization of the genera *Saccactis, Isocradactis* and *Isoulactis* with the genus *Oulactis:*

The identical structure of the column with adhesive verrucae and the marginal ruff consisting of delicate frond-like papillae in *Oulactis concinnata* (= *Isoulactis chilensis), Oulactis (Saccactis) coliumensis, Oulactis magna* (formerly called *Isocradactis magna),* and *Oulactis muscosa* (see discussion of the morphology of the marginal ruff)

The (at least facultative) presence of acrorhagi in *O. concinnata*, *O. coliumensis, O. magna,* and *O. muscosa*

The strong similarity of characteristic morphological features and habiti of *O. muscosa* and *O. concinnata* that can be seen in Dana’s (1846) original descriptions, on his drawings (Plate 5, figs 40-43; see Fautin, 2003) and on *in vivo* pictures of *O. muscosa*

Table 3: Comparison of the types of cnidae of 6 species with marginal ruff; $^{s}$: sporadic, $^{f}$: few, $^{c}$: common and $^{v}$: very common. Corresponding cnidae are arranged in the same row.

| Tissue / Species | *Oulactis concinnata* (values from own examination; *: cnidae types not found by Riemann-Zürneck & Gallardo, 1990 in the type material of *Isoulactis chilensis*) | *Oulactis magna sensu* Carlgren, 1924 (values from Riemann-Zürneck & Gallardo, 1990) | *Oulactis coliumensis* (values from Riemann-Zürneck & Gallardo, 1990; *: ranges from own examination that lay out of the here given ranges) | *Oulactis muscosa* (values from Carlgren, 1949: 134) | *Actinostella flosculifera* (values from Ocaña, 1994: 157) | *Onubactis rocioi* (values from López-Gónzalez, den Hartog & García-Gómez, 1995: 380)* |
|---|---|---|---|---|---|---|
| Tentacles | Spirocysts$^{v}$:<br>16.2-27 × 1.8-2.7 µm | Spirocysts:<br>25-30 × 2-2.5 µm | Spirocysts:<br>< 33 × 3-3.5 µm | Spirocysts:<br>not mentioned | Spirocysts$^{v}$:<br>13.7-29.1 × 1.8-2.3 µm | Spirocysts$^{v}$:<br>13-25 × 2.0-2.7 µm |
| | Basitrichs$^{v}$:<br>19.8–28.8 × 1.8-3.2 µm | Basitrichs:<br>20-24.5 × 2-2.5 µm | Basitrichs:<br>(19*)23-29 × 2-2.5 µm | Basitrichs$^{c}$:<br>19.7-25.4 × 2.5-3.5 µm | B-mast.$^{v}$:<br>16.4-25.5 × 1.6-2.3 µm | Spirulae$^{v\text{-}c}$:<br>21.4-27.6 × 2.2-2.7 µm |
| | | | | | B-mast.$^{c}$:<br>6.4-12.7 × 1.8-2.1 µm | Spirulae$^{s}$:<br>12.6-18.7 × 1.6-2.2 µm |
| Column | Basitrichs$^{c}$:<br>15.3-21.6 × 1.4-2.7 µm | Basitrichs:<br>15.5-18 × 2 µm | Basitrichs:<br>13-19(21*) × 2-2.5 µm | Basitrichs:<br>15.5-19.7 × 2.2-2.8 µm | B-mast.$^{v}$:<br>10-15.5 × 1.8 µm | Spirulae$^{c}$:<br>12.9-19.6 × 2.0-2.3 µm |
| | | | | Basitrichs$^{v}$:<br>22.6-29 × 3.5 µm | B-mast.$^{s}$:<br>22.8-36.4 × 2.5-2.7 µm | |
| | Rod-like basitr.$^{f*}$:<br>27.0-33.3 × 1.4-1.8 µm | Rod-like basitr.:<br>33-44 × 1.5-2 µm | | | | |
| | Holotrichs$^{f\text{-}c}$:<br>25.2-35.1 × 4.5-6.3 µm | | Holotrichs$^{*s}$:<br>19-21 × 4.8 µm | Atrichs:<br>19.7-33.8 × 4.2-5.6 µm | Holotrichs$^{f}$:<br>42.8-52.8 × 3.5-4.6 µm | |
| | | | | | Spirocysts: present | |
| Marginal ruff (papillae) | Basitrichs$^{f}$:<br>11.7-15.3 × 1.4-1.8 µm | not mentioned | Basitrichs:<br>14.5-19 × 2-2.5 µm | not mentioned | B-mastig.$^{v}$:<br>8.2-13.7 × 1.8-2.3 µm | Spirulae$^{f}$:<br>8.9-13.4 × 1.6-2.0 µm |
| | | | | | P-mastig.$^{S}$:<br>16.4 × 5.5 µm | |
| Actinopharynx | Basitrichs$^{c}$:<br>17.1-27.0 × 1.8-3.6 µm | Basitrichs 1:<br>26-32 × 3-3.5 µm | Basitrichs:<br>(21*)26-33 × 3 µm | Basitrichs$^{c}$:<br>27.5-32.4 × 4 µm | B-mast.$^{c}$:<br>24.6-31.9 × 1.8-3.2 µm | Spirulae$^{c\text{-}f}$:<br>21.4-30.3 × 2.5-2.9 µm |
| | | Basitrichs 2:<br>9.5-13.5 × 1.5-2 µm | | | B-mast.$^{v}$:<br>10.9-13.7 × 1.4-1.8 µm | |
| | Microbasi. amastig. A:<br>1 cnida<br>21.7 × 4.1 µm | P-mast. (opaque):<br>29 × 4-4.5 µm<br>P-mast.: 26 × 6-8 µm | | Microbas. p-mast.:<br>21-26.8 × 4.6-6 µm | P-mast.$^{c}$:<br>20.9-23.7 × 4.6-6.4 µm<br>P-mast.$^{s}$: 10.9 × 4.6 µm | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mesenterial filaments | Basitrichs$^{c}$:<br>13.5-19.8 × 1.4-2.3 µm<br>Microbas. b-mast.$^{c}$:<br>38.7-57.6 × 5.4-9.9 µm<br>Microbas. p-mast.$^{c*}$:<br>22.5-28.8 × 2.7-5.4 µm | Basitrichs:<br>9-12 × 2 µm<br>B-mast.:<br>46-55 × 6-7 µm | Basitrichs: (10*)<br>14.5-17.5 × 1.5-2.5 µm<br>B-mast.:<br>35-46(55) × 4.5-6.5 µm<br>P-mast.: 17.5-20(22*) × 3.5-4.5 µm<br>(*:not found) | Basitrichs:<br>15.5-18.3 × 2.2-2.5 µm<br>Basitrichs:<br>38-48x x5.6-7 µm | B-mast.$^{c}$:<br>9.1-13.7 × 1.4-2.1 µm<br>B-mast.$^{s}$:<br>22.8 × 2.7 µm | Spirulae$^{c}$:<br>14.2-18.2 × 1.3-1.8 µm<br>Spirulae$^{c}$:<br>21.8-34.7 × 3.6-4.9 µm<br>Penicilli B1$^{s}$:<br>13.4-17.8 × 3.1-3.8 µm |
| | Microbas. amast. A$^{f}$:<br>18.0-22.5 × 3.6-5.4 µm<br>Rod-like basitrichs$^{s*}$:<br>2 cnidae<br>33-34 × 1.5-2 µm | P- mast. (opaque):<br>22-26 × 3.5 µm<br>Rod-like basitr.:<br>35-48 × 6-7 µm | P-mast.?(opaque):<br>(18*)20-25 × 3-4.5 µm | Microbas. p-mast.:<br>22.6-26.8 × 4.5-5.5 µm | P-mast.$^{v}$:<br>18.2-27.3 × 4.6-5.9 µm | Penicilli A$^{f\text{-}c}$:<br>16.5-24.9 × 3.6-4.9 µm |
| Acrorhagi | Holotrichs 2$^{c}$:<br>43.2-54.9 × 4.5-8.1 µm<br>Holotrichs 1$^{v}$:<br>39.6-53.1 × 2.3-3.2 µm<br>(*: no acrorhagi present) | not present in this specimen | Holotrichs 1: 50-64(70*) × 5-6.5 µm<br>Holotrichs 2: (29*)<br>32-43.5 × 3.5-4 µm<br>Spirocysts:<br>23-25 × 1.5-2.5 µm<br>(*: not found) | Atrichs$^{v}$:<br>46.5-70.5 × 7 µm<br>Basitrichs$^{v}$:<br>36.6-45 × 2.8 µm | No acrorhagi present | No acrorhagi present |
| Pedal disc | Basitrichs$^{f\text{-}c}$:<br>15.3-21.6 × 2.3-2.7 µm<br>Some spirocysts present<br>(*: not examined) | not mentioned | Basitrichs: (14*)<br>17-20 × 2-2.5 µm<br>Spirocysts:<br>17-20(25*) × 2-2.5 | not mentioned | not mentioned | Spirulae$^{c}$:<br>13.4-22.7 × 2.0-2.7 µm<br>Spirocysts$^{v}$:<br>20.5-33.8 × 2.7-3.1 µm |

*: Spirulae are also called basitrichs respectively microbasic b-mastigophors; penicilli are also called microbasic p-mastigophors respectively microbasic amastigophors A (England, 1991).

(Carlgren, 1949a: Plate II) and *O. concinnata* (figs 3-4); this similarity was also mentioned by Verrill (1907)

To complete this revision, specimens of the other species of the genus *Oulactis*, *O. muscosa* (as the type species of the genus *Oulactis*), *O. mcmurrichi* (as the type species of the genus *Saccactis*) and *O. magna* (as the type species of the genus *Isocradactis*) from New Zealand and Australia have to be examined in life. There is no type material available for *O. muscosa* and *O. magna,* thus neotypes have to be designated and species re-described. As the type material of *O. mcmurrichi* was already in a rather poor condition in 1911 and almost disintegrated in 1990 (Riemann-Zürneck & Gallardo, 1990), it would be recommendable to also re-describe this species and designate a neotype.

The genus *Oulactis* seems to be most similar to the genus *Anthopleura* with the presence of adhesive verrucae on the column, large microbasic b-mastigophors in the filaments, and at least the facultative presence of acrorhagi and of holotrichs and rod-like basitrichs in the column ectoderm. This was already mentioned by Riemann-Zürneck & Gallardo (1990). On the other hand, we still do not know about the phylogenetic importance of characters such as verrucae, acrorhagi and the marginal ruff. Future molecular analysis might also help us to know which characters are phylogenetically preserved and could help to clarify phylogenetic relationships within the Actiniidae.

b) Synonymization of *Oulactis concinnata* with *Isoulactis chilensis*

Dana's (1846) description of *Metridium concinnatum* from central Perú is relatively short but provides a very good drawing of the living animal as well as of its position in the habitat (see Fautin, 2003). Unfortunately, there is no type material. The type material for the species described by Carlgren (1959) as *Isoulactis chilensis* still exists and is identical with the above described species.

Carter (1965) synonymized *Isoulactis chilensis* with *Oulactis concinnata*, which she called *Phyllactis concinnata*, without further explanation, but this has not been followed by other scientists. *Oulactis concinnata* is the only species with a marginal ruff found in southern Perú (Pax, 1912; Stefan Austermühle, in litt., 2002) that meets the description of Dana (1846). The description and the drawing provided by Dana (1846) in combination with the *in vivo* photos and the preserved specimens from Pucusana, Perú, leave no doubt that these two species are identical. The two are identical in colour, habitus, posture, habitat, behaviour and in morphological features like verrucae and marginal ruff.

c) Species formerly synonymized with *Oulactis concinnata*

Carlgren (1951) synonymized McMurrich´s (1893) *Oulactis californica* from the Gulf of California with *Oulactis concinnata*. This synonymization is hard to comprehend: according to McMurrich (1893), the species is elongate and small (15 mm diameter pedal disc, 30 mm high), with 48 tentacles, 24 pairs of mesenteries, 48 longitudinal rows of verrucae in the uppermost part of the column and a circumscribed sphincter. Carlgren's (1951) description mainly agrees with that of McMurrich; he additionally found zooxanthellae. However, neither fits Dana's description of *O. concinnata* at all. In fact, it seems obvious that McMurrich's *O. californica* belongs to the genus *Actinostella*. The specimens from Paita, northern Perú (fig. 2), examined by Pax (1912) and assigned to the species *O. concinnata*, most probably also belong to the species *Actinos-*

*tella californica*. Pax (1912) reports a circumscribed sphincter and small body size (20 mm broad and 20 mm high). It still has to be clarified if *A. californica* is identical with *A. bradleyi* (Verrill, 1869), a very similar species described earlier for the same region. Thus the latter species name would have priority.

d) Former descriptions of *Oulactis concinnata* and remarks on the description of the species *Oulactis coliumensis*

Carlgren (1959) believed that the lobing of the oral discs of his specimens of *Oulactis concinnata* was due to strong contraction. All larger individuals of *O. concinnata* observed in the field exhibit a strongly lobed oral disc in expanded state (fig. 3). In contrast to Carlgren's specimens, none of the specimens I examined had fertile directives. Carlgren (1959) described the longitudinal muscles of the tentacles of his specimens as endodermal, but the drawing he provides shows ectodermal musculature. The longitudinal muscles of the specimens I examined are clearly ectodermal. After examining the type specimen, Riemann-Zürneck & Gallardo (1990) doubted Carlgren's statement that *O. concinnata* would possess 280 to 290 tentacles, believing instead that this species had fewer tentacles. However, I regularly counted more than 400 tentacles in Chilean specimens. The specimens of *O. concinnata* examined by Carlgren had neither acrorhagi nor fighting tentacles, and were all from the intertidal. In addition to the cnidocysts Carlgren (1959) and Riemann-Zürneck & Gallardo (1990) described for *O. concinnata*, I found sparse rod-like basitrichs in the column and the filaments as well as additional p-mastigophors in the filaments.

The new material and field observations also add new insight into the biology of *Oulactis coliumensis*. This species was previously known only from depths between 40 and 55 m (Riemann-Zürneck & Gallardo, 1990). Two of the specimens of *O. coliumensis* I examined were dredged by the research vessel Kaikai of the Universidad de Concepción in 1998 from approx. 20 m depth. Additionally, observations of living animals revealed that the verrucae are adhesive (fig. 14). Unlike the seven specimens of the first description, the two specimens examined in this study showed slight variation in colour: the column of the smaller animal was light green and transparent in its most proximal region with transparent green tentacles (fig. 15), the other one had an ochre column with white verrucae and transparent brown tentacles (fig. 16); the tips of the ruff of both specimens were whitish (figs 14-15). The pedal discs were transparent whitish. Both examined individuals presented acrorhagi. In contrast to the description of Riemann-Zürneck & Gallardo (1990), the acrorhagi of living animals are situated close to the top on the oral side of the marginal lobe like in *O. concinnata*. The observation of Riemann-Zürneck & Gallardo (1990) might be an artifact due to contraction of the preserved specimens. The mouth openings of living animals are not wide and the lips are not prominent (fig. 15). The outer tentacles hang down, the inner are set upright (figs 15-16); the tentacles have small distal openings. Both examined specimens were able to contract completely. In the aquarium, they dug into the sandy substratum comparably fast with the pedal disc and attached their pedal disc to the glass bottom with only the ruff and the tentacular crown protruding out of the substratum. Both specimens survived several days in an aquarium in stagnating water without air supply. The cnidome given by Riemann-Zürneck & Gallardo (1990) could be confirmed; in addition sporadic holotrichs were observed in the column. In contrast to Riemann-Zürneck & Gallardo (1990), I found only few spirocysts in the smears as well as in the histological section of the pedal disc of the examined specimen of *O. coliumensis* (Häussermann, 1998). The specimen I sectioned was male, just as the specimens sectioned by Riemann-Zürneck & Gallardo (1990); its directives did not carry reproductive tissue.

e) The genus *Actinostella*

Carlgren (1949b) lists the genus *Actinostella* under synonymies of the genus *Phyllactis*. It is not clear why he does not use the senior synonym. He states that the genus possesses a column with verrucae in its "lower" (= proximal) part. In the next sentence, he mentions that there is a ruff between the verrucae and the tentacles. *Actinostella flosculifera* (Ocaña, 1994) as well as *Actinostella correae* (Schlenz & Belèm, 1988(92)) are described with verrucae in the "upper" (= distal) part of the column. It is most probable that Carlgren by a slip of the pen mixed up the words "upper" and "lower". Therefore, I propose to change this sentence in an amended diagnosis of the genus *Actinostella* to "usually with verrucae in its upper part". I also incorporated some other characters like the presence of 48 tentacles (Riemann-Zürneck & Gallardo, 1990) and the possible presence of zooxanthellae. This emended diagnosis is to be verified in a revision of the genus *Actinostella* including all its species.

## Fighting tentacles

Catch or fighting tentacles appear in addition to feeding tentacles and develop from them (Shick, 1991). As these tentacles are used in intraspecific agonistic behaviour rather than for catching prey, the name fighting tentacles is more appropriate than the name catch tentacles (Purcell, 1977). They are defined by their larger size, relative opacity and distinctive cnidome consisting especially of large, penetrating holotrichs (Shick, 1991). Fighting tentacles were thought to appear only within mesomyarian sea anemones; the counterpart of actiniid anemones was thought to be the acrorhagi (Williams, 1975). During the last decade, fighting tentacles containing holotrichs were discovered in a few actiniid anemones such as *Cnidopus japonicus* (Sanamyan & Sanamyan, 1998). Neither of these species possesses acrorhagi. A fighting tentacle of a member of *Oulactis concinnata* is up to three times longer than a feeding tentacle, and possesses a different equipment of cnidae (fig. 9). The colours of the fighting tentacles of *O. concinnata* in life are paler than those of feeding tentacles. In one specimen in the aquarium, I observed several of these tentacles, which were restricted to the same section of the tentacular crown where acrorhagi were present, suggesting that fighting tentacles, like acrorhagi, are used in agonistic behaviour in this species. I found no holotrichs in any of the several tentacles (from three different specimens) I examined, finding instead batteries of microbasic b-mastigophors that are larger and significantly wider than the cnidae of the feeding tentacles. In the aquarium, these tentacles were observed to make the searching movements typical of fighting tentacles. Williams (1975) already remarked that further work is required to ascertain whether holotrichs are characteristic of all tentacles exhibiting specialized "searching" and aggressive behaviour. Although I did not directly observe these tentacles being used in agonistic behaviour, I have no doubt that they have the same function as fighting tentacles. Therefore I propose to expand the definition of fighting tentacles to "different tentacles with larger size, relative opacity and a distinctive cnidome" which is not restricted to the presence of holotrichs.

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## Appendix 1

List of study sites (S 1-S 50) of VH and GF; *Oulactis concinnata* found (*); latitude/longitude (GPS respectively Microsoft Encarta, 2002; the latter without seconds); site description; dates visited. S (sporadically: 1-10 individuals seen in 45 min search), F (frequent: 11-30 animals seen), V (very abundant: more than 30 animals seen).

S 1. 18°30′S, 70°19′W, La Capilla, approx. 5 km S Arica. Intertidal. Extensive rocky plateau with tide pools and surge channels. 28.11.97.
S 2.* 18°30′S, 70°19′W, La Capilla, approx. 5 km S Arica. 0-6 m. Sand, shells, and boulders; alga *Lessonia trabeculata*; wave-exposed vertical wall. 31.11., 3.12., and 6.12.1997. R.
S 3. 18°30′S, 70°19′W, 500 m S La Capilla, Arica. Intertidal. Exposed rocky coast with tide pools, deep surge channels, and overhangs. 27.11.1997.
S 4. 18°32′S, 70°19′W, S Playa Corazones in front of caves, approx. 8 km S Arica. Intertidal. Exposed rocky coast with many tide pools. 26.11.1997.
S 5.* 20°56′S, 70°07′W, approx. 5 km N Rio Seco. Intertidal. Gently sloping rocky shore, bottom with cobble. 12.12.1997. R.
S 6. 20°56′S, 70°07′W, approx. 5 km N Rio Seco. 0-7 m. Gently sloping bottom with cobble, some boulders up to 1 m diameter, sand. 12.12.1997.
S 7.* 20°58′S, 70°08′W, Rio Seco. Intertidal. Extensive rocky plateaus with tide pools and small surge channels. 14.12.1997. V.
S 8. 21°01′S, 70°10′W, Punta Lobos S Rio Seco, 500 m offshore. 10-16 m. Bottom with boulders, some of them to 2 m diameter, covered with alga *Lessonia trabeculata*, shells. 14.12.1997.
S 9. 21°01′S, 70°10′W, Punta Lobos S Rio Seco. Intertidal. Shore with cobble, some rocky plateaus with small tide pools, some sand. 15.12.1997.
S 10. 23°32′S, 70°33′W, S end of Bahía Juán López, Antofagasta. Intertidal. Rocky plateau with few tide pools. 17.12.97.
S 11. 23°32′S, 70°33′W, S end of Bahía Juán López, Antofagasta. 0-19 m. Steeply sloping bare rock; from 19 m downward sloping gently, alga *Lessonia trabeculata* on some boulders to 1 m diameter; protected. 17.12.97.
S 12. 23°30′S, 70°35′W, bay W Juán López, Antofagasta. Intertidal. Rocky plateau with extensive tide pools. 18.12.97.
S 13. 23°30′S, 70°35′W, bay W Juán López, Antofagasta. 0-10 m. Cobble, sand, shells, and some boulders of various sizes to 3 m diameter; protected. 18.12.97.
S 14. 23°42′S, 70°26′W, Playa Huascar, Antofagasta. Intertidal. Sand, rocky plateau with tide pools and surge channels. 16.12.97.
S 15. 26°08′ S, 70°40′ W, Caleta Pan de Azúcar, national park Pan de Azúcar, Chañaral, 300 m offshore. 12-17 m. Bare boulders to 5 m diameter, with sand and broken shells. 21.12.1997.
S 16. 26°10′S, 70°39′W, Playa Los Piqueros, national park Pan de Azúcar, Chañaral. Intertidal. Pebbly shore, some large boulders to 5 m diameter including cracks and shallow tide pools. 20.12.97.
S 17.* 26°11′S, 70°39′W, S end of Playa Los Piqueros, national park Pan de Azúcar, Chañaral. 0-8 m. Gently sloping pebbly shore, some sand between small rocky islands. 21.12.97. V.
S 18. 29°56′S, 71°20′W, light house, Coquimbo peninsula. Intertidal. Rocky shore with tide pools and surge channels, partly covered with alga *Lessonia nigrescens* Bory, 1826. 31.12.1997.
S18a. 29°57′23.6′′S, 71°21′39.7′′W, Playa la Pampilla, Coquimbo peninsula. Extremely exposed rocky shore with large boulders up to several m diameter, tide pools and surge channels, partly covered with alga *Lessonia nigrescens*. 14.11.2002. 20./23.4.2003.
S18b. 29°56′00.1′′S, 71°20′11.1′′W, intertidal zone at cannon, end of the road, Coquimbo peninsula. Very exposed rocky shore with a small rocky plateau; towards the S many small to large boulders up to several m diameter. 7.11.2002. 22.4.2003.
S 19. 29°58′58.6′′S, 71°21′36.4′′W, Playa La Herradura, Coquimbo. Intertidal. Gently sloping shore with cobble, a boulder 10 m diameter in the middle of the beach with some tide pools on it. 2.1.1998. 19./21.4.2003.

S 20. 29°58′S, 71°20′W, Mole of Bahía La Herradura, Coquimbo. 0-9 m. Steel post of the dock. 30.12.1997.

S 21. 29°58′S, 71°21′W, middle of Bahía La Herradura, Coquimbo. 6-7 m. Sand, broken shells, pebbles. 30.12.1997.

S 22. 29°58′S, 71°21′W, S end of Bahía La Herradura. 10-16 m. Boulders to 1 m diameter, sloping quite steeply. 30.12.1997.

S 23. 29°57′57.7′′S, 71°21′11.7′′W, shore in front of the Universidad Católica del Norte, Coquimbo. Intertidal. Cobble. 2.1.1998.

S 24.* 30°03′S, 71°23′W, S end of beach of Totoralillo. Intertidal. Sandy shore with large boulders to 5 m diameter, shallow tide pools, surge channels. 30.12.1997. C.

S 25. 30°06′S, 71°23′W, Punta Lagunillas, on small peninsula 20 km S of Coquimbo. 0-9 m. Two large boulders 10-15 m diameter on both sides of beach, gently sloping shore with cobble, covered with *Lessonia trabeculata*, exposed. 29.12.1997.

S 26. 30°14′S, 71°30′W, north side of Tongoy peninsula. Intertidal. Rocky shore, some small tide pools. 28.12.1997.

S 27. 30°14′S, 71°30′W, north side of Tongoy peninsula. 0-12 m. Gently sloping sandy bottom, with boulders to 1 m diameter, many covered with algae *Lessonia trabeculata*. 28.12.1997.

S 28. 32°07′S, 71°32′W, Beach of Pichidangui. Intertidal. Protected rocky shore. 6.1.1998.

S 29. 32°07′S, 71°32′W, small island offshore of Pichidangui. 12-20 m. Boulders and steep rock, wave-protected. 6.1.1998.

S 30. 32°07′S, 71°32′W, mole of Pichidangui . 2-7 m. Boulders and cobble, occasional alga *Lessonia trabeculata*. 6.1.1998.

S 31. 32°14′S, 71°30′W, beach of Los Molles. Intertidal. Gently sloping exposed shore with boulders, some to 2 m diameter with tide pools, covered with alga *Lessonia nigrescens*. 7.1.1998.

S 32. 32°15′S, 71°28′W, S end of sandy beach of Los Molles. Intertidal. Large boulders to 10 m diameter with shallow tide pools on them. 7.1.1998.

S 33. 32°30′S, 71°27′W, beach of Papudo. Intertidal. Bottom sloping gently, boulders of various sizes, some to 2 m diameter. 8.1.1998.

S 34. 34°25′S, 72°03′W, beach of the small peninsula S Pichilemu. Intertidal. Large boulders to 5 m diameter, some tide pools. 10.1.1998.

S 35.* 34°54′S, 72°10′W, S end of the sandy beach of Caleta Duao. Intertidal. Exposed sandy shore, large boulders of various sizes with many tide pools, covered with alga *Lessonia nigrescens*. 11.1.1998. C.

S 36. 34°54′S, 72°11′W, exposed S end of beach of Caleta Duao, 500 m offshore. 19-23 m. Large boulders to 5 m diameter on flat sandy bottom, some broken shells. 12.1.1998.

S 37.* 34°54′S, 71°11′W, S end of the beach of Caleta Duao, 500 m offshore. 12-17 m. Large boulder 10 m diameter, surrounded by sand. 12.1.1998. S.

S 38. 35°27′S, 72°29′W, S end of the large sandy beach of Las Cañas, Constitución. Intertidal. Extensive rocky shore with shallow and deep tide pools, covered with various macroalgae. 13.1.1998.

S 39. 36°31′S, 72°56′W, sandy beach at the marine biology station of the Universidad de Concepción, Dichato. Intertidal. Protected rocky plateaus with tide pools and surge channels. 11.4.1998, 13.1.2001, 16.1.2001, 28.3.2001.

S 40. 36°31′S, 72°56′W, rocky ledge N of Pingueral, Dichato. 10-18 m. Boulders 1-2 m diameter. 14.1.1998, 15.1.1998, 5.4.1998, 13.1.2001.

S 41.* 36°31′ S, 72°56′ W, Pingueral, Dichato. 1-7 m. Small rocky island with many cracks and a small cave, surrounded by sand. 26.11.1997, 27.11.1997, 14.1.1998, 15.1.1998, 5.4.1998, 13.1.2001, 16.1.2001, 29.3.2001, 30.3.2001. V.

S 42. approx. 36°31′S, 72°56′W, Bahía Coliumo, Dichato. Approx. 20 m. Soft bottom. Samples collected by the research vessel KaiKai of the Universidad de Concepción. Early November 1997.

S 43. 36°35′S, 72°58′W, sandy beach of Cocholgüe. Intertidal. Extensive rocky plateaus with many tide pools and surge channels, surrounded by sand. 1994/1995, 8.4.1998, 8.12.1999, 30.3.2001.

S 44.* 36°45′S, 73°11′W, beach of Chome, Hualpén peninsula, Concepción. Intertidal. Old quay wall, bottom with boulders, some to 3 m diameter. 4.4.1998. S.

S 45.* 36°45′S, 73°11′W, Chome, Hualpén peninsula, Concepción. 0-18 m. Gently sloping bottom, cobble, regions with broken shells, some boulders to 5 m diameter. 3.4.1998, 7.4.1998. S.

S 46. 39°47′, 73°24′W, N end of Playa Calfuco, Valdivia. Intertidal. Bottom sloping gently with boulders, some to 2 m diameter, macroalgae (*Lessonia nigrescens* and *Durvillea antarctica*), brackish water through terrestrial fresh water input. 24.1.1998.

S46a.* 39°48′31.3′′, 73°23′50.8′′W, Playa Misión, Valdivia. Intertidal. Extensive rocky plateau with tide pools and surge channels covered with many macroalgae (*Lessonia nigrescens*, *Macrocystis* sp.). 31.11.02, 14.8.03. V.

S 46b.* 39°47′48.1′′S, 73°23′57.2′′W, Punta Misión, near Valdivia. Intertidal. 14.8.03. V.

S 47. 39°50′46.5′′S, 73°23′59.8′′W, rocky beach N of Los Molinos, Valdivia. Intertidal. Extensive rocky plateau with tide pools and surge channels covered with many macroalgae (*Lessonia nigrescens*, *Macrocystis* sp.), separated by small bays with boulders, brackish water through terrestrial sweet water input. 23.1.1998.

S 48.* 39°50′S, 73°24′W, rocky beach N of Los Molinos, Valdivia. 4-8 m. Small island, rocky ground, partly covered with *Macrocystis* sp., regions with broken shells. 25.1.1998, 26.1.1998. S.

S 49. 39°51′S, 73°27′W, Punta del Conde, Bahía Niebla, Valdivia. 18-23 m. Large boulders of different sizes. 25.1.1998.

S 50. 39°51′S, 73°27′W, Punta del Conde, Bahía Niebla, Valdivia. 8-14 m. Small rocky islands and large boulders in close to a colony of sea lions. 26.1.1998.

## Appendix 2

List of study sites of K.P. Sebens and R.T. Paine (P 1-P 22, numbers used as in Sebens & Paine, 1979): *Oulactis concinnata* found (*); longitude/latitude, site, date visited (if available). *O. concinnata*: A (abundant: more than 100 individuals seen in 1 h search), C (common: 6-100 seen), R (rare: fewer than 6 seen) (Sebens & Paine, 1979).

P 1.* 20°16′S, 70°08′W, Iquique lab. Intertidal. 30.9.1975, 1.10.1975. C.
P 2. 20°25′S, 70°11′W, Pozo Toyo. Intertidal. 1.10.1975, 3.10.1975.
P 3.* 20°42′S, 70°12′W, Cumbres Borascosas. Intertidal. 3.10.1975. R.
P 5.* 23°05′S, 70°30′W, Mejillones. Intertidal. 12.10.1975. A.
P 5. 23°02′S, 70°31′W, Mejillones. Subtidal.
P 6. 23°25′S, 70°36′W, Santa Maria. Intertidal. 7.10.1975.
P 7.* 23°41′S, 70°27′W, Antofagasta. Intertidal. R.
P 8.* 23°42′S, 70°27′W, S. Antofagasta. Intertidal. 5.10.1975. 6.10.1975. 10.10.1975. C.
P 8.* 23°42′S, 70°27′W, S. Antofagasta. Subtidal. 10.10.1975. R.
P 9. 23°49′S, 70°29′W, Pt. Jara. Intertidal. 8.10.1975.
P 12. 30°58′S, 71°39′W, B. El Teniente. Intertidal.
P 13.* 32°14′S, 71°32′W, Pt. Molles exposed. Intertidal.16.10.1975. 18.10.1975. R.
P 13. 32°14′S, 71°32′W, Pt. Molles protected. Intertidal.18.10.1975.
P 14.* 32°52′S, 71°33′W, Isla Concon. Intertidal. 22.10.1975. A.
P 15. 32°57′S, 71°32′W, Montemar exposed. Intertidal.
P 15. 32°57′S, 71°32′W, Montemar protected. Intertidal.
P 16. 33°22′S, 71°42′W, Algorroba. Subtidal.
P 16.* 33°30′S, 71°39′W, Pt. El Lacho. Intertidal. 25.10.1975. C.
P 17. 33°33′S, 71°38′W, San Antonio. Intertidal.
P 19.* 36°48′S, 73°11′W, Boca de Biobio. Intertidal. 28.10.1975. R.
P 21.* 39°23′S, 73°14′W, Mehuín. Intertidal. 2.11.1975. C.
P 22. 39°26′S, 73°16′W, I. Maiquillahue. Intertidal.1.11.1975.

## Appendix 3

List of study sites (R1–R16) in Perú; *Oulactis concinnata* found (*); latitude/longitude (Microsoft Encarta 2002 respectively GPS when minutes are given); scientist; date visited / date of publication. Depth. Abundance.

R 1. 03°29′17′′S, 80°23′10′′W, Tumbes. Subtidal. Stefan Austermühle, Aug. 2003.

R 2. 04°06′24′′S, 81°04′00′′W, Playa Vichayito, Mancora. Subtidal. Stefan Austermühle, Aug. 2003.

R 3. 04°06′24′′S, 81°04′00′′W, Playa Pocitas, Mancora. Subtidal. Stefan Austermühle, Aug. 2003.

R 4. 04°10′35′′S, 81°08′07′′W, Los Organos. Subtidal. Stefan Austermühle, Aug. 2003.

R 5. 04°14′55′′S, 81°14′09′′W, Punta Cabo Blanco. Subtidal. Stefan Austermühle, Aug. 2003.

R 6. 04°53′40′′S, 80°51′00′′W, Punta Mero. Subtidal. Stefan Austermühle, Aug. 2003.

R 7. 05°05′S, 81°06′W, Paita. Pax, 1912 (Pax's specimens are probably *Actinostella californica*).

R 8. 05°07′37′′S, 81°10′07′′W, Talara. Subtidal. Stefan Austermühle, Aug. 2003.

R 9. 05°07′38′′S, 81°10′07′′W, Caleta Yasila, Paita. Subtidal. Stefan Austermühle, Aug. 2003.

R 10. 05°12′24′′S 81°12′24′′W, Isla Foca, Paita. Subtidal. Stefan Austermühle, Aug. 2003.

R 11. 05°48′15′′S, 81°05′00′′W, Bahía de Sechura. Subtidal. Stefan Austermühle, Aug. 2003.

R 12. 05°48′15′′S, 81°04′99′′W, Playa Tantalean, Peninsula Bayovar. Intertidal (tidepools) and subtidal. Stefan Austermühle, Aug. 2003.

R 13*. 09°19′10-15′′S; 78°26′30′′W, Playa Las Salinas, aprox. 30 km S of Chimbote, December 2002. Intertidal. Several small animals in tide-pools, which never fall dry.

R 14*. 12°05′S, 77°12′W, San Lorenzo Island, Callao. Drayton, 1846 (type locality).

R 15*. 12°28′09′′S, 76°47′52′′W, near Punta Chuncho, Pucusana. Intertidal and subtidal. Stefan Austermühle, July and December 2002. Very common in sand-filled crevices between boulders in 2-3 m depth.

R 16. 14°02′40′′-14°03′50′′S, 76°15′60′′-76°16′70′′W, Playa Mendieta, cliffs and rocky islands forming the N limits of the bay Hueco de Zorra to its S limit point Mendieta; and from from the sand flat habitat to mouth of the bay Hueco de Zorra, Reserva Nacional de Paracas. Intertidal and subtidal. Stefan Austermühle, July and Dec. 2002, Aug. 2003.