

Re-description of *Phymactis papillosa* (Lesson, 1830) and *Phymanthea pluvia* (Drayton in Dana, 1846) (Cnidaria: Anthozoa), two common actiniid sea anemones from the south east Pacific with a discussion of related genera

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Key words: Actiniaria; Actiniidae; *Phymactis papillosa*; *Phymactis clematis*; *Phymanthea pluvia*; *Bunodosoma*; non-adhesive vesicles; Chile; Peru; Mexico; benthos.

Actiniid sea anemones possess few characteristics of taxonomic value, which makes columnar out-growths one of the most important features for systematic work. There are two species of actiniid sea anemones known from Chile and southern Peru that exhibit a column densely covered with non-adhesive vesicles: *Phymactis papillosa* (Lesson, 1830) (= *Phymactis clematis*) and *Phymanthea pluvia* (Drayton in Dana, 1846). Hereby both are re-described in detail. The re-descriptions are based on observations of about 100 living animals in their habitat and in aquaria and on the examination of 21 specimens of *P. papillosa* and seven specimens of *P. pluvia* collected in Chile between 1995 and 2003. In Chile, specimens of both species occur in tide-pools, on vertical and overhanging rock-walls in the intertidal zone and in shallow water down to depths of 16 m. Large size, numerous short tentacles, and acrorhagi characterize both species. *Phymactis papillosa* is a widely distributed species: its occurrence is confirmed from Playa Tantalean, Peninsula Bayovar, Peru (05°48'15"S, 81°04'99"W), to the Archipelago de los Chonos (44°24"S; 73°34'W), south Chile, for the Gulf of California (24°08'N; 110°15'W) and for the Pacific coast of Mexico (23°26'N; 110°15'W) as well as for some Pacific Islands. *Phymactis papillosa* occurs solitarily and in clonal aggregations and exhibits four distinct colour varieties: var. *rubra*, var. *viridis*, var. *cyanea* and var. *fusca* as well as some mixed morphs. *Phymanthea pluvia* can be found between Caleta Yasila, Paita, Peru (05°07'38"S, 81°10'07"W), and the region of Valparaíso, central Chile (33°02"S, 71°38'W). Specimens of *P. pluvia* always have a hardly varying orange colour; the apexes of its vesicles are whitish. Morphologically both species are quite similar; besides the colour they can be distinguished by the histological structure of the vesicles and by the numerous rod-like basitrichs in the acrorhagi of *P. papillosa*. Structure and histology of the vesicles of both species are described in detail and possible functions and the taxonomic value of vesicles are discussed. The distinctive characters of the genera *Phymactis* Milne Edwards 1857, *Bunodosoma* Verrill, 1899, and *Phymanthea* Carlgren, 1959 are given. Valid as well as doubtful species of all three genera are listed.

Las anémonas de la familia Actiniidae presentan pocos caracteres con valor taxonómico, lo que hace de los brotes columnares uno de los rasgos más importantes para el trabajo sistemático. En Chile y el sur de Perú, se conocen dos especies de la familia Actiniidae las cuales presentan una columna densamente cubierta con vesículas no-adhesivas: *Phymactis papillosa* (Lesson, 1830) (= *Phymactis clematis*) y *Phymanthea pluvia* (Drayton in Dana, 1846). Las dos están redescritas en detalle. Las descripciones están basadas en observaciones de unos 100 animales vivos en su hábitat y en acuario y en el examen de 21 especímenes

de *P. papillosa* y siete especímenes de *P. pluvia* recolectados en Chile entre 1995 y 2003. En Chile, especímenes de las dos especies se desarrollan o se distribuyen en charcos intermareales, en paredes verticales y sobre-inclinadas de la zona intermareal y en zonas de aguas someras hasta una profundidad de 16 m. Ambas especies están caracterizadas por su gran tamaño, sus tentáculos cortos y numerosos, y por presentar acroragios. *Phymactis papillosa* es una especie con distribución amplia: su presencia está confirmada desde Playa Tantalean, Peninsula Bayovar, Perú (05°48'15"S, 81°04'99"W), hasta el Archipielago de los Chonos (44°24"S; 73°34'W), Chile, para el Golfo de California (24°08'N; 110°15'W) y la costa pacífica de México (23°26'N; 110°15'W) como para unas islas pacíficas. *Phymactis papillosa* se desarrolla tanto de forma solitaria como en agregaciones (clones); expone cuatro diferentes morfas de color: var. *rubra*, var. *viridis*, var. *cyanea* y var. *fusca* y también algunas formas mixtas. *Phyanthea pluvia* se distribuye entre Caleta Yasila, Paita, Perú (05°07'38"S, 81°10'07"W), y la región de Valparaíso, Chile central (33°02"S, 71°38'W). Especímenes de *P. pluvia* siempre presentan un color anaranjado, apenas variable, siendo los ápices de sus vesículas blanquecinos. Morfológicamente ambas especies son bastante similares; además del color, ambas especies, se pueden distinguir por la estructura histológica de las vesículas y la presencia de numerosos basitrichos en los acrorragi de *P. papillosa*. Se describe en detalle la estructura y la histología de las vesículas de ambas especies y se discute posibles funciones y el valor taxonómico de las vesículas. Por último, se presentan los caracteres distintivos de los géneros *Phymactis* Milne Edwards 1857, *Bunodosoma* Verrill, 1899, y *Phyanthea* Carlgren, 1959 y una lista de especies válidas y dudosas de estos tres géneros.

Introduction

The Actiniidae are the largest and most varied sea anemone family (McCommas, 1991). In almost any rocky shallow water habitat, several species of actiniid anemones can be found, but they are often difficult to identify due to the low number of taxonomically informative characters and the scarcity of detailed descriptions and identification keys. Traditionally (Stephenson, 1921; 1935; Carlgren, 1949a) structures of the column like verrucae, vesicles, acrorragi and pseudoacrorragi are used to distinguish actiniid genera; histological characters and cnidae separate species. However, columnar outgrowths, such as verrucae and vesicles are controversially defined and often hard to tell apart in preserved specimens (den Hartog, 1987; Riemann-Zürneck & Gallardo, 1990; Daly, 2004). Information on the function of the columnar structures and on the biology of the species is often missing. Furthermore, histology and cnidae are difficult for non-experts to examine or interpret.

It is clearly desirable to introduce more reliable characteristics for identification (McCommas, 1991). Features of the animals *in situ* and *in vivo* including characteristics of fired cnidae and morphology of delicate structures can often facilitate taxonomic decisions. First of all it is necessary to provide detailed descriptions of the existing species including as much *in vivo* information as possible to create a base upon which new characteristics for identification can be introduced.

The actiniarian fauna of north and central Chile includes at least nine shallow water anemone species of the family Actiniidae (Häussermann, 1998), two of which have recently been described or re-described respectively (Häussermann & Försterra, 2001; Häussermann, 2003). In the present paper, two further common and eye-catching species, *Phymactis papillosa* and *Phyanthea pluvia*, are re-described. Detailed *in vivo* descriptions, observations and pictures including fired cnidae are provided. The genera *Phymactis* and *Phyanthea* are discussed in comparison with the closely related genus *Bunodosoma*. Structure and function of the vesicles in these genera are discussed.

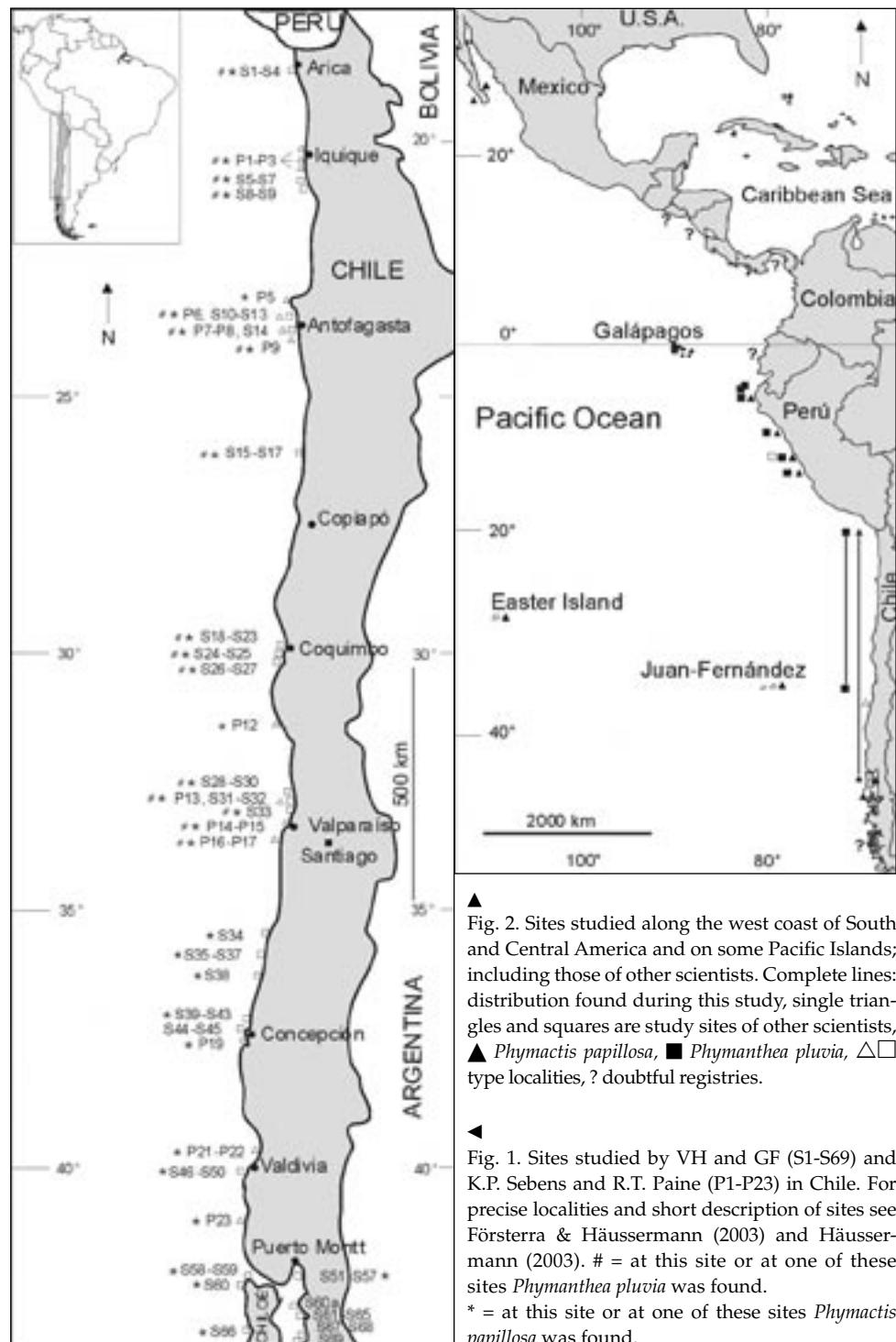


Fig. 2. Sites studied along the west coast of South and Central America and on some Pacific Islands; including those of other scientists. Complete lines: distribution found during this study, single triangles and squares are study sites of other scientists, ▲ *Phymactis papillosa*, ■ *Phymanthea pluvia*, △□ type localities, ? doubtful registries.

Fig. 1. Sites studied by VH and GF (S1-S69) and K.P. Sebens and R.T. Paine (P1-P23) in Chile. For precise localities and short description of sites see Försterra & Häussermann (2003) and Häussermann (2003). # = at this site or at one of these sites *Phymanthea pluvia* was found.

* = at this site or at one of these sites *Phymactis papillosa* was found.

Material and methods

Between 1994 and 2003, Günter Försterra and I observed and examined about 100 specimens of *Phymactis papillosa* and *Phymanthea pluvia* along the Chilean coast from Arica ($18^{\circ}28'S$, $70^{\circ}19'W$) to Cucao, Chiloé Island, ($42^{\circ}30'S$, $74^{\circ}07'W$) (fig. 1). Lists of all study sites up to S44 (Arica to Concepción) can be recalled in the online appendix of Häussermann & Försterra (2001) at <http://www.senckenberg.uni-frankfurt.de/odes/>. Lists and maps of study sites up to S50 (Arica to Valdivia) and S51 to S97 respectively (Puerto Montt to Puerto Chacabuco) and R1 to R16 (Peru) can be recalled in Häussermann (2003) and Försterra & Häussermann (2003). This study also utilizes information gathered in 2002 and 2003 by S. Austermühle who collected and observed several specimens in Peru (fig. 2). I also examined specimens of *P. pluvia* collected in 1975 by K.P. Sebens & R.T. Paine (fig. 1) and I include data on specimens of *P. papillosa* collected and observed in Mexico in November 2002 by M. Daly (fig. 2).

The studies were carried out in the intertidal zone during low tide and by means of SCUBA-diving. Some specimens were kept in aquaria for several days for detailed examinations. Nineteen specimens of *P. papillosa* and six specimens of *P. pluvia* were preserved.

Specimens were relaxed with menthol crystals for 30–120 min and fixed in 10–15% seawater formalin. Specimens of both *Phymactis papillosa* and *Phymanthea pluvia* need

Table 1. Size and distribution of cnidae of *Phymactis papillosa* (letters A-M refer to Fig. 13), 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 cnidae 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 (C)	13.5-26.1	21.5	3.31	1.8-3.1	2.6	0.37	5/5	41	
basitrichs ^c (D)	17.1-21.6	20.1	1.39	1.8-2.7	2.3	0.40	3-5	5/5	54
ACRORHAGI									
holotrichs ^v (H)	(45) 70.2-88.2	77.2	9.41	4.5-9.0	6.8	1.01	5/5	44	
rod-like basitrichs ^v (I)	77.4-115.2	98.2	9.61	2.3-3.6	2.6	0.32	5/5	40	
COLUMN									
basitrichs ^f (A)	13.5-18.9	15.8	1.18	1.8-2.7	2.5	0.32	4-5	5/5	41
ACTINOPHARYNX									
small basitrichs ^c (E)	15.3-18.9	17.3	0.97	1.8-2.7	2.2	0.38	5/5	42	
large basitrichs ^{f-c} (F)	24.3-32.4	28.1	2.48	2.3-3.2	2.7	0.16	6-8	5/5	17
microbasic amastigophors A ^f (G)	23.4-26.1	25.1	1.26	4.5-5.4	4.9	0.42	~10	5/5	12
							-13		
MESENTERIAL FILAMENTS									
b-mastigophors ^c (J)	27.0-42.3	36.5	3.22	3.6-6.3	5.0	0.60	2	5/5	44
microbasic amastigophors A ^c (K)	21.6-25.2	23.6	0.97	4.5-5.4	5.0	0.45		5/5	41
basitrichs ^s (L)	13.5-17.1	14.6	1.33	1.8-2.7	2.2	0.41	4-5	5/5	10
microbasic p-mastigophors B ^s (M)	11.7-13.5	12.5	0.81	1.4-2.3	1.8	0.23	2/5	~4-5	12
PEDAL DISC									
basitrichs ^f (B)	16.2-21.6	19.0	1.51	1.8-2.7	2.6	0.33	4-5	4/4	21

up to several hours of exposure to menthol crystals until they are relaxed completely and, even in maximal relaxation, do not expand completely, probably due to the auto-elasticity of the thick mesogloea. Specimens were kept in formalin for at least 4 months before being transferred to 70% alcohol. Pieces of three specimens of *P. papillosa* and of two specimens of *P. pluvia* were embedded in paraffin, sectioned at 8 µm and 9 µm respectively, and stained with Azocarmine triple staining.

For cnidae examination, squash preparations of small amounts of tissue from three living and four preserved specimens of *Phymactis papillosa* and two living and three preserved specimen of *Phymanthea pluvia* 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. Cnidae did not discharge readily. 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 sucked off carefully with a tissue. Then a solution of 1:1 sea water:glycerin with few drops of phenol and formalin on 100 ml 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). Size ranges of Table 1 and 2 are values taken from a single preserved specimen.

Table 2. Size and distribution of cnidae of *Phymanthea pluvia* (letters A-J refer to Fig. 26), 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 cnidae 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 (A)	16.2-31.5	24.3	5.47	1.8-3.2	2.4	0.44	4/4	40	
basitrichs ^c (B)	19.8-29.7	24.1	2.29	2.3-2.7	2.6	0.22	4-5	4/4	40
ACRORHAGI									
holotrichs ^v (G)	38.7-58.5	49.7	4.44	4.5-7.7	6.4	0.54	4/4	42	
COLUMN									
basitrichs ^c (C)	15.3-19.8	17.3	1.24	2.3-3.2	2.6	0.24	~4	4/4	40
ACTINOPHARYNX									
basitrichs ^c (D)	17.1-32.4	25.6	3.61	1.8-3.6	2.7	0.28	5-7	4/4	46
microbasic amastigophors A ^s (E)	24-27						8-9	2/4	5
MESENTERIAL FILAMENTS									
microbasic amastigophors A ^c (H) ¹	18.9-22.5	21.0	0.78	3.6-5.4	4.4	0.33	7-9	4/4	42
b-mastigophors ^{f,c} (I)	27.0-38.7	33.4	2.61	4.1-5.4	4.7	0.49		4/4	42
basitrichs ^{f,c} (J)	15.3-23.4	20.1	1.83	1.8-3.2	2.5	0.34	4-7	4/4	40
PEDAL DISC									
basitrichs ^f (F)	16.2-22.5 (25, 27.1)	18.7	2.26	1.8-2.7	2.6	0.24	3-4	3/3	40

¹ In some preparations short thread visible in the unfired cell

² countless

Table 3. Diagnostic characters of the genera *Phymactis* Milne Edwards, 1857, *Bunodosoma* Verrill, 1899 and *Phymanthea*

Characters	<i>Phymactis</i> Milne Edwards, 1857
Column	Densely covered with rounded non-adhesive vesicles of uniform colour, simple or compound, often of irregular shape; in vivo vesicle rows generally undistinguishable; column rarely visible between vesicles
Structure of vesicles	Ectoderm with mucus gland cells, mesogloea thin, endoderm without muscles
Nematocyst batteries on vesicles	Absent
Endodermal sphincter	Diffuse
Retractor muscle	Diffuse, band-like
Acrorhagi	Single acrorhagus on oral side of marginal vesicles; not every marginal vesicle with acrorhagus; rarely absent especially in juv. animals
Cnidae of acrorhagi	Numerous large holotrichs; numerous large rod-like basitrichs; some spirocysts
Reproductive tissue on:	All incomplete mesenteries except the last cycle, sometimes also on youngest perfect cycle, never on first and second cycle
Tentacles	short, at about as long as half diameter of oral disc, very numerous
Siphonoglyphs and directives	In hexamerous animals 2 siphonoglyphs connected to 2 directives, in asexually reproduced animals several siphonoglyphs not connected with directives or directives missing
Distribution	West coast of Central and South America, some Pacific Islands, St. Helena (Atlantic)

Water temperature in the habitat during sampling ranged from 12.0-23.0°C (*Phymactis papillosa*) to 13.0-22.8°C respectively (*Phymanthea pluvia*) and salinity from 30.5-36.0‰ (*P. papillosa*) to 33.5-36.0‰ respectively (*P. pluvia*).

Results

Amended diagnoses of the genera *Phymactis* and *Phymanthea*

Family Actiniidae Rafinesque, 1815
Genus *Phymactis* Milne Edwards, 1857
Rivetia Pax, 1912

Diagnosis after Carlgren (1949a), amended, with changes in bold: Actiniidae with well-developed pedal disc. Column **densely covered with rounded, non-adhesive vesicles**; **vesicles simple or compound**. **Acrorhagus containing holotrichs, rod-like basitrichs and some spirocysts; situated on the oral side of an enlarged marginal vesicle**. Margin distinct, with well-developed fosse. Sphincter **diffuse, strong**. Tentacles short, **at about half diameter of oral disc, conical**, usually hexamerously arranged,

Carlgren, 1959.

Bunodosoma Verrill, 1899	Phymanthea Carlgren, 1959
The whole or almost the whole column covered with rounded non-adhesive (or only weakly adhesive) vesicles that are never compound; in vivo vesicle rows generally visible and column generally visible between vesicles; vesicles may or may not have nematocysts	Densely covered with rounded non-adhesive vesicles, simple or compound, especially marginal vesicles strongly compound and enlarged; in vivo vesicle rows more or less discernable in proximal and distal region; distal column generally visible between vesicles when expanded
Ectoderm with mucus gland cells, mesogloea thickened at apex, endoderm without muscles	Ectoderm with mucus gland cells missing at apex of vesicle, mesogloea thinner at apex than at sides of vesicles, endoderm without muscles
Present in some species?	Absent
Circumscribed	Diffuse
Diffuse, band-like	Small, circumscribed-diffuse
Each marginal projection typically bears a single acrorhagus; rarely absent	Single acrorhagus on oral side of enlarged and compound marginal vesicles; not every marginal vesicle with acrorhagus
Numerous holotrichs	Numerous holotrichs
All perfect mesenteries, sometimes except directives	All incomplete mesenteries except the last cycle, sometimes also on younger perfect cycles
Shorter than diameter of oral disc	Short, at about as long as half diameter of oral disc, very numerous
In hexamerous animals 2 siphonoglyphs connected to 2 directives, rarely several siphonoglyphs not connected with directives	2 siphonoglyphs connected to 2 directives
Mainly tropic and subtropic distribution: Caribbean Sea, subtropical west Atlantic, east Atlantic and east Pacific, India	Southern Perú and northern Chile

their longitudinal muscles ectodermal, **in some animals partly mesogloal**. Radial muscles of oral disc **ectodermal to mesogloal**. As a rule, two aborally prolonged **siphonoglyphs and two pairs of directives; or several siphonoglyphs not connected with directives or directives lacking**. Numerous perfect mesenteries, at least the two oldest cycles **sterile**. At least in larger mesenteries **oral and marginal stoma present**. **Retractors diffuse, band-like**. Parietobasilar and basilar muscles well-developed. **No zoanthellae**.

Cnidae: spirocysts (**in tentacles and acrorhagi, sporadic in pedal disc**), basitrichs (**in all tissues except acrorhagi**), microbasic *b*-mastigophores (**in filaments**), microbasic amastigophores A (**in filaments and pharynx**), holotrichs (**in acrorhagi**), rod-like basitrichs (**in acrorhagi**).

Genus *Phymanthea* Carlgren, 1959

Diagnosis after Carlgren (1959), amended, changes in bold: Actiniidae with **well-developed** pedal disc. Column **densely** covered with **rounded, non-adhesive vesicles, simple or, especially towards the margin, enlarged and compound**. Vesicles in the proximal part of the column smaller and more numerous, **distally and proximally distinguishable rows**. **Acrorhagus on the oral side of an enlarged marginal vesicle**

containing numerous holotrichs. Margin distinct, with well-developed fosse. Sphincter diffuse, strong. Tentacles very numerous, conical, short, **at about half diameter of oral disc, hexamerously arranged**, their longitudinal muscles ectodermal. **Radial muscles of oral disc ectodermal.** Two distinct, aborally prolonged siphonoglyphs and two pairs of directives. Numerous perfect mesenteries, **at least the two oldest cycles sterile, medium-sized mesenteries fertile.** At least in larger mesenteries oral and marginal stoma present. Retractors small, circumscribed-diffuse. Parietobasilar and basilar muscles well-developed. No zooxanthellae.

Cnidae: spirocysts (in tentacles, sporadic in pedal disc), basitrichs (in all tissues except acrorhagi), microbasic b-mastigophores (in filaments), microbasic amastigophores A (in filaments), holotrichs (in acrorhagi).

The diagnostic characters of the genera *Phymactis*, *Bunodosoma* and *Phymanthea* are compared (tab. 3) and their valid and doubtful species are listed (tab. 4).

Differential diagnoses of the species *Phymactis papillosa* and *Phymanthea pluvia*

Both *Phymactis papillosa* and *Phymanthea pluvia* are large-sized species of the intertidal and shallow subtidal with pedal disc diameter up to 100 mm or 160 mm respectively; column densely covered with rounded, non-adhesive, simple or compound vesicles; tentacles relatively short, marginal. Acrorhagi generally present on oral sides of enlarged marginal lobes.

In the field, uniform red, green, blue or brown colour distinguishes *Phymactis papillosa* from *Phymanthea pluvia* and from *Bunodosoma grandis* (Verrill, 1969)¹, the latter only occurs north of Chile. *Phymanthea pluvia* is orange with white vesicle tips and *B. grandis* is green to brown, with 12 rows of light vesicles alternating with 3 rows or more of dark vesicles (Verrill, 1869). Central American *Bunodosoma californica* (Carlgren, 1951) can be distinguished from the above-described species by the low number of tentacles: approx. 80 (Daly, 2004). Cnidae of the acrorhagi (numerous holotrichs and rod-like basitrichs) characterize preserved specimens of *P. papillosa*; acrorhagi of *P. pluvia* present numerous holotrichs only. In addition, *P. papillosa* and *P. pluvia* are distinguished from all other described species of *Bunodosoma* by their diffuse sphincter and by the presence of at least some compound vesicles. *Phymanthea pluvia* can be found in more light-exposed habitats than *P. papillosa*; its distribution maximum is located in the subtidal instead of the intertidal.

Material (if not otherwise mentioned all collected by G. Försterra (GF) and V. Häussermann (VH).— **Chile:** *Phymactis papillosa*: 1 specimen (var. *rubra-viridis*) from Arica/Playa Corazones (S1), collected 4.xii.1997, intertidal (Ex. 65 = ZSM 20030295); 6 specimens (var. *rubra-fusca*, juv.) from Playa Los Piqueros, national park Pan de Azúcar, Chañaral (S16) collected 21.xii.1997, intertidal (Ex. 92-97 = ZSM 20030296); 3 specimens (var. *cyanea*) from Playa La Pampilla, Coquimbo (S18a), collected 14.xi.02, intertidal (Ex. 1-3 = ZSM 20030297); 1 large specimen (var. *rubra*) from Aquarium Coquimbo

¹ Data taken from old literature. I have not seen specimens and thus do not know if it is a valid species.

(originally S22), collected 23.iv.2003, with porcellanid crab *Allopetrolisthes spinifrons* (Milne Edwards, 1837) (ZSM 20030298); 1 small specimen (var. *viridis*) from Aquarium Coquimbo (originally S22), collected 23.iv.2003 (ZSM 20030298); 1 specimens (var. *viridis*) from Pingueral (S41), collected 31.x.1997 (Ex.7 = ZSM 20030299), 6 m depth; 3 specimens (var. *rubra* and var. *viridis*) from Aquarium Dichato, collected 10.xi.1997 (Ex. 26-28 = ZSM 20030300); 2 specimens from Pingueral (S41), collected 1.iv.1995, 7 m depth (MZUC 23164); 1 specimen (var. *viridis*) from Punta Misión, Valdivia (S46b), collected 14.viii.2003, intertidal (Universidad Austral de Chile, IZUA-CNI-0041); 2 specimens from Mar Brava (S56), collected 27.i.2001, intertidal (Ex. 64, 65 = ZSM 20030301 and 20030302, one preserved in 96% EtOH). Several specimens of *P. papillosa* can also be found in the collection of Chilean sea anemones of K.P. Sebens and R.T. Paine deposited in the National Museum of Natural History Naturalis, Leiden, Netherlands (RMNH Coel. 33015-33022).

Phymanthea (Actinia) pluvia: 2 specimens from Arica/Playa Corazones (S1), collected 4.xii.1997, intertidal (Ex. 63, 64 = ZSM 20030303); 3 specimens from Playa La Pampilla, Coquimbo (S18a), collected 14.xi.02, intertidal (Ex. 4-6 = ZSM 20030304); 1 specimen from Playa La Herradura, Coquimbo (S19), collected 3.i.1998, intertidal (Ex. 138 = ZSM 20030305), 1 specimen from Aquarium Coquimbo (originally S22), collected 23.iv.2003, intertidal (ZSM 20030304); 3 specimens from Pozo Toyo (P2), collected 1.x.1975 by K.P. Sebens and R. T. Paine, intertidal (RMNH Coel. 32163).

Sites, where *Phymactis papillosa* and *Phymanthea pluvia* respectively were found in Chile: *P. papillosa*: S1, S3-7, S9-19, S22, S24, S26, S28, S31-35, S38-39, S41, S43-48, S50, S55-58, S60, S66. *Pa. pluvia*: S1-8, S11-17, S19, S22, S25, S27, S30-31, S33, R9-10.

Sites where *Phymactis papillosa* and *Phymanthea pluvia* were found in Peru by S. Austermühle in 2002 and 2003 (fig. 2): *P. papillosa*: R12 (intertidal, high density); R13 (intertidal, high density, several small animals in tide-pools which never fall dry); R14 (locality of syntype); R15 (intertidal and subtidal down to 3 m depth); R16 (intertidal). *Pa. pluvia*: R9 (subtidal, down to 4 m depth); R10 (subtidal, down to 4 m depth); R12 (intertidal and subtidal down to 3 m depth); R13 (intertidal, high density, several small animals in tide-pools which never fall dry); R14 (type locality); R15 (subtidal down to 7 m depth); R16 (subtidal). (for detailed description of sites see Försterra & Häussermann, 2003; Häussermann, 2003).

Holotypes.— *Phymactis (Actinia) papillosa* (Lesson, 1830), Talcahuano, Chile. No type material (Fautin, 2003); = *Phymactis (Actinia) clematis* (Drayton in Dana, 1846), Museum of Comparative Zoology, Yale University, Syntype 297 (1), Valparaíso, Chile = *Phymactis (Actinia) florida* (Drayton in Dana, 1846), Museum of Comparative Zoology, Yale University, Syntype 298 (3), Callao, Peru. For original drawings of *Phymactis papillosa* (Lesson, 1830), *Phymactis clematis* (Drayton in Dana, 1846) and *Phymactis florida* (Drayton in Dana, 1846) see Fautin (2003: *Phymactis papillosa*, *P. clematis*)

— *Phymactis (Actinia) sanctaeheleneae* (Lesson, 1830). No type material (Fautin, 2003). For original drawings see Fautin (2003: *Phymactis sanctaeheleneae*).

— *Phymanthea (Actinia) pluvia* (Drayton in Dana, 1846) San Lorenzo, Callao, Peru (approx. 12°05'S, 77°12'W). No type material (Fautin, 2003). For original drawings see Fautin (2003: *Phymanthea pluvia*).



Fig. 3-4. *Phymactis papillosa*. Fig. 3. Oral disc and tentacles of a specimen var. *rubra*; note prominent, deeply coloured mouth opening and numerous tentacles at the margin of the oral disc. Fig. 4. Lateral view of a specimen var. *cyanæa*; note column densely covered with vesicles and lobed oral disc.

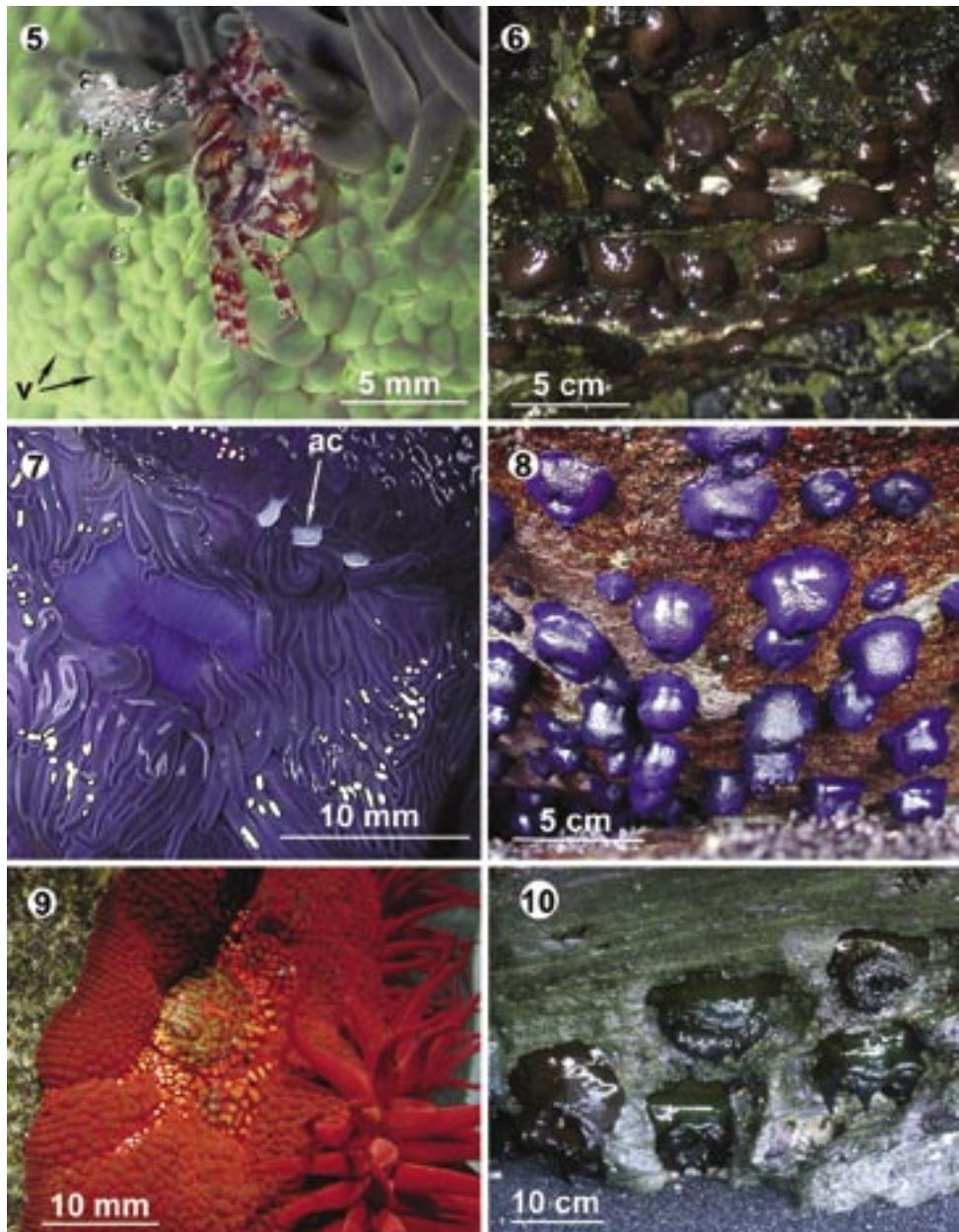


Fig. 5-10. *Phymactis papillosa*. Fig. 5. Specimen var. *viridis* with a juvenile of the porcellanid crab *Allopelotristhes spinifrons* clinging to the column; note rounded, irregularly-shaped vesicles. Fig. 6. Intertidal aggregation (at least partly clonal) of middle-sized specimens var. *fusca*; note some specimens neighboured animals. Fig. 7. Mouth opening and acrorhagi (white) of an emersed specimen var. *cyannea*. Fig. 8. Intertidal aggregation of middle-sized specimens var. *cyannea*; note different sizes. Fig. 9: Specimen var. *rubra* with the porcellanid crab *Allopelotristhes spinifrons* clinging to the column; note density of vesicles. Fig. 10. Intertidal aggregation of solitary specimens of different colours on the underside of a very exposed overhang.

Phymactis papillosa (Lesson, 1830)

Actinia papillosa; Lesson, 1830: 78 (Talcahuano, Chile to Lima, Peru).

Cereus papillosum; Milne Edwards, 1857: 267.

Phymactis papillosa; Stephenson, 1922: 285; Sebens & Paine, 1979: 222 (Iquique to Montemar, Chile); Carlgren, 1949a: 51 (Payta, Peru).

Bunodes papillosa; Verrill, 1869: 468; Andres, 1884: 215.

Bunodactis papillosa; Carlgren, 1949: 66 (Peru, Chile).

Rivetia papillosa; Pax, 1912: D6 (26 spec., Payta, Peru).

Actinia clematis; Drayton in Dana, 1846: 130 (Valparaíso, Chile); Gay, 1854: 448; Drayton in Dana, 1859: 6.

Phymactis clematis; Verrill, 1869: 476; Dana, 1872: 22; Andres, 1884: 217 (var. *cyanæa*, *viridis* and *rubra*);

Carlgren, 1899: 17 (Peru to Valparaíso, Chile, 59 spec.); McMurrich, 1904: 259 (North and Central Chile, Juan-Fernandez Islands, 24 spec.); Carlgren, 1920: 145 (3 spec., Easter Island); Stephenson, 1922: 285; Carlgren, 1925: 12; Carlgren, 1939: 795 (short note); Carlgren, 1945: 9; Carlgren, 1951: 419 (2 spec., Gulf of California); Carlgren, 1949a: 51 (only list: Lower California, San Salvador, Nicaragua, Panama, Pearl Island, W coast of S America to S Tierra del Fuego, Juán Fernández, Easter Island); Carlgren, 1959: 17 (>180 spec., Iquique to Archipel de los Chonos, Chile); Carter, 1965: 149 (Montemar, Chile); Stotz, 1977: 27 (Valdivia, Chile); Stotz 1979: 181 (Valdivia, Chile); Sebens & Paine, 1979: 222 (Iquique to Llahue Peninsula); Brace, 1981: 85; Baeza & Stotz, 1995: 255 (Coquimbo, Chile); Häussermann, 1998 (Arica to Chiloé Island, Chile); Baeza, Stotz & Thiel, 2000: 3726; Baeza & Stotz, 2001: 341; Häussermann & Försterra, 2001: 221 (Chile); Rivadeneira & Oliva, 2001; Baeza, Stotz & Thiel, 2002: 189; Baeza & Stotz, 2003: 25; Häussermann, 2003

Non *Phymactis clematis*; Milne Edwards, 1857: 275 (Brazil) (*sensu* Verrill, 1869); ?Stephenson, 1918: 23 (South Trinidad Island, Antarctica) (*sensu* Carlgren, 1939); ?Orlando Muñoz, Atkinson & Idler, 1976; Zamponi, 1977: 137 (Argentina); Zamponi, 1981; Pollero, 1983; Patronelli, Zamponi, Bustos & Vega, 1987; Zamponi, 1989; Excoffon & Zamponi, 1991; Zamponi, 1993; Acuña & Zamponi, 1995; Genzano, Acuña, Excoffon & Perez, 1996; Acuña & Zamponi, 1996a; 1996b; Zamponi & Pérez, 1996; Acuña, Zamponi & Pérez, 1996; Excoffon & Zamponi, 1997; Zamponi, Belém, Schlenz, & Acuña, 1997 (1998); Gomes, Belém & Schlenz, 1998; Excoffon, Genzano & Zamponi, 1999; Zamponi, Genzano, Acuña & Excoffon, 1998; Zamponi, 2000.

Actinia florida Drayton in Dana, 1846: 131 (Callao, Peru) (*sensu* Andres, 1884 and Carlgren, 1899); Drayton in Dana, 1859: 6; Gay, 1854.

Phymactis florida; Milne Edwards, 1857: 274; Verrill, 1869: 476; Andres, 1884: 218.

?*Cladactis grandis* Verrill, 1969: 472 (Paita, Peru, Panama, Pearl Island, Nicaragua); Andres, 1884: 443 (*sensu* McMurrich, 1904: 259).

?*Eucladactis grandis*; Pax, 1912: D27 (footnote).

?*Phymactis capensis*; Pax, 1912: D26 (San Salvador, Panama, Peru, Chile) (footnote).

?*Phlyctenactis tuberculosa*; Zamponi, 1992 (1995) (Concepción, Chile).

External anatomy (figs 3-12).— Middle-sized to large species up to 100 mm pedal disc diameter; column red, green, blue or brown; tentacles and oral disc slightly paler than column. Column densely covered with rounded, non-adhesive, generally compound vesicles (figs 5, 9). Acrorhagi present, rarely in several rows. Oral disc in large animals slightly lobed (fig. 4); mouth opening prominent. Numerous short and conical tentacles situated at margin of oral disc. Contracted animals shaped like cylindrical stump of cone, with crater-like hole at apex (figs 6, 8). Young individuals up to 10 mm pedal disc diameter often with dense, white radial lines on the centre of the oral disc, mouth opening dark (fig. 11); with fewer, relatively larger vesicles. Individuals in the field found single or in aggregation. Preserved animals bluish, greenish or reddish-brown initially; colour tends to fade over time. The cnidom of *Phymactis papillosa* contains just a few characteristic elements, which distinguish it from the cnidom of *Phy-*

manthea pluvia: the large holotrichs (fig. 13H), the rod-like basitrichs in the acrorhagi (fig. 13I), and the microbasic amastigophores A in the pharynx (fig. 13G).

Size (in life).—Solitary individuals: pedal disc diameter to 100 mm, typically 70 mm; column diameter to 90 mm, typically 60 mm; column height to 70 mm, typically 50 mm high; oral disc diameter to 90 mm, typically 65 mm; longest tentacles 40 mm, typically 25 mm. Clonal individuals: pedal disc diameter to 50 mm, typically 40 mm; column diameter to 45 mm, typically 35 mm; column height to 40 mm, typically 30 mm; oral disc diameter to 45 mm, typically 35 mm; longest tentacles to 20 mm, typically 15 mm.

Colouration.—Four easily distinguishable colourations: red, green, blue and brown. Each of these constitutes a variety: var. *rubra* (red), var. *viridis* (green), var. *cyanea* (blue), var. *fusca* (brown). Andres (1884) mentioned var. *rubra*, var. *viridis* and var. *cyanea*; var. *fusca* is herein described for the first time. Specimens also occur as mixed morphs, with vesicles or oral disc coloured differently from column; these constitute varieties *rubra-fusca*, *rubra-viridis*, *viridis-fusca*, and *rubra-cyanea*. Varieties are distinguished only by colouration; they do not vary in terms of anatomy or cnidae. If not otherwise mentioned, the varieties were found all along the Chilean coast.

Var. *rubra* (figs 3, 9, 11): Column with vesicles, oral disc and tentacles bright red, pedal disc red or rose-coloured, acrorhagi light red; moderately common.

Var. *viridis* (figs 5, 10): Vesicles bright green to olive green, oral disc light green, tentacles darker green, pedal disc whitish, greenish or yellowish, acrorhagi yellowish; common.

Var. *cyanea* (figs 4, 7, 8): Vesicles, oral disc and tentacles bright blue, pedal disc and acrorhagi white or light blue; generally very rare, but common in some regions (e.g. Coquimbo, North Chile); present at least between Valdivia, south Chile and Arica, north Chile as well as in Pucusana, Peru.

Var. *fusca* (fig. 6): Column with vesicles, oral disc and tentacles reddish brown or bright brown to dark brown, pedal disc whitish to brown, acrorhagi whitish brown; common.

Var. *rubra-viridis* (fig. 11): Column (hardly visible) and oral disc red, vesicles green, may look emerald green with reddish margin, tentacles brownish red, pedal disc red or rose-coloured, acrorhagi reddish or greenish; common (this morph was called *P. papillosa*, see Fautin (2003: *Phymactis papillosa*).

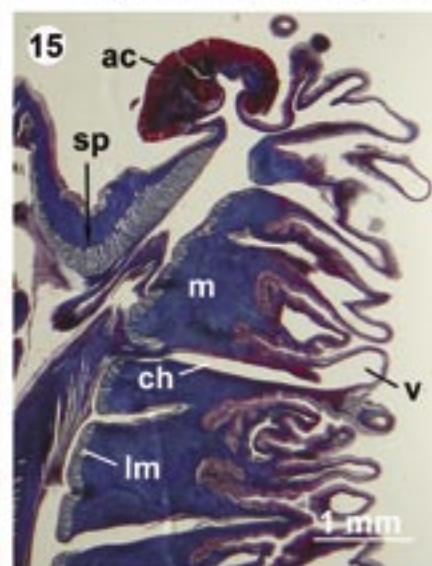
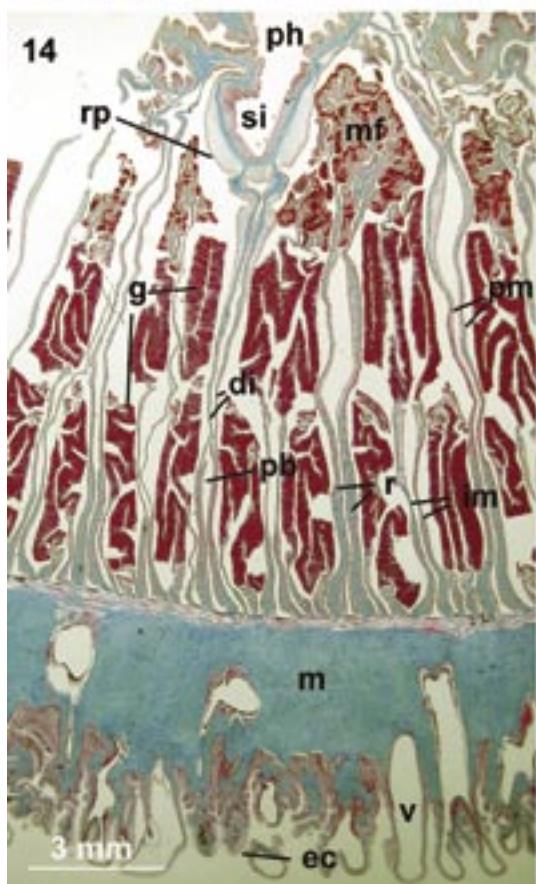
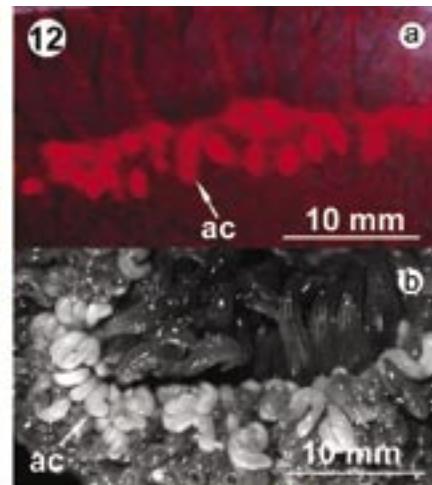
Var. *rubra-fusca* (fig. 10): Column with vesicles, oral disc and tentacles brownish red, pedal disc whitish to brownish red, acrorhagi brownish red; very common.

Var. *viridis-fusca* (fig. 10): Column with vesicles and tentacles brownish green, oral disc light greenish, mouth opening brown, pedal disc whitish to brownish green, acrorhagi lighter; common.

Var. *rubra-cyanea* (see original drawings in Fautin, 2003): Column red, vesicles, oral disc and tentacles blue, pedal disc whitish, acrorhagi white to reddish; very rare. Only observed in northern Chile.

Pedal disc.—Diameter slightly greater than or equal to that of column; robust, slightly lobed. Limbus weakly notched. In life coloured opaque, in some specimens red or slightly shaded in the main colour. Insertions of mesenteries are visible in the outer, more delicate and transparent region. Strongly adhesive to the substratum.

Column.—Stout, densely covered from margin to limbus with rounded, non-adhesive vesicles (figs 5, 9). Vesicles simple or, especially distally, compound; vesicle size



increases slightly towards horizontal midline of column. Vertical arrangement of vesicles difficult to discern due to their irregular size: in some animals, vesicles arranged linearly in proximal and distal region where vesicles are smaller. Size and number of vesicles partially a function of size of animal: large animals bear a greater number of vesicles, but small specimens have relatively larger vesicles (fig. 11). Most distal, largest "crown vesicles" often bear an acrorhagus on oral side; largest acrorhagi on the largest of the crown vesicles; acrorhagi generally lighter coloured than vesicles (figs 7, 12). Number of acrorhagi per specimen variable; distribution irregular in some individuals; rarely some individuals, especially juveniles, may lack acrorhagi. Rarely up to three rows of acrorhagi, which appear to be distributed over the most distal region of the column when being inflated (fig. 12). Fossa very distinct.

Oral disc and tentacles.— Oral disc circular to slightly lobed in large animals, about equal in diameter to column and slightly smaller than pedal disc (figs 3, 4). Oral disc paler than column, with radial lines visible at margin indicating insertions of mesenteries. Oral disc with central prominent mouth; mouth the same colour as oral disc but in most animals more intensely coloured (fig. 3); pharynx opaque white; with deep longitudinal furrows and two siphonoglyphs. Margin of oral disc bears numerous conical, short, retractile tentacles with broad base and circular terminal opening. First cycles of the tentacles of the large, solitary individu-

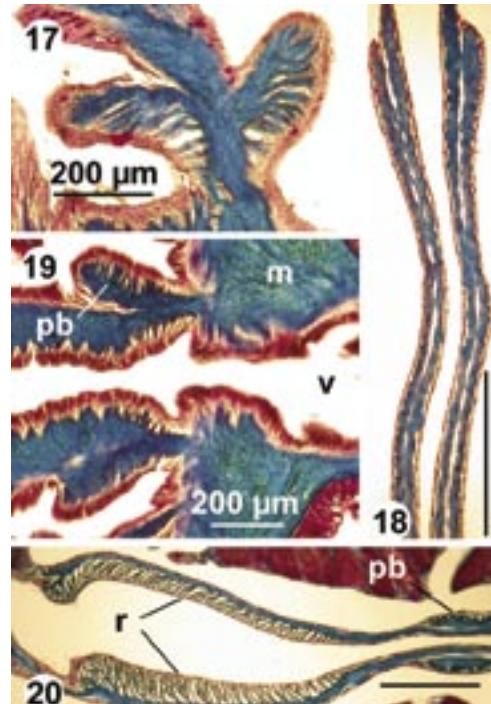


Fig. 17-20. *Phymactis papillosa*: Histological details of musculature (azocarmine triple staining). Fig. 17. Basilar muscles. Fig. 18. Long parietobasilar muscles in the distal region of the animal. Scale 1 mm. Fig. 19. Shorter parietobasilar muscles (pb) in the proximal region of the animal; note channel of endocoel (v). M: mesogloea. Fig. 20. Retractor muscle (r) and free pennon of parietobasilar muscle (pb). Scale 1 mm.

◀ Fig. 11-12; 14-16. *Phymactis papillosa*. Fig. 11. Var. *rubra-viridis* ZSM 20030295. Fig. 12. Juvenile specimen in a tide pool; note relatively large vesicles and acrorhagi. Fig. 14. Transverse section (azocarmine triple staining). Fig. 15. Histological section of upper column of large animal (azocarmine triple staining); note compound distal vesicles; Mesogloea blue, ectoderm and endoderm red. Fig. 16. Detail of a vesicle; note that apex and side of vesicle is identical in structure. Legend: Acrorhagi (ac), narrow channel of vesicle (ch), column (co), directives (di), ectoderm (ec), pair of imperfect mesenteries (im), endodermal longitudinal muscles (lm), mesogloea (m), trilobated mesenterial filament (mf), mucus gland cells (mg), parietobasilar muscle (pb), lumen of actinopharynx (ph), pair of perfect mesenteries (pm), retractor muscle (r), reticulated pad (rp), siphonoglyph (si), endodermal diffuse sphincter (sp), tentacles (te), vesicles (v).

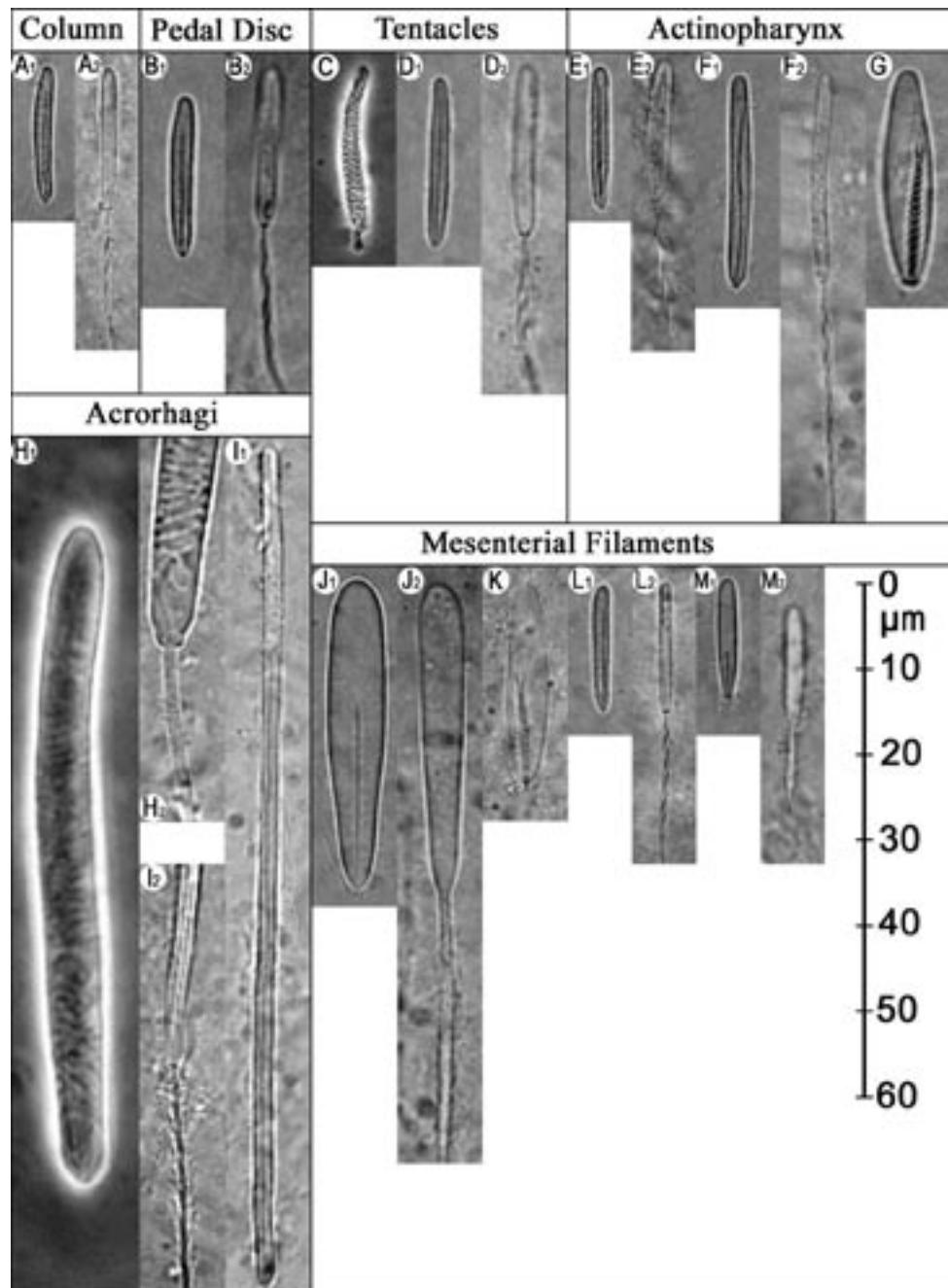


Fig. 13. Cnidae of *Phymactis papillosa*. Letters A–M correspond to cnidae types listed in Table 1.

als hexamerously arranged. Tentacles paler than column, may be slightly transparent, number to 400 in large animals; largest tentacles slightly shorter than half the diameter of the oral disc (fig. 4); inner tentacles hardly longer than outer ones. In preservation, tentacles furrowed longitudinally.

Internal anatomy (figs 14-20).—Mesenteries more or less hexamerously arranged in up to seven cycles. Up to approx. 200 pairs of mesenteries counted; a fourth to half of mesenteries perfect. Stotz (1977) counted up to 243 pairs of mesenteries. Mesenteries hard to count as very numerous with thin mesogloea. Youngest mesenteries connect to pharynx with a small lappet only. Approximately same number of mesenteries proximally and distally. Strongest mesenteries meet at centre of pedal disc. Large oral stoma and smaller marginal stoma; marginal stoma present at least in larger mesenteries, situated more proximally in older ones.

Actinopharynx long, up to more than 2/3 of the column, with fine, deep longitudinal furrows, two aborally prolonged siphonoglyphs and two pairs of directives; rarely with more siphonoglyphs not connected to directives or directives missing (Stotz, 1977).

Two of eight specimens examined fertile: the sectioned fertile specimen was male. Sexes separate (see also Carter (1965) and Stotz (1977)). Gonads mainly on medium sized and small imperfect and sometimes on youngest perfect mesenteries, arranged in long strings (fig. 14). Reproductive tissue may appear on all incomplete mesenteries except very small ones. At least two oldest cycles of mesenteries and directives sterile.

Musculature.—Sphincter endodermal, diffuse and well developed, strong, tapering at both ends (fig. 15). Circular endodermal musculature of body wall strong, absent in vesicles. Longitudinal muscles of tentacles ectodermal. Circular musculature of oral disc endodermal to meso-endodermal, radial muscles ectodermal to mesogloea (see Stotz, 1977). Mesenterial retractors diffuse, very variable in shape, restricted to inner half or inner fourth of mesentery (figs 14, 20). Parietobasilar muscles strong; in proximal column short (fig. 19), in distal column parietobasilar of a larger mesentery may be connected to mesentery over a half of mesentery's span (figs 14, 18). Basilar muscles strong (fig. 17).

Epithelia.—Vesicles hollow, rounded evaginations of body wall formed by all three tissue layers (fig. 16); endocoelic. Mesogloea of column and vesicle layer exceptionally thick, 2-3 mm and 2-6 mm respectively. Each vesicle connected with gastrocoel by narrow channel (figs 15, 19). All tissue layers show modifications in vesicle, compared to column: endodermal circular musculature absent in whole vesicle; mesogloea thin, especially at apex of vesicle ectoderm with many globular mucus gland cells (fig. 16). Ectoderm at apex of vesicle not differentiated from ectoderm at sides of vesicle. Endoderm of tentacles and vesicles with dark pigment granules; these pigments probably are responsible for the colouration (fig. 16). Siphonoglyphs each with long cilia and strongly developed reticulated pads (fig. 14).

Cnidae (fig. 13).—Spirocysts (in tentacles, some in acrorhagi, sporadic in pedal disc), basitrichs (in all tissues), microbasic *b*-mastigophores (in filaments), microbasic amastigophores A (in pharynx and filaments), microbasic *p*-mastigophores B (in filaments), holotrichs (in acrorhagi and sporadic in proximal region of column), rod-like basitrichs (in acrorhagi) (fig. 13). See table 1 for information on size and distribution.

Cnidae size data for a single, medium-sized specimen of *P. papillosa* var. *rubra-viridis*

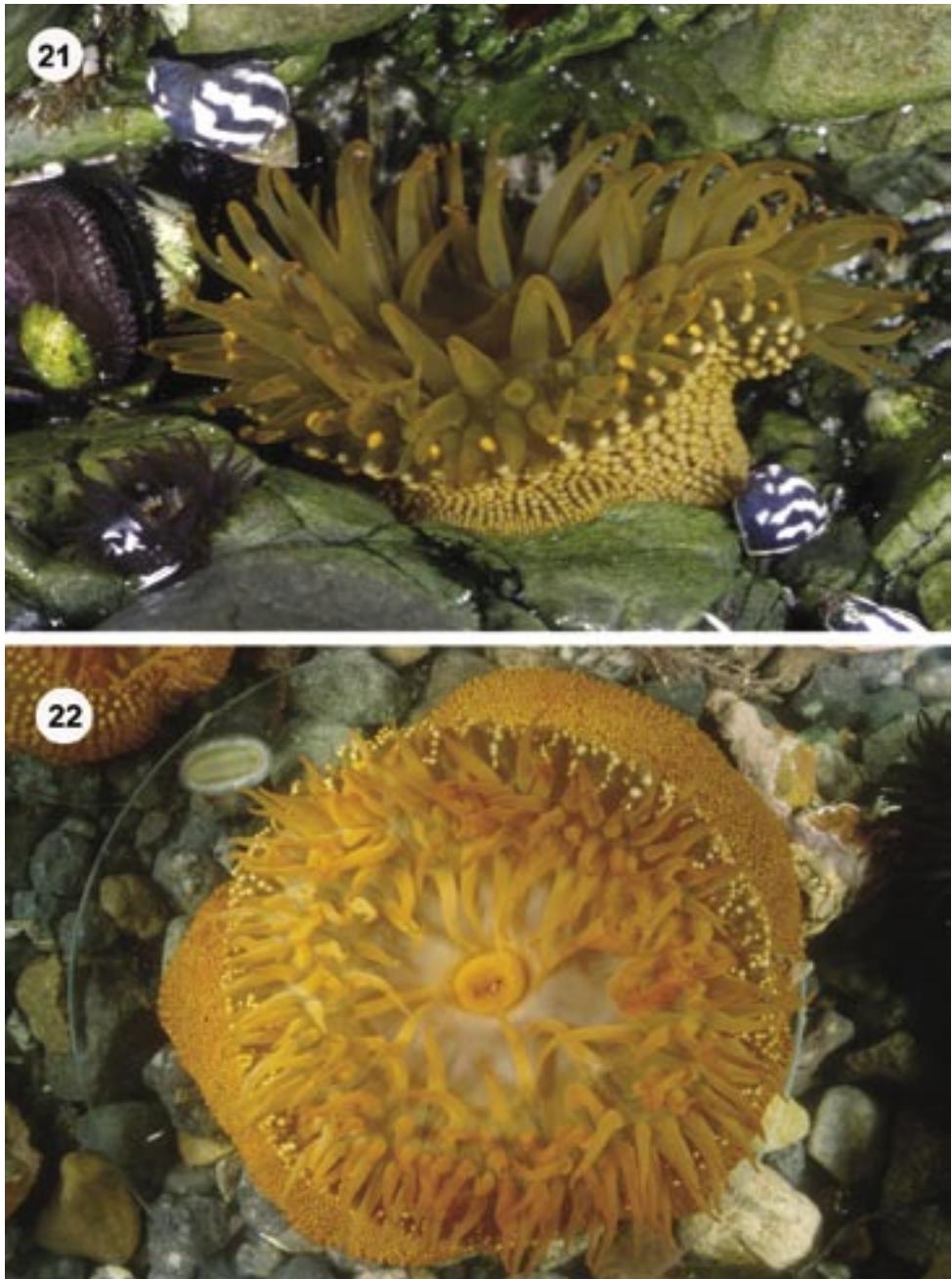


Fig. 21-22. *Phymanthea pluvia*. Fig. 21. Specimen in a tide pool; note acrorhagi on most distal vesicles, longitudinal rows of vesicles on proximal region of column and juvenile specimen of *P. papillosa* on lower left side. Fig. 22. Oral disc and tentacles; note deeply coloured, prominent mouth opening and enlarged marginal vesicles corresponding with smaller marginal vesicles.

(ZSM 20030295) (table 1) are comparable to those for specimens of roughly the same size belonging to var. *rubra* and var. *cyanea*. Smaller individuals of var. *cyanea* and var. *fusca* had somewhat smaller cnidae. A length by width range of holotrichs and rod-like basitrichs from acrorhagi of juvenile specimen varies considerably from those given in Table 1: holotrichs 36–54 µm, basitrichs 47–54 µm.

Distribution and zoogeography.— *Phymactis papillosa* is a wide-spread species, found in abundance on the Pacific coast of Central and South America in Mexico, Peru and Chile, and in the Sea of Cortez (fig. 2).

Within Chile, *Phymactis papillosa* is reported from the Chilean coast between Arica, north Chile ($18^{\circ}28'S$, $70^{\circ}19'W$), and the exposed coasts of the Archipago de los Chonos ($44^{\circ}24'S$; $73^{\circ}34'W$) (figs 1–2), south Chile (Carlgren, 1959), as well as on Easter Island (Carlgren, 1920) and the Júan Fernández Islands (McMurrich, 1904) (fig. 2). During this study we found *P. papillosa* between Arica and Cacao on Chiloé Island ($42^{\circ}35'S$; $74^{\circ}07'W$), south Chile (fig. 1). A single specimen was found in the subtidal of Seno Reloncaví close to Lenca ($41^{\circ}35'37,0''S$; $72^{\circ}42'10,9''W$). Despite intense sampling in the fjord region, *P. papillosa* was neither found in the inner fjords between Lenca and Puerto Chacabuco ($45^{\circ}27'S$; $72^{\circ}49'W$) nor in Puerto Natales ($51^{\circ}38'S$; $72^{\circ}28'W$) where the surface water is characterized by a prominent low salinity layer (LSL) with salinities <10‰. It was not found in the exposed regions between Bahía TicToc and Raul Marin Balmaceda ($43^{\circ}35'59,0''S$, $72^{\circ}55, 25,2''W$ – $44^{\circ}00'26,7''S$, $73^{\circ}05'35,4''W$) or around Fuerte Bulnes in the Strait of Magellan ($53^{\circ}30'S$; $70^{\circ}56'W$).

In Peru, Lesson (1830) described *Phymactis papillosa* from Paita (= Payta) ($5^{\circ}05'S$, $81^{\circ}06'W$) southward; Stefan Austermühle (in litt., 2003) reported it from Paracas ($14^{\circ}02'40''$ – $14^{\circ}03'50''S$, $76^{\circ}15'60''$ – $76^{\circ}16'70''W$) to the Peninsula Bayovar ($05^{\circ}48'15''S$, $81^{\circ}04'99''W$), but not further north between Tumbes ($03^{\circ}29'17''S$, $80^{\circ}23'10''W$) and Bahía de Sechura ($05^{\circ}48'15''S$, $81^{\circ}05'00''W$) (fig. 2).

In a recent study, specimens of *Phymactis papillosa* have been collected and identified intertidally from both the Pacific ($23^{\circ}26'N$; $110^{\circ}15'W$) and the Gulf of California coast ($24^{\circ}08'N$; $110^{\circ}18'W$) of southern Baja California, Mexico (Daly, in litt. 2003). *Sensu* Daly (in litt., 2003), *P. papillosa* was, together with *Anthopleura dowii* Verrill, 1869, the most abundant sea anemone in this region.

Natural history.— *Phymactis papillosa* is one of the most common Chilean sea anemones of the upper littoral and may be the most common species of the intertidal. Specimens of this species occur intertidally and subtidally to depths of 16 m, generally attached to bare rock, which is free from macroalgae (figs 6, 7).

Apart from species which only occur in tide or splash pools *Phymactis papillosa* is the species settling in the highest areas of the intertidal zone. The highest densities of *P. papillosa* occur between the lowest low tide level and the mean tide level in exposed positions below overhangs and on vertical and overhanging rock walls (figs 6–8), where specimens of this species frequently form large, more or less dense aggregations of up to 100 or more individuals. In habitats which are protected from direct sunlight and in tide pools, specimens can even reach the mean high tide level. Young specimens were found in small, protected tide pools of the high intertidal, often between mytilids (figs 11, 21). They can withstand direct sunlight for several hours during low tide (fig. 6). *P. papillosa* lives in habitats with strong surge surf and can tolerate direct wave exposure. In very exposed habitats, specimens of this species live in cracks, holes and under rocks

Table 4. List of valid and doubtful species of the genera *Phymactis* Milne Edwards, 1857, *Bunodosoma* Verrill, 1899 and *Phymanthea* Carlgren, 1959.

Genus *Phymactis* Milne Edwards, 1857

Urticina p.p. Duchassaing, 1850; *Phymactis* p.p. Milne Edwards, 1857; p.p. Andres, 1883; *Bunodes* p.p. Verrill, 1864; McMurrich, 1889; *Bunodactis* p.p. Pax, 1922, 1926; *Cladactis* Verrill, 1869; *Eucladactis* Verrill, 1899.

Genotype: *P. (Actinia) papillosa*^d (Lesson, 1830) = *P. (Actinia) clematis* (Drayton in Dana, 1846) = *P. (Actinia) florida* (Drayton in Dana, 1846): Archipelago de los Chonos, south Chile to Peninsula Bayovar, Perú, Juan Fernández Islands, Easter Islands, Gulf of California: intertidal and upper littoral down to 16 m, on stones and rocks, in tide pools.

- *P. (Actinia) sanctaehelenae* (Lesson, 1830): St. Helena, Atlantic Ocean; upper littoral.

Species with unknown status:

- ?*P. (Actinia) pustulata* (Couthouy in Dana, 1846) = *P. clematis* Stephenson, 1918 = *B. cavernata* Verrill, 1864 = ?*P. braziliensis* Carlgren, 1939: Cape Hatteras along Central American east coast down to Mar del Plata, Argentina; intertidal - at least Gulf of Mexican populations with adhesive verrucae (den Hartog, 1987) thus species might belong to another genus (species formerly put into the genus *Bunodosoma* by den Hartog, 1987); this species was nor found by Correa (1964) neither during other recent studies of the Brazilian anemone fauna (Gomes, in litt., 2003).

Genus *Bunodosoma* Verrill, 1899

Rivetia Pax, 1912

Genotype: *B. (Actinia) granulifera*^d (Le Sueur, 1817) = *Bunodes taenitus* McMurrich, 1889 = *Urticina lessonii* Duchassaing, 1850: Caribbean Sea (West India, Jamaica, Puerto Rico, Panama, Bahamas, Barbados, Curaçao, Guadeloupe, Martinique, St. Thomas, Brazil).

- *Bunodosoma caissarum*^d Corrêa in Belém, 1987: Brazil.
- *Bunodosoma cangicum*^d Corrêa in Belém & Preslercravo, 1973: Brazil (name not valid *sensu* Fautin, 2003).
- *Bunodosoma spherulata* Duerden, 1902: Porto Rico.
- *Bunodosoma kiikenthali* Pax, 1910: Barbados, Curaçao, Loango.
- *B. (Actinia) cavernata* (Bosc, 1802): South Carolina to cape Hatteras; Caribbean Sea (Cuba, Puerto Rico, Florida); intertidal and low-water - Gulf of Mexican populations with adhesive verrucae (McCommas & Lester, 1980); *sensu* Daly (in litt., 2003), the vesicles of *B. cavernata* can attach foreign material presumably due to their cnidae, but never really adhere it in the way verrucous species do.
- *Bunodosoma californica*^d Carlgren, 1951: Pacific coast of Baja California and Gulf of California, Mexico to El Salvador; intertidal.
- *B. (Cladactis) grandis* (Verrill, 1869): Peru to Nicaragua, Pearls Islands.
- *B. (Actinia) diadema* (Drayton in Dana, 1846): Cape Verde Islands, Porto Praya, ?Morocco.
- *Bunodosoma goanensis*^d den Hartog & Venham, 1993: west India; intertidally attached to smooth rock.

Species, which might belong to another genus and need to be re-examined:

- ?*B.**. (*Bunodes*) *biscayensis*^d (Fischer, 1874): French and Spanish Atlantic coast; low water; with adhesive verrucae (den Hartog, 1987); probably belongs to the genus *Anthopleura* (Daly, in litt., 2003).
- ?*B. (Actinia) capensis* (Lesson, 1830): South Africa from Lüderitz Bay to Durban (following England (den Hartog, 1987) probably belongs to another genus).

Species with unknown status:

- ?*B. polydactyla* Hutton, 1878: New Zealand; most probably this species does not exist and specimens belong to another species (Ocaña, in litt., 2003).
- ?*P. crucifer* Verrill, 1907: Bermuda; status unknown (never cited since first description).

- ?B. (*Bunodactis*) *fallax* (Pax, 1922): New Amsterdam Island (*sensu* den Hartog & Vennam (1993) the generic identity of this species cannot be determined by the material and thus needs confirmation).

Genus *Phymanthea* Carlgren, 1959

Genotype: *P. pluvia* Carlgren, 1959: Paita, Perú to Valparaíso, Chile; intertidal and subtidal to 16 m, on stones and rocks, in tide pools.

and large stones (fig. 10). Although the solitary individuals are most common in the subtidal, they can also be found in tide pools, in crevices, and on rock walls of the exposed intertidal (fig. 10). In south Chile, medium-sized specimens form a narrow band below the mytilid zone and are often found between and under the green alga *Ulva lactua* Linnaeus, 1753 (Stotz, 1977). In tide pools, *P. papillosa* can be found associated with the sea anemones *Anemonia alicemartinae* Häussermann & Försterra, 2001 (Häussermann & Försterra, 2001) and *Oulactis concinnata* (Drayton in Dana, 1846) (Häussermann, 2003). *P. papillosa* and *A. alicemartinae* both live in exposed positions; *P. papillosa* even can stand moderate wave exposure; *O. concinnata* can be found in sand-filled crevices. Juvenile and adult specimens of the porcellanid crab *Allopelotisthes spinifrons* were observed sitting on the column of *P. papillosa* (figs 5, 9). *Sensu* Stotz (1977) this symbiosis is more abundant in shaded places protected from waves; the crab rapidly moves between tentacles, oral disc and column without any reaction of the anemone. Tides at Antofagasta, north Chile, are 0.8 m on average and 1.6 m at spring tide, and show little variation along the exposed coast of the study region (Guiler, 1959). Tides in the fjords are much higher, e.g. up to 7.3 m in the fjord Comau (own observation).

In the sublittoral, the population density decreases rapidly; below 7 m *P. papillosa* can be found only occasionally. Larger solitary individuals in the sublittoral generally live on the lower portion of large rocks and can occasionally be found on the ascidia *Pyura chilensis* Molina, 1782 and on the polychaet *Phragmatopoma virgini* Kinberg, 1867 (Stotz, 1977). A general decrease in size can be seen from the upper to the lower intertidal and subtidal (see also Stotz, 1977). *Sensu* Stotz (1977) a vertical migration of individuals of different age and a fluctuation of the population throughout the year can be observed; populations strongly decrease in winter.

Phymactis papillosa var. *cyanea*, and to a lesser extent var. *viridis* appear to avoid sun exposure; specimens belonging to these varieties were typically found in well-shaded places like overhangs (fig. 8), caves or under stones. In the aquarium, they expand in the darkness. In contrast, specimens belonging to var. *rubra* are often found in well-illuminated positions.

In Baja California Sur, Mexico, specimens of *Phymactis papillosa* occur in more exposed habitats and further down in the intertidal, compared to *Anthopleura dowii*, another very common Mexican intertidal sea anemone; *P. papillosa* is found in the mid to low intertidal and subtidally (Daly, in litt., 2003). *Sensu* Daly (in litt., 2003), var. *rubra* is by far the most common on the Pacific coast, and is the only colour morph found within the Gulf of California. Some olive green specimens were found at Los Cerritos, on the Pacific coast; a single patch of mustardy yellow animals was found within one aggregation of green specimens at this locality. On both the Pacific and Gulf coasts, individuals occur in loose aggregations; animals within an aggregation typically do not touch one another, and vary in size from about 10 to 50 mm diameter (Daly, in litt., 2003). Soli-

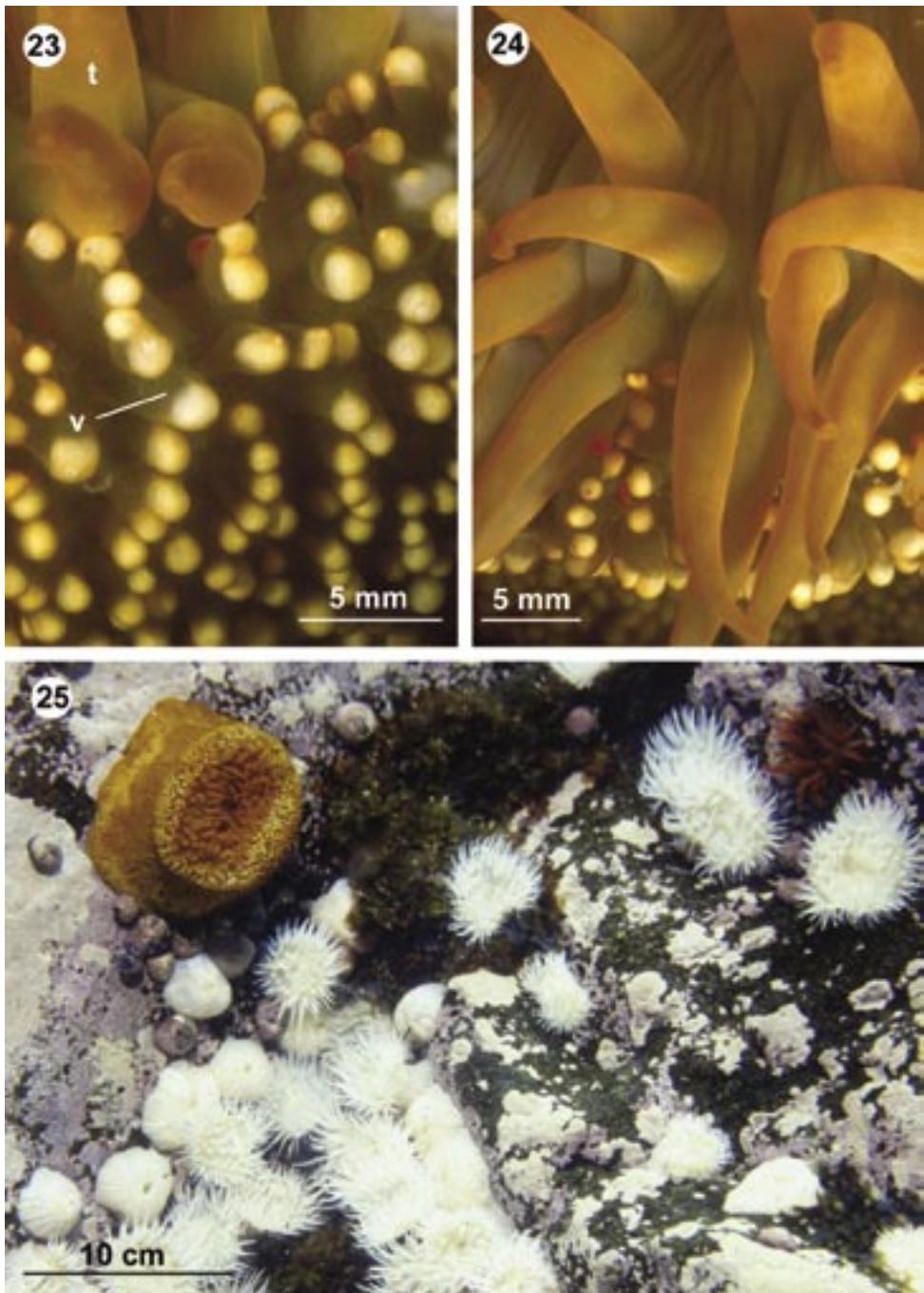


Fig. 23-25. *Phymanthea pluvia*. Fig. 23. Compound, most distal vesicles; note white apices. Fig. 24. Outer region of oral disc with tentacles; note mesenterial insertions. Fig. 25. Typical position and appearance of *Pa. pluvia* in subtidal habitat, associated with *Anthothoe chilensis* (white) and *Anemonia alicemartiae* (red).

tary specimens do not exceed these sizes, but live at lower depth than aggregations, in semi-permanent pools that are free of algae and where water may get very warm during low tide (Daly, in litt., 2003).

Large solitary *Phymactis papillosa* show agonistic behaviour towards neighbouring individuals (Sebens & Paine, 1979); individuals within aggregations show agonistic behaviour against members of other aggregations (Daly, in litt., 2003). *Sensu* Sebens & Paine (1979), the anemones extend the body and swing it in a circle while inflating their acrorhagi and using them to sting any close neighbours. Brace (1981) reports intraspecific aggression between colour morphs taken from aggregations in Montemar, central Chile. No agonistic behaviour against members of the same species was observed during this study.

Specimens of *Phymactis papillosa* are quite mobile, and move through the aquarium by somersaults. When somersaulting specimens encountered specimens of *Antholoba achates* (Drayton in Dana, 1846), they did not avoid contact, resulting in injuries for both themselves and their opponents (fig. 3). A specimen of *P. papillosa* var. *viridis* as well as several specimens of *Anthopleura* aff. *hermaphroditica*, which had been kept at large distance in the same, very large aquarium, were found burned badly by a specimen of *P. papillosa* var. *rubra* during two subsequent mornings. The numerous red patches on the burned specimens contained nematocysts from the aggressor. The injured specimens stayed in contracted condition for two days, when the foreign tissue started being secreted with mucus.

One specimen carrying a porcellanid crab *Allopetrolisthes spinifrons* presented three rows of acrorhagi (fig. 12), which it could inflate and deflate within minutes. These acrorhagi were not visible most of the time (fig. 9). Stotz (1977) has already reported several rows of acrorhagi from some specimens.

The adhesion of the pedal disc to the substratum is very strong in *Phymactis papillosa*. Specimens are very difficult to remove from the rough rock without damaging the pedal disc, but generally reattach within a few hours in the aquarium.

No signs of asexual reproduction were observed in large, solitary *Phymactis papillosa*. The aggregated (clonal) form of *P. papillosa* may exhibit scars from longitudinal fission, but was rarely observed in state of fission.

Phymanthea pluvia (Drayton in Dana, 1846)

Actinia pluvia (partly) Drayton in Dana, 1846: 144 (San Lorenzo, Callao, Peru); Drayton in Dana, 1859: 9. *Bunodes pluvia*; Gosse, 1860; Verrill, 1869: 468; Andres, 1884: 226.

Bunodactis pluvia; Carlgren, 1949a: 66 (Peru).

Cereus pluvia; Milne Edwards, 1857: 267.

Phymanthea pluvia; Carlgren, 1959: 17 (14 spec., Iquique, Chile); Carter, 1965: 148 (Montemar, Chile);

Sebens & Paine, 1979: 222 (Iquique to Pto. El Lacho, Chile); Baeza & Stotz, 1995: 255 (Coquimbo, Chile); Häussermann, 1998 (Arica to Papudo, Chile); Häussermann & Försterra, 2001: 221 (Chile); Baeza, Stotz & Thiel, 2002: 190; Baeza & Stotz, 2003: 25; Häussermann, 2003.

?*Phymactis clematis*; McMurrich, 1904: 258 (Chile).

External anatomy (figs 21-25).— Large species of hardly variable bright orange colour. Column densely covered with rounded, simple or, especially distally strongly compound non-adhesive vesicles with whitish tips. Acrorhagi present. Numerous

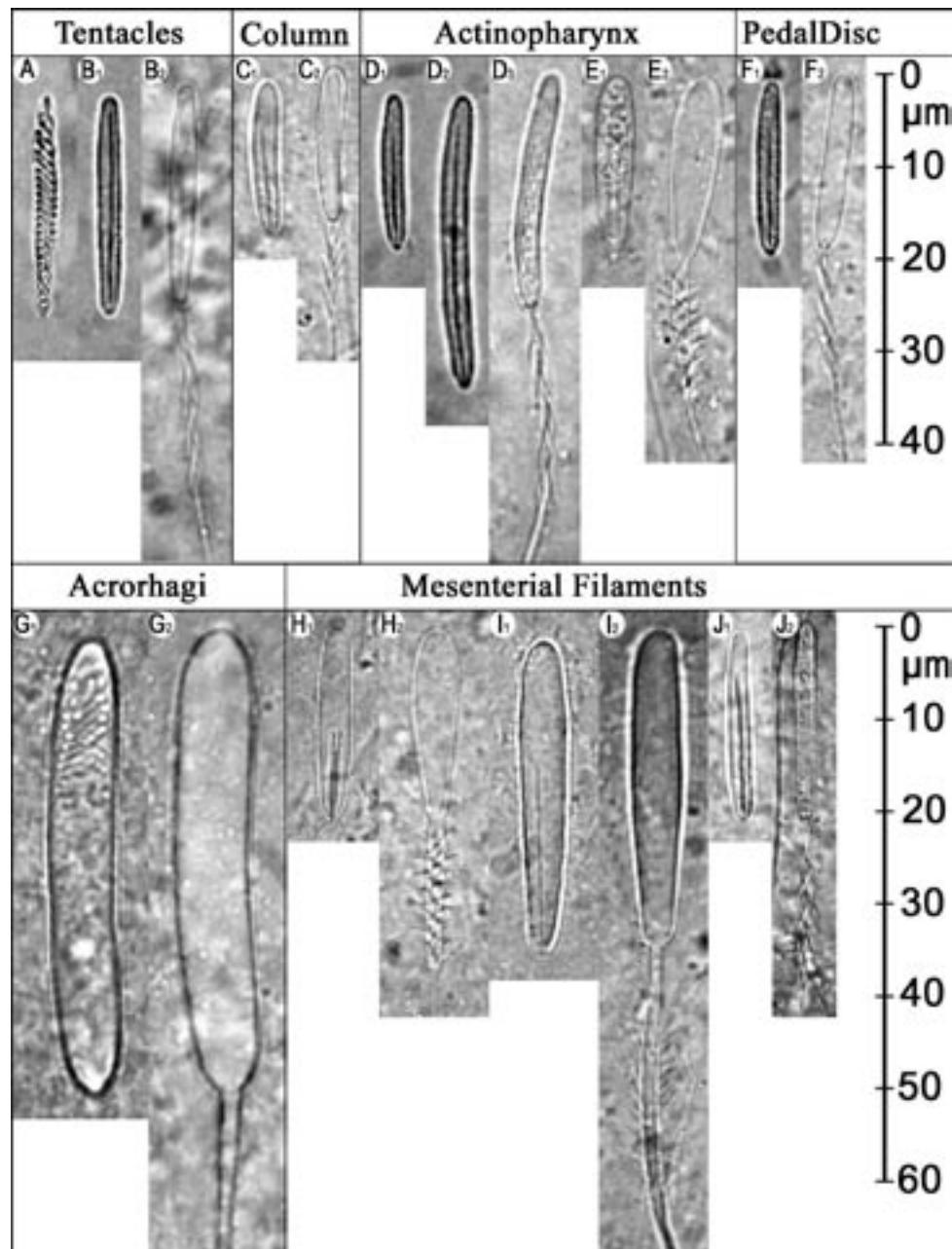


Fig. 26. Cnidae of *Phymanthea pluvia*. Letters A–J correspond to cnidae types listed in Table 2.

short, conical tentacles situated only on outer half of oral disc; mouth opening prominent. Contracted animals shaped like the stump of a cone with a crater-like hole in the middle; few specimens contract completely. Solitary. Preserved animals beige. The cni-dom of *Phymanthea pluvia* contains only a few characteristic elements which distinguish it from *Phymactis papillosa*: the smaller holotrichs (fig. 26G) and the lack of rod-like basitrichs in the acrorhagi, the lack of microbasic *p*-mastigophores B in the filaments and the extreme scarcity of microbasic amastigophores A in the pharynx.

Size (in life).— Pedal disc diameter to 160 mm (typically 100 mm); column diameter to 160 mm (typically 100 mm), column height to 140 mm (typically 80 mm); oral disc diameter to 180 mm (typically 110 mm); longest tentacles 50 mm (typically 35 mm).

Colouration.— Column and vesicles transparent orange, vesicles with whitish orange tips (fig. 23); oral disc pale transparent orange (fig. 22); tentacles orange, acrorhagi whitish orange (fig. 21); pedal disc white to slightly orange-coloured. Colouration within Chile very uniform, most observed specimens were bright orange, some slightly brownish orange.

Pedal disc.— Circular and robust, strongly attached to substratum; white, rarely with a slight orange colouration; mesenterial insertions visible. Limbus weakly notched.

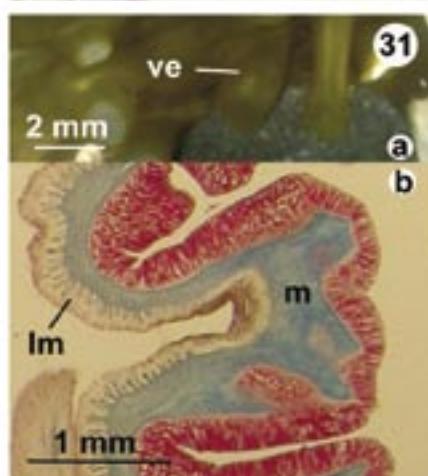
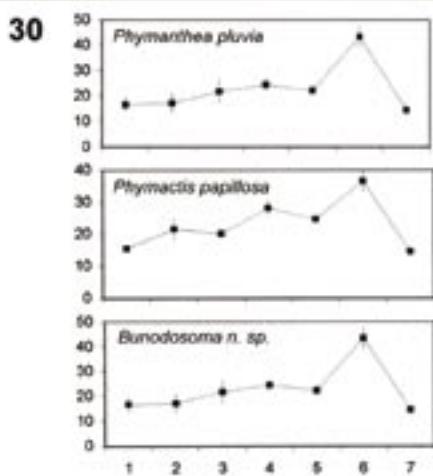
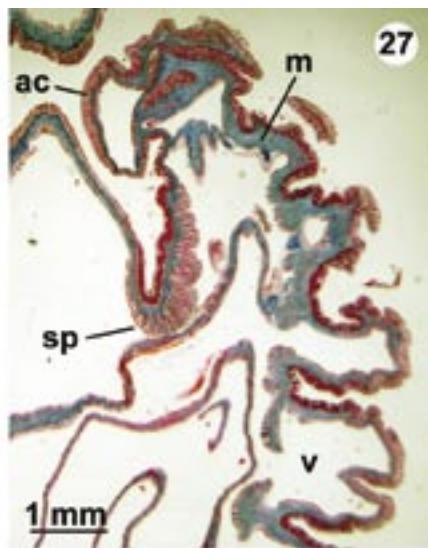
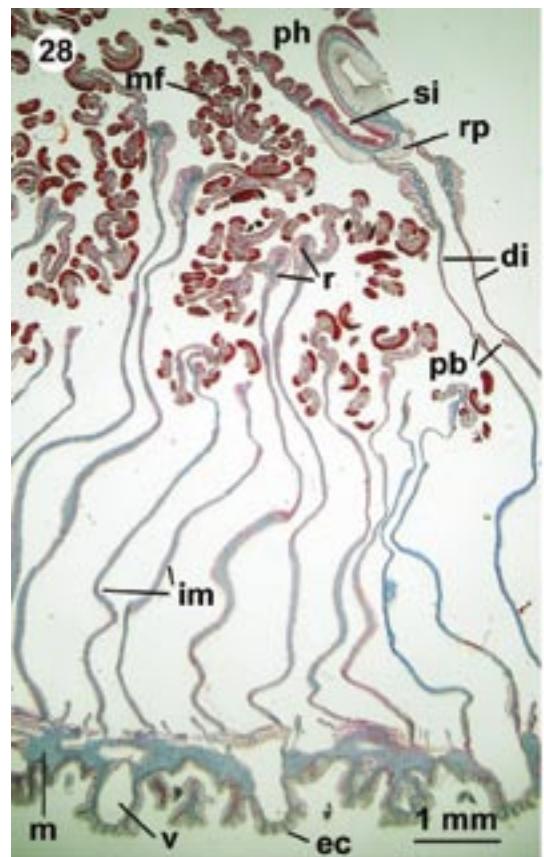
Column.— Broader than high, covered from margin to limbus with rounded, non-adhesive vesicles (fig. 21). Vesicles simple or, especially in distal region, strongly compound (fig. 23); vertical rows of vesicles more or less vague, distinguishable proximally and distally (fig. 21); more rows of smaller vesicles proximally. Distal-most, large, crown vesicle (71 and 85 counted in a medium-sized and a small specimen) with branches on outer side and generally a whitish orange acrorhagus on oral side (fig. 21). Crown vesicles of older cycles largest, alternate with smaller ones (figs 22-24). Number of acrorhagi variable; distribution irregular in some individuals; largest acrorhagi on largest crown vesicles; not every marginal vesicle with acrorhagi; acrorhagi rarely absent (Carlgren, 1959). Fossa deep.

Oral disc and tentacles.— Oral disc circular to slightly lobed, especially in large animals, transparent orange. Insertions of mesenteries visible as orange lines on oral disc (fig. 22); mouth prominent and bright orange; two well-developed siphonoglyphs. Medium-sized specimens 300 or more tentacles; tentacles conical, with broad base and circular terminal opening, length about half diameter of oral disc; situated at margin of oral disc. Inner tentacles slightly longer than outer ones. In preservation, tentacles longitudinally furrowed.

Internal anatomy (figs 27-29, 32-34).— Mesenteries more or less hexamerously arranged in up to seven cycles, a fourth to half of which perfect. Mesenteries hard to count as very numerous and thin. Youngest ones connected to pharynx with a small lapet only. Approximately same number of mesenteries proximal and distal. Strongest mesenteries meet at centre of pedal disc. At least in older mesenteries large oral stoma and small marginal stoma present, the latter situated more proximal in older mesenteries.

Actinopharynx long, up to more than 2/3 of the column, with fine, deep longitudinal furrows and two aborally prolonged siphonoglyphs. Two pairs of directives.

One of six specimens examined fertile: the fertile specimen was male. Reproductive tissue on middle-sized and small mesenteries; it may appear on all incomplete mesenteries except very small ones and on youngest ones of perfect cycles; reproductive tissue irregularly distributed within specimen. Oldest mesenteries and directives sterile.



Musculature.— Sphincter endodermal, diffuse and well developed with numerous folds (fig. 27), now more concentrated, now more elongate; tapering at both ends. Circular endodermal musculature of body wall strong, absent in vesicles (fig. 27). Longitudinal muscles of tentacles ectodermal. Radial musculature of oral disc ectodermal, circular musculature endodermal. Mesenterial retractors small, diffuse restricted, reniform to circumscribed, situated at inner end of mesentery (figs 28, 32, 33). Parietobasilar muscles form a distinct deep fold on the mesenteries, strong; connected with mesentery over a long distance (figs 28, 32). Basilar muscles strong (fig. 34).

Epithelia.— Vesicles, hollow, rounded evaginations of body wall formed by all three tissue layers (fig. 29). Mesogloea of column and vesicle layer thick, but in animals of same size generally somewhat thinner than in *Phymactis*. Vesicles connected with gastrocoel by narrow channels (fig. 27). All tissue layers show modifications in vesicle, compared to column: endodermal circular musculature absent in whole vesicle, mesogloea thin; ectoderm with many globular mucus gland cells; ectoderm at apexes of vesicles differentiated from ectoderm at sides of vesicles: mucus gland cells are missing at apexes of vesicles (fig. 29). Endoderm of tentacles and on sides of vesicles with dark

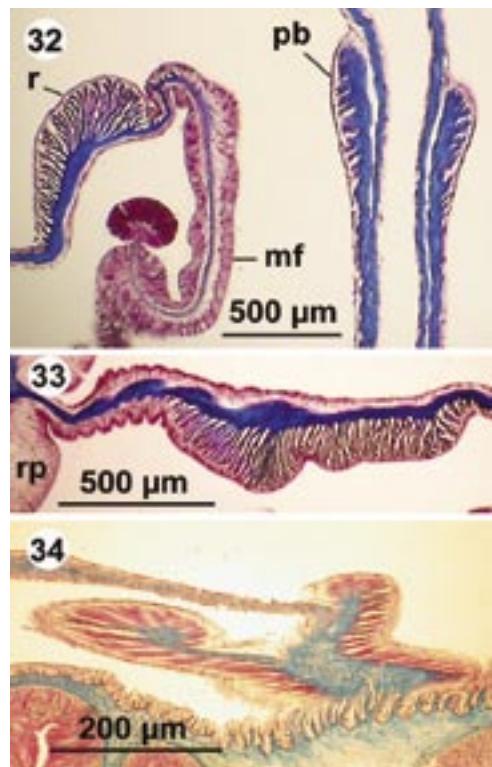


Fig. 32-34, *Phymanthea pluvia*. Histological details of musculature (azocarmine triple staining). Fig. 32. Retractor muscle (r) and free pennon of parietobasilar muscle (pb) in distal region of animal. Fig. 33. Retractor muscles on directive mesentery; rp: reticulated pad of siphonoglyph. Fig. 34. Basilar muscles.

◀ Fig. 27-31. Fig. 27-29, *Phymanthea pluvia*. Fig. 27. Histological section of upper column of small animal (azocarmine triple staining); note compound distal vesicles; Mesogloea blue, ectoderm and endoderm red. Fig. 28. Transverse section (azocarmine triple staining). Fig. 29. Detail of vesicle; note different structure of apex and side of vesicle: mucus gland cells at vesicle side and lacking endodermal muscles. Fig. 30. Cnidocyst diagrams of *Phymactis papillosa* and *Phymanthea pluvia* modified after Schmidt (1972). Fig. 31. Verruca of *Oulactis concinnata*, *in vivo* and preserved state; note lacking endodermal muscles and dark pigments at apex of verruca. Legend: Acrorhagi (ac), column (co), directives (di), ectoderm (ec), pair of imperfect mesenteries (im), endodermal longitudinal muscles (lm), mesogloea (m), trilobated mesenterial filament (mf), mucus gland cells (mg), parietobasilar muscle (pb), lumen of actinopharynx (ph), pair of perfect mesenteries (pm), retracting muscle (r), reticulated pad (rp), siphonoglyph (si), endodermal diffuse sphincter (sp), tentacles (te), vesicles (v), verrucae (ve). 1: basitrichs (column), 2: spirocysts (tentacles), 3: basitrichs (tentacles), 4: basitrichs (pharynx), 5: microbasic amastigophores A (filaments), 6: large b-mastigophores (filaments), 7: small basitrichs (filaments); x-axis: tissue, y-axis: mean value of cnidocysts in µm, vertical line standard deviation.

pigment granules (fig. 27); these pigments probably are responsible for the colouration. Siphonoglyphs each with long cilia and strongly developed reticulated pads (fig. 28).

Cnidae.—Spirocysts (in tentacles, sporadic in pedal disc), basitrichs (in all tissues), microbasic *b*-mastigophores (in filaments), microbasic amastigophores A (in filaments, extremely scarce in pharynx), holotrichs (in acrorhagi) (fig. 26).

Table 2 provides data on cnidae size of specimen ZSM 20030303 (Ex. 63). Cnidae of other examined middle-sized specimens (ZSM 20030304) approximately matched the size ranges of Table 2. Smaller individuals had somewhat smaller cnidae.

Distribution and zoogeography.—*Phymanthea pluvia* is distributed between Paita, Peru ($05^{\circ}07'38"S, 81^{\circ}10'07"W$), and Montemar, central Chile ($32^{\circ}57'24"S, 71^{\circ}33'25"W$) (figs 1-2). Drayton in Dana (Dana, 1846) described *P. pluvia* from San Lorenzo, Peru ($5^{\circ}05'S, 81^{\circ}06'W$); Stefan Austermühle (in litt., 2003) reported it from Paracas ($14^{\circ}02'40"-14^{\circ}03'50"S, 76^{\circ}15'60"-76^{\circ}16'70"W$) to Paita, Peru ($05^{\circ}07'38"S, 81^{\circ}10'07"W$), but not further north between Talara ($05^{\circ}07'37"S, 81^{\circ}10'07'W$) and Tumbes ($03^{\circ}29'17"S, 80^{\circ}23'10'W$) (fig. 2). We found *P. pluvia* in the intertidal zone and down to depths of 16 m between Arica ($18^{\circ}28'S, 70^{\circ}19'W$), north Chile, and Papudo, central Chile ($32^{\circ}29'S, 71^{\circ}27'W$) (fig. 1). Between Arica and Coquimbo ($29^{\circ}53'S, 71^{\circ}22'W$), *P. pluvia* was common but never abundant, south of Coquimbo this species became less abundant. The distribution of *P. pluvia* (fig. 2) lies within the zoogeographical unit known as the Peruvian Province (Olsson, 1961) or the warm-temperate Southeast Pacific Province (Sullivan Sealey & Bustamante, 1999).

Natural history.—Because of its large size and distinctive colour, *Phymanthea pluvia* is one of the most eye-catching sea anemones of northern Chile. Specimens of this species occur in the lower rocky intertidal zone close to the mean low tide level, in tide pools up to the mean tide level (fig. 21) and subtidally to 16 m, generally attached to bare vertical rocks that are free from macroalgae. *P. pluvia* lives in more protected places than *Phymactis papillosa*, such as tide pools with regular water movement but without direct surf surge. Intertidal specimens can sometimes be found exposed at low tide and tolerate direct sunlight. When exposed, *P. pluvia* is able to completely cover the tentacles with the column. In tide pools, *P. pluvia* can be found associated with the sea anemones *P. papillosa*, *Anemonia alicemartinae* (Häussermann & Försterra, 2001) and *Oulactis concinna* (Häussermann, 2003).

In the sublittoral, *Phymanthea pluvia* can grow very large. Specimens generally inhabit vertical or slightly overhanging portions of bare rock on the leeward side of the current (fig. 25), but I also found them on the rhizome of the brown algae *Lessonia trabeculata* (Villouta & Santelices, 1986) and close to Antofagasta, north Chile, on the introduced giant ascidia *Pyura praeputialis* (Heller, 1878). *P. pluvia* can often be found together with the sea anemones *Anthothoe chilensis* (Lesson, 1830) and *Anemonia alicemartinae* (fig. 25). *P. pluvia* and *A. alicemartinae* occupy more exposed positions than *A. chilensis*. Typically, specimens of *P. pluvia* are found expanded or with the column covering half the length of the tentacles (fig. 25).

Juvenile and adult specimens of the porcellanid crab *Allopsetrolistes spinifrons* were observed sitting on the column of *Phymanthea pluvia* (figs 5, 9). Specimens of *P. pluvia* show agonistic behaviour towards neighbouring individuals (Sebens & Paine, 1979). No agonistic behaviour could be observed during this study.

The adhesion of the pedal disc to the substratum is very strong in *Phyanthea pluvia*. However, the pedal disc is robust and, if the substratum is not too rough, specimens are quite easy to remove from the rock and generally reattach within one hour in the sampling jar or in the aquarium. The tentacles strongly stick to human skin. If placed at an unsuitable spot in the aquarium, *P. pluvia* may be quite mobile.

No signs of asexual reproduction were observed.

On a vertical rocky wall at Pan de Azúcar (S15), north Chile ($26^{\circ}9'S$, $70^{\circ}39'W$), a specimen of *Phyanthea pluvia* was observed with a complete sea urchin in its gastrocoel. The diameter of the sea urchin was larger than the column diameter of the sea anemone and the expanded body wall of *P. pluvia* showed every single spine.

Discussion

Distribution of *Phymactis papillosa*

The records of *Phymactis papillosa* from Argentina refer to a different species. The Argentinean species (Zamponi, 1977) does not fit the description of *P. papillosa*, but exhibits some characters of the closely related genus *Bunodosoma* (see table 3): the colouration of the described species is different, the specimens only have 24 tentacles, the sphincter is circumscribed, the mesogloea narrow. Only the first cycle is perfect and sterile, the others are imperfect and fertile. The Argentinean species will be described as a new species of *Bunodosoma* (Gomes, in litt. 2004).

In his species list, Carlgren (1949a) reports that *Phymactis papillosa* is distributed along the whole Chilean coast to South Tierra del Fuego. Sebens & Paine (1979) confirm this distribution although during their study they found *P. papillosa* just as far south as Llahue Peninsula ($42^{\circ}41'S$; $72^{\circ}52'W$). I did not find any proof for a distribution south of this region in the literature such as mention of collected or observed specimens. This southern distribution limit could be an additional hint for the existence of a zoogeographical barrier around the Golfo de Penas ($46\text{--}47^{\circ}S$) (Lancellotti & Vásquez, 1999; Häussermann & Försterra, in review).

In Carlgren's species list (1949a) *Phymactis papillosa* is mentioned for lower California, San Salvador, Nicaragua, Panama and Pearl Island. However, I did not find any records of sea anemones in the literature for the northern part of South America or for Central America that can be attributed to *P. papillosa* except Carlgren's (1951) report of two small sterile specimens of uncertain status from Puerto Escondido, Gulf of California. Specimens identified as *P. papillosa* have recently been found in the Gulf of California and on Baja Peninsula (see above). Although McMurrich (1904) examined specimens of *P. papillosa* from Ecuador, from the collection of the Museum of Turin, it is uncertain to which species the specimens belong, because he does not distinguish between *P. papillosa*, *Phyanthea pluvia* and *Eucladactis grandis*. It is noteworthy that *P. papillosa* was not found at any of the Peruvian study sites north of Peninsula Bayovar. A study of the fauna between northern Peru and Mexico is necessary to reveal whether the distribution of *P. papillosa* is continuous or patchy. If not continuous, molecular studies could help to reveal whether Mexican populations are on their way to speciation. To determine the limits of distribution of *P. papillosa*, the region north of the Gulf of California

and Baja Peninsula, where this species is still abundant, and the exposed regions south of the Archipelago de los Chonos in south Chile must be sampled.

Senior synonym of South American *Phymactis* species

Lesson's (1830) description of *Phymactis papillosa* is not very detailed and no type material is available (Fautin, 2003). However, the described features all match *P. papillosa* very well and the drawing accompanying Lesson's (1830) description of *P. papillosa* clearly shows a specimen belonging to the variety *rubra-viridis* of *P. clematis* (see Fautin, 2003: *P. papillosa*). The latter species therefore is synonymized with *P. papillosa*. Besides, I extensively sampled the region where Lesson collected his material and found only one species of the genus *Phymactis*, which I identified as *P. papillosa*.

Phymactis papillosa was only mentioned under this name in five further publications, three of which are pure species lists. Pax (1912) based his identification on Lesson's drawing mentioning the poor description; Sebens & Paine (1979) probably identified the species the same way. Although the name *Phymactis clematis* is commonly used in Chile and Peru, *P. papillosa* has priority following the code of nomenclature.

The genus *Phymactis* currently contains two species, one of which, *P. sanctaehelena* (Lesson, 1830), is very poorly known. Unfortunately there is no type material available (Fautin, 2003). All described morphological characters of the *P. sanctaehelena* including cnidae agree very well with *P. papillosa* (Carlgren, 1941). According to the descriptions, there is no difference that would justify keeping the two species apart. Nevertheless, the large geographic separation, one in the South East Pacific, the other one in the centre of the southern Atlantic Ocean, prevents me from synonymizing the two species. Recent material of *P. sanctaehelena* should be collected and examined to solve this problem. Its description appears in the same publication some pages before the description of *P. papillosa* (Lesson, 1830), thus in case of a synonymization, *P. sanctaehelena* would become the senior synonym.

Aggregational and solitary individuals of the species *Phymactis papillosa*

In Chile, members of *Phymactis papillosa* occur both as medium-sized aggregated and as large-sized solitary individuals (Stotz, 1977; Sebens & Paine, 1979; Häussermann, 1998) (figs 3-4, 6-7). Aggregations of medium-sized individuals are supposed to be clonal groups of organisms resulting from longitudinal fission (Stotz, 1977; Sebens & Paine, 1979). These aggregations can exclusively be found in the intertidal (figs 6, 8). The larger solitary occurring individuals are always more or less hexamerously arranged and live in the lower intertidal and in the subtidal.

A similar pattern is known for some species of the genus *Anthopleura*. As far as known, all *Anthopleura* species reproduce sexually through planula larvae, which settle down and grow into polyps (Geller & Walton, 2001). In some species, all polyps remain solitary, whereas in other species polyps divide, usually by longitudinal fission, and form clonal aggregations (Geller & Walton, 2001). However, the solitary form of *A. elegans* Brandt, 1835, has been described as a separate species, *A. sola* Pearse & Francis, 2000, based upon allozyme differentiation and differences in life history and growth mode (Pearse & Francis, 2000).

Both growth forms of *Phymactis papillosa* look identical in the field, and with examination of several specimens of each form, I did not find a morphological difference between these two forms. However, this is also the case for *A. elegantissima* and *A. sola* (Pearse & Francis, 2000). At least in Mexico, aggregations of *P. papillosa* are less dense and more heterogeneous in terms of size compared to aggregations of *Anthopleura elegantissima* and the difference in size between clonal and solitary specimens are less obvious (Daly, in litt., 2003). Relatively large distances between specimens and relatively large variation in sizes might indicate that some individuals of the aggregations have been produced sexually. Nevertheless, at least some of the specimens in the aggregations are produced asexually by longitudinal fission. Because *P. papillosa* lives in very exposed habitats, fission has to take place very fast and thus it can be expected to be difficult to observe. Monitoring a population or molecular examinations would test the hypothesis that some aggregations are produced exclusively asexually. Groups of large individuals of different colours not touching each other (fig. 10) can be the result of a casual aggregation in a suitable habitat.

Colour morphs of *Phymactis papillosa*

Phymactis papillosa shows high colour variability (see description): red, green, blue and brown varieties as well as mixed forms (figs 3-12). Interestingly, there seem to be no mixed forms between the blue and the green morph or the blue and the brown morph, but very sporadically red-blue morphs can be observed (Sebens & Paine, 1979; pers. obs.). At least some of these varieties differ in habitat preference: var. *cyanea* (Sebens & Paine, 1979) and to a lower extend also var. *viridis* were found in shaded places like overhangs and on the lower portion of boulders at wave-exposed sites (fig. 8). Stotz (1977) hypothesizes that var. *rubra* can tolerate direct sunlight better than the other varieties, because it reflects light of longer wavelength and thus heats up less and loses less water through evaporation than the other varieties; var. *cyanea* can be found at the other end of this scale. During their study, Sebens & Paine (1979) observed a predominance of the red-green morph in exposed areas and similar frequencies of all varieties in protected regions. They suggested the possibility of a polymorphism maintained by heterosis. Although Sebens & Paine (1979) suggested that var. *cyanea* is in the process of undergoing speciation through reproductive isolation, the occurrence, albeit sporadic, of a mixed red-blue morph suggests that interbreeding does take place. Neither Stotz (1977) nor I were able to detect any morphological differences among the colour morphs.

Cnidae of *Phymactis papillosa*

Phymactis papillosa has a rather simple cnidome with few cnidae types, dominated by basitrichs, which is typical for actiniid sea anemones. Size ranges become very broad when many specimens of different sizes are included. Thus characteristic cnidae, such as holotrichs and rod-like basitrichs are helpful to distinguish this species from similar species.

Stotz (1977) presented data on the size and distribution of cnidae from twenty specimens of *Phymactis papillosa*. These size ranges are much broader than the ranges I

found in the specimens I examined. The lower limit generally lies slightly below, the upper limit up to 15 µm above this of specimen ZSM 20030295 (tab. 1). The only exceptions to this rule are the *b*-mastigophores of the filaments of Stotz's (1977) specimens, which are up to 10 µm smaller, but not larger than these of specimen ZSM 20030295. These differences may be due to differences in size of the specimens examined and the result of pooling values from twenty specimens.

There is great variation in the sizes of acrorhagial cnidae in animals of different sizes. The ranges of the basitrichs and holotrichs of the acrorhagi (Stotz, 1977) were much broader than the ranges I measured. Carlgren (1920) presented two different categories of acrorhagial holotrichs for the specimens of *Phymactis papillosa* he examined; in later publications (Carlgren, 1945; 1951) he gave a single range that differed from the combination of the two size classes. Because of this variability among specimens, the sizes of basitrichs and holotrichs in the acrorhagi should not be used as a distinctive taxonomic feature.

Descriptions of *Phymanthea pluvia*

Although Drayton's description of *Phymanthea pluvia* from San Lorenzo, Peru, in Dana (1846) is short and not very detailed, in combination with his drawing (Fautin, 2003) it is sufficient to differentiate the species from other South American actiniids. Drayton's specimens did not exhibit acrorhagi (Dana, 1846). Although McMurrich (1904) suspected that Drayton overlooked these structures because of their inconspicuous colouration (see fig. 21), Drayton may have examined a specimen that had lost or maybe never developed its acrorhagi. Acrorhagi are known to be facultative in other actiniid species (Riemann-Zürneck & Gallardo, 1990; Häussermann, 2003), and one of Carlgren's (1959) specimens neither possessed these structures.

Drayton (1846) described *Phymanthea pluvia* as very variable in colour: a bright orange morph, a morph with dull red or pale red tentacles, and a brownish green morph with white-tipped, bright orange vesicles. I only observed pure orange specimens, few of which had a very light brownish element. The material from Chile Carlgren (1959) examined and described as *P. pluvia* was orange. Similarly, Carter (1965) found only orange specimens in Montemar, central Chile. Most probably, the red colour variations described by Drayton (1846) were individuals belonging to *Phymactis papillosa*.

Status and comparison of the genera *Phymactis*, *Bunodosoma* and *Phymanthea* (see tab. 1)

The genera *Phymactis* and *Phymanthea*

Carlgren (1959) introduced the new genus *Phymanthea* with hesitation, claiming that it might well be a subgenus of *Phymactis*. According to him, the only difference between *Phymanthea* and *Phymactis* are the rod-like basitrichs and spirocysts in the acrorhagi of *Phymactis*, which are lacking in *Phymanthea* (see fig. 13 and fig. 26). However, in my experience, spirocysts occur sporadically in the acrorhagi of members of *Phymactis papillosa*, making this a less useful character for separating *Phymactis* and *Phymanthea*. Although rod-like basitrichs are found in abundance in the acrorhagi of

members of *Phymactis* and are lacking in members of *Phymanthea*, in other genera belonging to Actiniidae (Häussermann, 1998; 2003) the occurrence of this kind of nematocyst is considered a species-level character.

However, the two genera differ in the structure of the vesicles of the column. In contrast to the vesicles of *Phymactis*, the vesicles of *Phymanthea* lack mucus gland cells in their apex (fig. 29). Vesicles of *Bunodosoma californica* e.g. resemble those of *Phymactis papillosa* (fig. 16) (Daly, 2004). In addition, the marginal vesicles of *Phymanthea* tend to be strongly compound and enlarged while the marginal vesicles of *Phymactis* are comparable to these of its column. As the evaginations of the column are generally considered a generic character within Actiniidae (Stephenson, 1922; Carlgren, 1949a), I propose that *Phymanthea* and *Phymactis* be recognized as distinct genera.

The genera *Phymactis* and *Bunodosoma* and other related genera

Living specimens belonging to the genera *Phymactis* and *Bunodosoma* are hard to distinguish. Both species are intertidal and shallow water species, have short tentacles, and have a nearly cylindrical column densely covered with non-adhesive vesicles. The primary difference is the morphology of the marginal sphincter: it is diffuse in *Phymactis* and "more or less circumscribed" in *Bunodosoma* (Carlgren, 1949b). Stephenson (1922) synonymized *Phymactis* and *Bunodosoma*, arguing that sphincter-detail alone is insufficient to separate genera. Carlgren (1925) concurred that sphincter alone might not separate *Phymactis* and *Bunodosoma*. Sphincter morphology is a species level character in *Anthopleura*; in this genus, the sphincter shape may vary even within a single species (England, 1987).

However, sphincter morphology is not the only difference between these two genera. In species belonging to *Phymactis*, at least the two oldest cycles of mesenteries are sterile, whereas in species belonging to *Bunodosoma* the mesenteries of the first cycle are fertile. In my opinion, this difference, in conjunction with sphincter morphology, justifies maintaining *Phymactis* and *Bunodosoma* as separate genera.

As Carlgren (1925) pointed out, there is a great agreement in the whole morphological organisation of *Phymactis*, *Bunodosoma*, *Phymanthea*, *Phlyctenactis*, *Phlyctenanthus*, and *Cladactella*. The latter three are very similar to one another, and share many characters with *Phymactis* and/or *Bunodosoma*, including the vesicles on the column. One of the main differences is the lack of acrorhagi in *Phlyctenactis*, *Phlyctenanthus*, and *Cladactella* (Carlgren, 1949a). However, this character varies among species of other actiniid genera such as *Oulactis* (Häussermann, 2003), and rarely acrorhagi may also lack in *Phymactis* and *Phymanthea*. Therefore a revision of these genera and a detailed examination of the structure of their vesicles would be helpful.

Distinction and function of columnar outgrowths: vesicles and verrucae

Definition and distinction

Daly (2004) defined a verruca as "an adhesive, hollow evagination of all three layers of the column wall, with thick, glandular ectoderm that lacks nematocysts, relatively thin mesogloea (especially at the centre, where it may form a cinclis), and relatively thin, un-muscular endoderm" (see fig. 31). The term vesicle is applied to a more heterogeneous group of structures, including the columnar outgrowths of members of the

family Aliciidae, which bear nematocyst batteries, as well as the columnar evaginations of genera like *Phymactis*, which are typically non-adhesive. According to Daly (2004), vesicles may or may not have nematocysts. In preserved animals these structures are difficult to distinguish because verrucae tend to drop their attached shells and vesicles become deflated and appear flat, like verrucae (Daly, 2004). In contrast to the preserved state, in living animals vesicles are easily distinguishable from verrucae by their shape, function and adhesiveness: verrucae are adhesive and generally cup-like with a lighter spot in the centre whereas vesicles are rounded (figs 5, 23, 31).

The vesicles of living members of *Phymactis papillosa* and of *Phymanthea pluvia* look quite similar at first sight, but differ in anatomical detail. In *P. pluvia* the apex of a vesicle differs from its side: the large mucus gland cells are missing (figs 16, 29, 31). In life, the apex of the vesicles of *P. pluvia* is characterized by a whitish colour (fig. 23), while the vesicles of *P. papillosa* are uniformly coloured (figs 5, 7, 9). With the knowledge of the structure of vesicles of other species, different types might be distinguished.

Function of vesicles

When removed from the water, specimens of *Phymactis papillosa* are covered with mucus secreted by the large circular mucus gland cells of the epithelium (figs 6, 8). *Sensu* Stotz (1979) the vesicles collapse slightly when exposed to air and adhere to each other, forming a continuous layer without increasing the exposed surface. The large lumina of the vesicles are connected to the coelenteron with narrow ducts equipped with muscle fibres and thus, by controlling the quantity of water inside the vesicles, might form a well controllable evaporation and cooling system (Stotz, 1979) (figs 15, 19). The same narrow ducts between the vesicles and the coelenteron and the circular mucus gland cells, at least at the sides of the vesicles, can be found in *Phymanthea pluvia* (fig. 27). Although less commonly observed in immersed state than *P. papillosa*, dry specimens of *P. pluvia* are also covered with mucus; thus vesicles of *P. pluvia* probably have a similar function. The same is known for species of *Bunodosoma* (Ocaña, in litt., 2004)

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