AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Williams, R. B., 1981. A sea anemone, *Edwardsia meridionalis* sp. Nov., from Antarctica and a preliminary revision of the genus *Edwardsia* de Quatrefages, 1841 (Coelenterata: Actiniaria). *Records of the Australian Museum* 33(6): 325–360. [28 February 1981].

doi:10.3853/j.0067-1975.33.1981.271

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

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A SEA ANEMONE, *EDWARDSIA MERIDIONALIS* SP. NOV., FROM ANTARCTICA AND A PRELIMINARY REVISION OF THE GENUS *EDWARDSIA* DE QUATREFAGES, 1841 (COELENTERATA: ACTINIARIA).

R. B. WILLIAMS

2 Carrington Place, Tring, Herts., HP23 5LA, England

SUMMARY

A newly recognized sea anemone, *Edwardsia meridionalis* sp. nov., from McMurdo Sound, Antarctica is described and compared with other *Edwardsia* species. Its habitat and geographical distribution are described.

The generic name *Edwardsia* de Quatrefages, 1841 and the familial name Edwardsiidae Andres, 1881 are invalid. A summary of a proposal made to the International Commission on Zoological Nomenclature to conserve these names is given.

The genus *Edwardsia* is defined and its known synonyms are given. A review of the published descriptions found of nominal *Edwardsia* species revealed many *nomina nuda*, *nomina dubia*, synonyms and homonyms. The remaining *nomina clara* comprize forty currently accepted nominal species, which are listed with their known synonyms and geographical distributions.

The following nomenclatural changes are instituted: *E. carlgreni* nom. nov. is proposed as a replacement name for *E. pallida* Carlgren, 1921, a junior primary homonym of *E. pallida* Verrill, 1879; *E. neozelanica* Farquhar, 1898, a subjective synonym of *E. elegans* Farquhar, 1898, is proposed as a replacement name for *E. elegans* Farquhar, which is a junior primary homonym of *E. elegans* Verrill, 1869; *E. claparedii* (Panceri, 1869) is regarded as the valid name of *E. callimorpha* (Gosse, 1853) (*sensu* Stephenson, 1935) whilst *E. callimorpha* (Gosse, 1853) (*sensu stricto*) reverts to *Scolanthus callimorphus* Gosse, 1853; *E. perdita* nom. nov. is proposed as a replacement name for *E. grubii* Andres, 1883, a junior secondary homonym of *E. grubii* (A. Costa, 1869); *Fagesia janthina* comb. nov. is proposed for *E. janthina* Andres, 1881; *E. horstii* Pax, 1924b is a simultaneously published synonym of *Isoedwardsia curacaoensis* Pax, 1924b and its valid name is here regarded as *Scolanthus curacaoensis* (Pax, 1924b).

Further research may reveal invalid names amongst the currently accepted nominal species: notes are made on some of those which might prove to be invalid. Furthermore, any of the *nomina dubia* might be raised to the status of *nomina clara* if type material were found, but their validity would still remain to be established.

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INTRODUCTION

The coelenterate genus *Edwardsia* de Quatrefages, 1841 is one of the largest known within the order Actiniaria (sea anemones) and its distribution is world wide: all members of the genus burrow into mud, sand or gravel. It is a curious fact that although Actiniaria have frequently been collected from McMurdo Sound in Antarctica, no species of *Edwardsia* have hitherto been reported there. However, during studies on the diversity and structure of benthic communities in the Sound, large numbers of an un-named *Edwardsia* species were collected in 1970 by Dr J. K. Lowry (then at the University of Canterbury, Christchurch, New Zealand; currently at the Australian Museum, Sydney). Through the kindness of Dr Lowry and Mr J. S. Oliver in supplying specimens I have been able to make the following description of the species for which I propose the name *Edwardsia meridionalis* sp. nov.: the trivial name refers to its southerly distribution.

Carlgren (1949), in a survey of the world's sea anemones, listed 55 species of *Edwardsia* which he apparently regarded as valid and several more have since been described. An examination of the original and some subsequent descriptions of these and all the other nominal species of *Edwardsia* which were found in the literature revealed the need for a review of the genus. The number of presently accepted species is reduced to forty and the remaining nominal species are classified as *nomina nuda*, *nomina dubia*, synonyms or homonyms. It should be emphasized that some of the presently accepted nominal species listed in appendix II might prove to be conspecific: some of the possible synonyms are noted, but further research is necessary to assess their status. Furthermore, any of the *nomina dubia* might be raised to the status of *nomina clara* if type material were found but their validity would still remain to be established.

SYSTEMATICS: DESCRIPTION OF *EDWARDSIA MERIDIONALIS* SP. NOV. **Edwardsia** de Quatrefages, 1841*, p.427

- *Edwardsia.* de Quatrefages, 1842, p.68; Carlgren, 1921, p.27; Stephenson, 1935, p.52; Carlgren, 1949, p.22; Manuel, 1977, p.484.
- Actinia. Stimpson, 1853, p.7 (pro parte); [non Actinia Browne, 1756, = Actinia auct., e.g. Stephenson, 1935†].
- Milnea. Reichenbach in Wright, 1866, p.782; (see appendix I).

Urophysalus. — A. Costa, 1869, p.56; (see below).

Halcampa. — Panceri, 1869, p.6 (pro parte).

Edwardsiella. — Andres, 1883, p.305 (*pro parte*); McMurrich, 1913, p.551; Verrill, 1928, p.27.

* The usage of this genus-group name which is preoccupied by Edwardsia O. G. Costa, 1834, is discussed in appendix I. No nominal species were included at the time the genus was established.

[†] Actinia Browne, 1756, being published before the starting point of zoological nomenclature, is an unavailable name: the valid name of this genus is *Priapus* Linnaeus, 1758.

Diphtera[‡]. — Sluiter, 1888, p.233; Sluiter, 1889, p.47; (see below.)

Edwardsioides. — Danielssen, 1890, p.100.

REMARKS. The name *Scolanthus* Gosse, 1853, p.157, has long been considered to be a junior synonym of *Edwardsia* de Quatrefages, 1841 (see Gosse, 1855a; Haddon, 1889; Stephenson, 1935.) Hence *Scolanthus callimorphus* Gosse, 1853 has been known for over a century as *Edwardsia callimorpha* (Gosse, 1853) (see Stephenson, 1935.) However, it has recently been found that *S. callimorphus* Gosse, 1853 is synonymous with *Isoedwardsia (Edwardsia) lucifuga* (Fischer, 1888) (Manuel, in preparation). *Scolanthus* Gosse, 1853 is therefore a senior subjective synonym of *Isoedwardsia* Carlgren, 1921 and the latter name is here regarded as invalid: for this reason, *Scolanthus* is no longer regarded as a synonym of *Edwardsia*. (However, *Scolanthus* (sensu Holdsworth, 1855, p.85) is a synonym of *Sagartia* Gosse, 1855a, p.272.) The valid name of *E. callimorpha* (sensu Stephenson, 1935) is here considered to be *E. claparedii* (Panceri, 1869) (*q.v.*), with which Mr Manuel concurs.

Lecythia Sars, 1829, p.27, was synonymized by implication with Edwardsiella Andres, 1883 by Andres (1883) and by Delage and Hérouard (1901) because the type-species by monotypy, L. brevicornis Sars, 1829 was synonymized doubtfully by Andres (1883) with Edwardsia (Edwardsiella) sarsii Düben and Koren, 1847. Although Carlgren (1921) subsequently synonymized L. brevicornis with Paraedwardsia sarsii (Düben and Koren, 1847) and furthermore, used the morphological data of Sars (1829) to add to his own description of P. sarsii, it is clear from his text that he really regarded Lecythia Sars, 1829 as a nomen dubium. If this were not the case the name Lecythia Sars, 1829 would have had priority over Paraedwardsia Carlgren, 1905. Lecythia is regarded here also as a nomen dubium and is therefore not synonymized with either Edwardsia (Edwardsiella) or Paraedwardsia.

Although Urophysalus A. Costa, 1869 is synonymized here with Edwardsia, as it was by Andres (1883), the only included species (U. grubii, q.v.), which Andres (1883) considered to be synonymous with E. claparedii (Panceri, 1869) is here regarded as a nomen dubium. Similarly, the type-species by monotypy (D. octoplax, q.v.) of Diphtera Sluiter, 1888 is here regarded as a nomen dubium although Diphtera is clearly a synonym of Edwardsia.

The generic definition of *Edwardsia* de Quatrefages, 1841 given below is that of Manuel (1977) which is based on that of Carlgren (1949).

"Edwardsiidae (sensu Carlgren, 1949) with column divisible into physa, scapus, scapulus and capitulum. Physa never with periderm (cuticle) or nemathybomes; morphologically and functionally differentiated from the scapus. Scapus long, always with periderm and nemathybomes, the latter being externally opening cavities sunk in the mesogloea which contain nematocyst batteries. Eight perfect mesenteries (macrocnemes) and at least four imperfect ones (microcnemes), the latter very weak and restricted to the most distal part of the column. Gonads, filaments, parietal and retractor muscles on the macrocnemes only. Parietals well developed; retractors strong, diffuse to circumscript-diffuse. Cnidom: spirocysts, basitrichs, microbasic *b*-mastigophores and microbasic *p*-mastigophores."

For general terminology, see Stephenson (1928) and Carlgren (1949). Fig. 1 (a-c) is a diagrammatic representation of the general structure of an *Edwardsia*. Various species

[‡] Mistakenly listed Diphthera by Neave (1939) in his Nomenclator Zoologicus.



Figure 1. — Schematic diagrams of a generalized *Edwardsia*, to various scales: (a) transverse section through capitulum of a species with 16 tentacles (which are superimposed over the mesenteries); (b) external features of a whole specimen; (c) internal features — a longitudinal section passing through X-X of fig. 1a.

ac = actinopharynx; ca = capitulum; go = gonad; mc = macrocneme; mcl = macrocoel; me = mesenterial filament; mi = microcneme; ne = nemathybomes; pa = parietal muscle; prd = periderm; prs = peristome; ph = physa; re = retractor muscle; scl = scapulus; scp = scapus; si = siphonoglyph.

may differ in detail, particularly in the structure and arrangement of the mesenteries. Cnidae are named according to Weill's (1934) system as modified by Carlgren (1940). Recent research has suggested that basitrichs and *b*-mastigophores may belong to the same category (Westfall, 1965; Schmidt, 1969) but until there is more general agreement amongst researchers on nematocyst nomenclature, it may be better to retain Carlgren's (1940) modification.

Edwardsia meridionalis sp. nov. Fig. 2a-b

? E. intermedia. — Carlgren, 1899, p.6; 1927a, p.4; 1959, p.11 (pro parte(?)); [non McMurrich, 1893, p.136].

Edwardsia sp. — Dayton and Oliver, 1977, table 1, p.57.

Definition: *Edwardsia* typically with sixteen white-tipped tentacles in two cycles each of eight, the inner longer than the outer; eight macrocnemes and eight microcnemes. Nemathybomes not visible to the naked eye, concentrated in a band along the centre of each macrocoel, containing microbasic *b*-mastigophores measuring in the region of 29.0-50.7 x 2.6-4.7 μ m. Actinopharynx containing microbasic *p*-mastigophores measuring in the region of 14.5-25.9 x 3.6-5.7 μ m and two types of microbasic *b*-mastigophores measuring 14.5-23.8 x 1.6-2.6 μ m and 35.7-40.3 x 2.6-4.1 μ m. Physa imperforate.

TYPE SPECIMENS. The holotype is deposited in the Australian Museum, Sydney; regd no. G.15050; type locality Cape Bird, McMurdo Sound, Antarctica. The following information appears on the label: *"Edwardsia meridionalis* sp. nov.; holotype, dissected. Collected by Dr J. K. Lowry (University of Canterbury, Christchurch, New Zealand) on 28 December, 1970 as part of sample CB2 (depth 65 m) from Cape Bird, Ross Island, McMurdo Sound, Antarctica (77°13′S, 166°25′E). Deposited by Dr R. B. Williams (Tring, England), August 1978." The specimen has 16 tentacles and is 1.2 cm long and 1.5 mm in diameter. The capitulum and scapulus are polygonal , the latter being corrugated, and the physa is slightly puckered at the tip. The colour of the scapus is mainly beige, tan-coloured just above the physa.

Two paratypes are deposited in the British Museum (Natural History), London; regd nos. 1978. 9. 1. 1-2. Three further paratypes (sectioned material) are in the author's private collection.

DESCRIPTION. This is based on examinations of both living and fixed material: the numbers examined are given where appropriate. Measurements of features in living or stained microscopical preparations were made, using an eyepiece micrometer and an oil immersion objective, to an accuracy of $\pm 0.26 \mu$ m after calibration. Measurements are all rounded off to the nearest 0.1μ m. Specimens fixed in 70% alcohol were sectioned at 10 μ m and stained with Masson's Trichrome (Pantin, 1964). The material examined consisted of fixed specimens from Cape Bird (Ross Island, McMurdo Sound) collected by Dr J. K. Lowry, taken from samples CB1 (25 December, 1970) and CB2 (28 December, 1970); and living specimens from Cape Armitage (Ross Island, McMurdo Sound) collected by Mr J. S. Oliver in January, 1976.

Column. Divisible into physa, scapus, scapulus and capitulum, the last being rather indistinct. In fixed, contracted specimens the column was between 4 and 19 mm long and between 0.75 and 2 mm in diameter at its widest point. In living, buried specimens the column was up to 35 mm long and up to 2.5 mm in diameter. It is likely, however, that in relaxed undisturbed specimens, the column may be even longer.



Figure 2. — Photographs of *E. meridionalis* in its natural position in a gravel substrate, viewed through the side of an aquarium (scales = 5 mm): (a) expanded at surface; (b) tentacles retracted but column still extended below surface.

The physa is translucent when distended, revealing the mesenterial insertions. It is bluish-grey, has no nemathybomes or periderm and is imperforate. Its extremity may become tucked in rosette-like but is not introvertible.

The scapus is corrugated and opaque in contraction, smooth and translucent when extended. The periderm likewise becomes translucent when stretched and ends in a ragged edge where the scapus joins the scapulus distally and the physa proximally. When contracted, the periderm is greyish-brown or ochre, modified by adhering foreign matter, but when stretched, the scapus shows through, being bluish-grey like the physa for most of its length (fig. 2b). The scapus bears non-tuberculate nemathybomes concentrated in a band along the centre of each macrocoel (fig. 3). (The arrangement is similar to that in *E. andresi* but in that species the nemathybomes are relatively smaller (see Carlgren, 1921, fig. 18). For comparison, note the scattered arrangement in E. norvegica (see Carlgren, 1942, fig. 68) and an intermediate arrangement in E. danica (see Carlgren, 1921, fig. 17).) Nemathybomes in live anemones measured from 39.0 to 58.5μ m across and were not visible to the naked eye in fixed or living material. In transverse sections of the column they were not present at the distal end of the scapus, although periderm was still present at that level. (This could simply have been a result of the column being contracted: fig. 3 was drawn from a live expanded specimen and so represents the nemathybomes in their natural arrangement.)

Figure 3. — Distribution of nemathybomes between two mesenterial insertions on the scapus of *E*. *meridionalis*, 0.7 mm in diameter; scale = 200μ m.

The scapulus has no nemathybomes. Its proximal part is pink or deep chestnut brown: this coloration extends a little way onto the distal scapus where it fades out. The distal part of the scapulus is translucent and bluish-grey, and the actinopharynx, which is pinkish-brown, is clearly visible through it. There are eight prominent chalk-white blotches, longitudinally elongated and each corresponding with a macrocoel, which occur on the chestnut coloured region just above the distal edge of the periderm (fig. 2a). The scapulus narrows slightly towards the rather indistinct capitulum which bears a narrow semi-opaque white streak in the middle of each macrocoel, each about half the length of the white markings on the scapulus (fig. 2a).

Disc. The disc is circular, its diameter less than that of the scapulus. It bears a prominent hypostome which, together with the tapering scapulus, approximates to the shape of a truncated cone in living anemones (fig. 2a). The colour of the disc varied from opaque deep chestnut brown to almost colourless and translucent. The hypostome was always off-white and the macrocneme insertions were frequently marked with continuations of the hypostome pigment, extending over the margin just onto the capitulum.

Tentacles. Typically, the tentacles numbered 16 in two cycles of 8, presumably the normal adult pattern. The endocoelic (inner) tentacles were longer than the exocoelic (outer) tentacles. All the tentacles were colourless and translucent except for a more or less strongly marked white tip. Table 1 shows the numbers of tentacles counted on 25 specimens (16 from fixed samples and 9 living). The range was from 12 to 18 with a mode of 16 (80% of the specimens). Only one specimen had supernumerary tentacles. The tentacles were delicate in form and, in living specimens of about 2.5 mm diameter scapus, they tapered from just over 0.4 mm in diameter at the base to a fine point: inner tentacles about 11.25 mm long, outer tentacles about 9 mm long. In unburied specimens the tentacles tended to be blunter and shorter by about one half. In the fixed specimens, the tentacles were either completely withdrawn or contracted to 1 mm or less.

TABLE 1: Numbers of tentacles counted on 25 specimens of E. meridionalis

Number of tentacles	12	13	14	15	16	17	18
Number of specimens	1	0	1	2	20	0	1
Percentage of specimens	4	0	4	8	80	0	4

Anatomy. The description is based on dissections of nine whole fixed specimens and two living specimens, and examinations of two series of transverse sections and one series of longitudinal sections. The arrangement of the tentacles and mesenteries of *E. meridionalis* presents nothing unexpected, the two cycles of eight tentacles being associated with eight microcnemes (present only at the level of the capitulum) and eight macrocnemes. This is typical of an *Edwardsia* species with sixteen tentacles (see fig. 1a; Stephenson, 1935, fig. 45B; Carlgren, 1949, plate I, fig. 1). The fact that the inner tentacles are longer than the outer is, however, rather unusual.

The retractor muscles, at all levels of the column (figs. 4 to 7), had in cross-section a branched process (rarely two) in the outer part and between two and six other less branched or single processes in the inner part. The parietal muscles, however, varied in cross section depending on the level in the column. In the distal column, they were hastate in cross-section (figs. 4 and 5), becoming foliiform with six to ten processes more proximally (figs. 6 and 7). The extension of the parietal muscles onto the distal column wall was slight. However, towards the proximal end of the column, it became progressively more marked, though nowhere greatly exceeding the maximum width of the foliiform portion (figs. 4 to 7). Circular muscle was attached to the inner surface of the mesogloea at the base of the endoderm (figs. 4 to 8). The cnidoglandular tracts of the mesenterial filaments possessed many secretory cells containing granules about 1μ m in diameter.

The mesogloea, at least in fixed and contracted specimens, was thinnest at the extreme distal and proximal ends of the column. At the distal end, it bore short radial



Figure 4. — Transverse section of macrocneme and part of body wall at the level of the scapulus of E. meridionalis, 0.9 mm in diameter; scale = $100 \,\mu$ m.

c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p= parietal muscle; r = retractor muscle.



Figure 5. — Transverse section of macrocneme and part of body wall at the level of the upper scapus of *E. meridionalis*, 0.9 mm in diameter; scale = $100 \,\mu$ m. c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p

= parietal muscle; pe = periderm; r = retractor muscle.



Figure 6. — Transverse section of macrocneme and part of body wall at the level of the middle scapus of *E. meridionalis*, 0.9 mm in diameter; scale = 100μ m. c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; p = parietal muscle; pe = periderm; r = retractor muscle.





c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea; mf = mesenterial filament; n = nemathybome; p = parietal muscle; pe = periderm; r = retractor muscle.



Figure 8. — Longitudinal section of physa and lower scapus of *E. meridionalis*, 1 mm in diameter; scale = 100μ m.

c = circular muscle; ec = ectoderm; en = endoderm; m = mesogloea containing a nemathybome; ma = macrocnemes; p = periderm; r = retractor muscle.



Figure 9. — Stylized representation of the cnidom of *E. meridionalis;* scale = $10 \,\mu$ m. Nb = microbasic *b*-mastigophore of nemathybome.

Ap = microbasic *p*-mastigophore of actinopharynx; Ab1 and Ab2 = microbasic *b*-mastigophores of actinopharynx; As = spirocyst of actinopharynx.

Cb = microbasic *b*-mastigophore (?) of column.

Tb = microbasic p-mastigophore of tentacle; Ts = spirocyst of tentacle.

Mb = microbasic p-mastigophore of mesenterial filament; Mp = microbasic p-mastigophore of mesenterial filament.

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processes projecting into the ectoderm (figs. 4 and 5): such processes did not occur anywhere else. In addition, there were thickenings of the mesogloea in the form of longitudinal ridges extending into the ectoderm opposite each macrocoel which gave a polygonal appearance to the scapulus in fixed specimens. The nemathybomes were embedded in the scapus mesogloea (possibly not extending to the most distal part) and contained from about seven to at least fifteen nematocysts of one type (microbasic *b*-mastigophores) and numerous granules up to about 2.1μ m in diameter. In a transverse section, usually only one nemathybome was cut through in each macrocoel but occasionally two were seen.

The periderm plus the closely associated foreign material (including sand, detritus and diatoms) was up to $65\,\mu$ m thick (the periderm alone being about $2.6\,\mu$ m thick) in contracted specimens. The periderm must be much thinner when stretched as in fig. 2b. The imperforate physa was morphologically differentiated from the scapus by its lack of circular muscle, of periderm and of nemathybomes, and by its thick ectoderm and thin mesogloea (fig. 8).

The sexes are probably separate (data from fixed specimens collected in December, during the Antarctic summer). The sperm heads were pointed as is usual in *Edwardsia* species (see Schmidt, 1974), about 3.1 μ m long and 2.1 μ m wide. The oocytes were spherical or elliptical in shape: the smallest measured was 22.8 μ m in diameter (nucleus 10.3 μ m diameter, nucleolus 5.2 μ m diameter) and the largest was 147.9 μ m in diameter (nucleus 31.0 μ m diameter, nucleolus 13.4 μ m diameter).

Cnidom. The description is based on examinations of four living specimens, twelve fixed specimens (including the holotype and both paratypes) and series of transverse sections of two further specimens. Up to fourteen cnidae of each type were measured from each tissue sample. The cnidom is summarized in table 2 and the types of cnidae are shown in stylized form in fig. 9. Besides those in the nemathybomes, nematocysts in the column wall are probably very rare: only two were found in seven tissue samples. Examination of stained transverse sections confirmed their rarity but it was still not possible to be absolutely certain of their type since no discharged examples were seen. They are shown as microbasic b-mastigophores, but may be basitrichs, these types being difficult to distinguish when undischarged (see Carlgren, 1940 and p.329). The larger microbasic *b*-mastigophores in the actinopharynx were found in only two out of five tissue samples; they are unlikely to have been contaminants since the nematocysts closest in appearance to them occur in the nemathybomes and furthermore the latter type is usually slightly curved whilst that in the actinopharynx is usually straight (see fig. 9). However, the spirocysts found in two out of five actinopharynx samples might possibly be contaminants from the tentacles or disc, although Carlgren (1940) noted the presence of spirocysts in the actinopharynges of some other Actiniaria. The microbasic p-mastigophores in the mesenterial filaments were found in only two out of four tissue samples and were rare in these; they appear to be similar to those in the actinopharynx. Microbasic *b*-mastigophores were found in the mesenterial filaments, which confirms the presence of this type of nematocyst in Edwardsia filaments noted for the first time by Manuel (1977).

Variation. The appearance of the living specimens examined was fairly constant: figs. 2a and b show typical specimens. Only two variants were observed which, although similar in form to the other specimens, bore only white pigment. This occurred at the tips of the tentacles, on the hypostome and in the form of eight blotches just above the junction of scapus and scapulus, all as described for normal specimens. However, the actinopharynx was also white but other parts of these specimens were devoid of pigment, being translucent.

Tissues Tentacle tips	Cnidae Spirocysts Microbasic <i>b</i> -mastigophores	Mean sizes 23.4 x 4.1 22.5 x 2.7	Ranges 10.3-39.3 x 2.1-5.2 20.7-26.9 x 2.1-3.6	Abundance Common Common
Column	Microbasic <i>b</i> -mastigophores (?)	12.4 x 2.1	10.3-15.5 x 2.1	Very rare
Nemathybomes	Microbasic <i>b</i> -mastigophores	39.0 x 3.6	29.0-50.7 x 2.6-4.7	See p.336
Actinopharynx	Microbasic <i>b</i> -mastigophores Microbasic <i>p</i> -mastigophores Microbasic <i>b</i> -mastigophores Spirocysts	19.3 x 1.9 22.1 x 4.9 37.6 x 3.1 17.6 x 2.6	14.5-23.8 x 1.6-2.6 14.5-25.9 x 3.6-5.7 35.7-40.3 x 2.6-4.1 14.5-22.8 x 2.1-3.1	Predominant Few Rare Very rare
Mesenterial filaments	Microbasic <i>b</i> -mastigophores Microbasic <i>p</i> -mastigophores	23.1 x 2.2 22.8 x 5.0	18.6-25.9 x 1.6-3.1 20.7-25.9 x 3.6-6.2	Predominant Rare

TABLE 2: The cnidom of *E.* meridionalis (measurements in μm)

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ECOLOGY: HABITAT OF E. MERIDIONALIS

The information in this part was provided by Dr J. K. Lowry and Mr J. S. Oliver.

In McMurdo Sound *E. meridionalis* inhabits a zone between 30 and 180 m in depth along the western Cape Bird coastline at the northern end of Ross Island; and between 5 and 40 m in depth at Cape Armitage at the southern end of Ross Island and also on the western side of the Sound. Population densities at various depths are shown in table 3.

TABLE 3:	Numbers	per	m²	of	Ε.	meridionalis	at	various	depths	(Antarctic	summer
	samples)*	• -							-		

Depth	Ross	Marble	New	Ferrar	McMurdo	Cape	Cape
(m)	Sea	Point	Harbour	Glacier	Station Jetty	Armitage	Bird
6	-					2,744	
7			224				
9						7,560	
10			7,560				
18						560	
20			12,700		19,000		_
25			1,230			500	
30		2,770		0-50			
35							23,500
50							19,250
65							10,800
500	0-3			-	_		<u> </u>

* Data provided by Mr J. S. Oliver and Dr J. K. Lowry — No data

At Cape Bird between 30 and 50 m depth the substrate is medium to very fine sand with a mean particle diameter of 170 μ m. E. meridionalis lives here in a community dominated by the tube building spionid polychaete Spiophanes tcherniai Fauvel; these two species along with the myodocopid ostracod Philomedes heptathrix Kornicker and the tanaidacean Nototanais dimorphus Beddard make up about 77% numerically of the total animal population. At Cape Armitage E. meridionalis lives in mud, sand, gravel, sponge spicule and cobble substrates, comprizing zones, I, II and III of Dayton, Robilliard and Paine (1970); the gravel with which the living anemones used in this study were received came from a depth of 10 m and analysis by sieving showed it to have a mean particle diameter of 540um. In shallow water, Edwardsia is most abundant just above the level of the dense maldanid and spionid polychaete tubes; these tubes cannot be maintained towards extreme shallows because they probably provide a substrate for ice crystal formation. Edwardsia does not have this problem and flourishes just above the tube zone and below the zone of permafrost or the anchor ice carpet. On the other side of McMurdo Sound at New Harbour, the tube zone is not present and Edwardsia is more abundant somewhat deeper in the shallows. Benthic diatom growth or the grazing activities of asteroids and ophiuroids may control the lower limit of this dense zone at New Harbour (i.e. in depths greater than ca 20 m). E. meridionalis is the un-named Edwardsia species included by Dayton and Oliver (1977) amongst "other Vermes" in the Antarctic benthic samples in their table 1.

Littlepage (1965) has summarized the physical conditions in southern McMurdo Sound at depths from 3 to 275 m: the annual mean temperature is -1.87° C (range -2.15 to -1.40° C); the annual mean salinity is $34.70^{\circ}/_{oo}$ (range 33.96 to $34.99^{\circ}/_{oo}$).

GEOGRAPHICAL DISTRIBUTION OF E. MERIDIONALIS

E. meridionalis has been found at several localities in McMurdo Sound, *viz.* Cape Bird, Ross Island (77°13'S, 166°25'E); Cape Armitage, Ross Island (77°51'S, 166°41'E); McMurdo Station Jetty (77°54'S, 166°38'E); Ferrar Glacier (77°42'S, 163°36'E); New Harbour (77°34'S, 163°34'E); Marble Point (77°25'S, 163°47'E) and also in the open Ross Sea (74°58'S, 170°48'E). (These co-ordinates are approximate and were estimated from maps.) In McMurdo Sound, it appears to be most abundant at depths from 6 to 65 m and is much less frequent at 500 m in the Ross Sea (table 3).

As noted previously, it is possible that some of the specimens assigned to *E. intermedia* by Carlgren (1899,1927a, 1959) may belong to *E. meridionalis*. If this is so, then the distribution may include Graham Land, South Georgia, Tierra del Fuego and Southern Chile, all these records being from depths within the range recorded for *E. meridionalis* from McMurdo Sound and the Ross Sea. Records of *E. meridionalis* and of specimens identified as *E. intermedia* by Carlgren (1899, 1927a, 1959) are shown in fig. 10.

DIFFERENTIATION OF E. MERIDIONALIS SP. NOV. FROM OTHER NOMINAL EDWARDSIA SPECIES

The most useful diagnostic features of *Edwardsia* species are the types and sizes of the nematocysts in the nemathybomes; the arrangement and prominence of the nemathybomes on the scapus; the types and sizes of the nematocysts in the actinopharynx; the arrangement of the mesenteries and tentacles in adult specimens; and in some species, the branching patterns seen in transverse sections of retractor and parietal muscles. The appearance of the nemathybome arrangement and, maybe to a lesser extent, that of the retractor muscles may be affected by the degree of contraction of an anemone and severe distortion may occur in preserved specimens. Transverse sections of longitudinal muscles also may vary in appearance depending on the level of the section through the column. Other anatomical features and patterns of coloration may under some circumstances serve to identify incompletely described specimens, but only when especially distinctive and known to be consistent.

An attempt has been made to trace all the published descriptions of nominal *Edwardsia* species. Each has been compared with the foregoing description of *E. meridionalis*. Discounting the invalid species listed in appendix III, 39 nomina clara (sensu Smith, 1963) remain. These may be differentiated from *E. meridionalis* by a process of elimination using various combinations of the diagnostic features noted above. For the sake of brevity, only some of the distinctive features are given here: further details may be obtained from the references given.

(1) First, those *Edwardsia* species with two nematocyst types in the nemathybomes and (with the exception of *E. delapiae*) having a different arrangement of nemathybomes from that of *E. meridionalis* are excluded as follows:—

E. beautempsii de Quatrefages, 1842. Nemathybomes in eight longitudinal lines (Manuel, 1977).

E. timida de Quatrefages, 1842. Nemathybomes scattered (Manuel, 1977).

E. tuberculata Düben and Koren, 1847. Tuberculate nemathybomes in eight longitudinal lines (Carlgren, 1921).

E. sipunculoides (Stimpson, 1853). Nemathybomes scattered (Carlgren, 1931).

E. sulcata Verrill, 1866. Nemathybomes possibly in eight longitudinal lines, but at any rate not scattered (Carlgren, 1950a).

E. claparedii (Panceri, 1869). Tuberculate nemathybomes in eight longitudinal lines (Carlgren and Stephenson, 1928 as *E. callimorpha* (Gosse)).



Figure 10. — Geographical distribution of *E. meridionalis* (\blacksquare) and specimens identified by Carlgren as *E. intermedia* (\bullet), some of which may be conspecific with *E. meridionalis*. The *E. meridionalis* symbol in McMurdo Sound represents 6 separate localities (see p.339). The *E. intermedia* symbol off Chile represents 8 separate localities (see Carlgren, 1959).

E. elegans Verrill, 1869. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

E. neozelanica Farquhar, 1898. Nemathybomes scattered giving granulous appearance (Carlgren, 1924 as *E. tricolor* Stuckey).

E. californica (McMurrich, 1913). Nemathybomes in eight longitudinal lines (Carlgren, 1936).

E. tinctrix Annandale, 1915. Tuberculate nemathybomes in eight longitudinal lines (Annandale, 1915; Carlgren, 1925).

E. danica Carlgren, 1921. Nemathybomes more or less scattered (Carlgren, 1921).

E. longicornis Carlgren, 1921. Tuberculate nemathybomes in eight longitudinal lines, physa perforate (Carlgren, 1921).

E. delapiae Carlgren and Stephenson, 1928. Nemathybomes in a wide band in the centre of each macrocoel (Carlgren and Stephenson, 1928).

E. maroccana Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

E. octoradiata Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

E. capensis Carlgren, 1938. Nemathybomes in eight longitudinal lines (Carlgren, 1938).

E. sanctaehelenae Carlgren, 1941. Nemathybomes in eight longitudinal lines (Carlgren, 1941).

E. annamensis Carlgren, 1943. Nemathybomes in eight longitudinal lines (Carlgren, 1943).

E. ivelli Manuel, 1975. Tuberculate nemathybomes in eight longitudinal lines (Manuel, 1975).

E. carlgreni nom. nov. Nemathybomes in closely packed groups (Carlgren, 1921 as *E. pallida* Carlgren).

(2) Second, those species with only one type of nematocyst (of a size range not or only slightly overlapping that in *E. meridionalis*) in the nemathybomes (which, with the exception of *E. andresi*, are differently arranged) are excluded as follows:—

E. and resi Danielssen, 1890. Nemathybomes (nematocysts 48-67 x $3.5-4 \mu$ m) irregularly arranged but concentrated in the centres of the macrocoels, physical perforate (Carlgren, 1921).

E. vegae Carlgren, 1921. Nemathybomes (nematocysts 84-101 x 3μ m) visible to the naked eye and scattered, physa perforate (Carlgren, 1921).

E. kameruniensis Carlgren, 1927b. Nemathybomes (nematocysts 45-63 x 3.5-4.5,*u*m) scattered (Carlgren, 1927b).

E. armata Carlgren, 1931. Nemathybomes (nematocysts 43-70 x 3.5-4.5µm) scattered (Carlgren, 1931).

E. japonica Carlgren, 1931. Nemathybomes (nematocysts 74-101 x 2.5-3.5 μ m) scattered (Carlgren, 1931).

E. norvegica Carlgren, 1942. Nemathybomes (nematocysts 47-58 x 3μ m) scattered (Carlgren, 1942).

E. jonesii Seshaiya and Cuttress, 1969. Nemathybomes (nematocysts 48-72 x 4.5-5.5 μ m) in eight longitudinal lines (tending to become sixteen lines around mid-scapus) (Seshaiya and Cuttress, 1969).

(3) Third, those species with types and sizes of nematocysts in the actinopharynx differing from those in *E. meridionalis* (and having other significant differences) are excluded as follows:—

E. pudica Klunzinger, 1877. Retractor muscles extremely diffuse (Faurot, 1895 as *E. adenensis* Faurot; Carlgren, 1931).

E. fusca Danielssen, 1890. Distinctive coloration different from that of *E. meridionalis* (cf. Carlgren, 1921).

E. vitrea (Danielssen, 1890). Nemathybomes scattered, physa perforate (Carlgren, 1921).

E. arctica Carlgren, 1921. Tuberculate nemathybomes in eight longitudinal lines, physa perforate (Carlgren, 1921).

E. finmarchica Carlgren, 1921. Nemathybomes scattered, physa perforate (Carlgren, 1921).

E. islandica Carlgren, 1921. Nemathybomes scattered (Carlgren, 1921).

E. bocki Carlgren, 1931. Nemathybomes scattered (Carlgren, 1931).

E. duodecimtentaculata Carlgren, 1931. Maximum of twelve tentacles (Carlgren, 1931).

E. stephensoni Carlgren, 1950b. Nemathybomes scattered (Carlgren, 1950b).

(4) Last, those species not falling into the first three groups, but having other distinctive characters, are excluded as follows:—

E. carneola (Verrill, 1928). Has twenty-four tentacles and a distinctive coloration different from that of *E. meridionalis* (cf. Verrill, 1928 as *Edwardsiella carneola* Verrill).

E. gilbertensis Carlgren, 1931. Nemathybomes in eight longitudinal lines (Carlgren, 1931).

E. vivipara Carlgren, 1950c. Nemathybomes scattered, twelve tentacles and diffuse retractors (Carlgren, 1950c).

THE STATUS OF ANEMONES DETERMINED AS E. INTERMEDIA MCMURRICH, 1893

The name *E. intermedia* McMurrich, 1893 is here regarded as a *nomen dubium* (see p. 349). The holotype was sectioned and I do not know its whereabouts, if indeed it still exists. However, Carlgren (1899, 1927a, 1959) has determined several anemones from Subantarctic regions and South American waters as this species. Since some, at least, of these specimens have features in common with *E. meridionalis*, their status is discussed in detail. Although the single type-specimen of *E. intermedia* was incompletely described, the fact that its nemathybomes were scattered and visible to the naked eye immediately differentiates it from *E. meridionalis*, but not from some other *Edwardsia* species.

The anemones from the Magellan Strait (Chile), Ushuaia (Tierra del Fuego) and South Georgia determined by Carlgren (1899) as *E. intermedia* may belong to two or more species. They were described as having scattered nemathybomes. Later (Carlgren, 1927a), some of the same specimens were re-examined and the measurements of the nematocysts in their nemathybomes were given. Similar but more extensive data were also given for further anemones from South Georgia and Graham Land (Carlgren, 1927a) and they appear to be similar to those of *E. meridionalis* from McMurdo Sound (table 4). Further details of the cnidom of specimens from Chile (Carlgren, 1959) are also included in table 4.

Compared with the McMurdo Sound populations of *E. meridionalis*, Carlgren's specimens show great variation in numbers of tentacles on each individual (Carlgren, 1899, 1927a, 1959). In the case of an edwardsiid with a finite number of tentacles in the adult state, one would expect a population to have most individuals with tentacles up to and including this number, as in, for example, *Nematostella vectensis* Stephenson, 1935 (see Williams, 1975). This appears to be true of *E. meridionalis* since only one specimen examined had supernumerary tentacles, the adult number apparently being 16 (table 1). However, Carlgren's specimens have from 16 to 28 tentacles; so it is extremely unlikely that the adult number can be 16 if they are all the same species. It is remarkable, moreover, that with the great variation in the numbers of tentacles and also in the appearance of transverse sections of the retractor muscles (see figs. 2 and 3 of Carlgren

	E. meridionalis		E. intermedia	
	present study: McMurdo Sound	Carlgren (1927a): Magellan Strait, Ushuaia, South Georgia	Carlgren (1927a): South Georgia, Graham Land	Carlgren (1959): Chile
Tentacles	10.3-39.3 x 2.1-5.2 (sp.) 20.7-26.9 x 2.1-3.6 (m. <i>b</i> -m.)		14-24 x 1.5-3.5 (sp.) 21-26 x 2-2.5(?)	15-36 x 2.5-3 (bas.)
Column	10.3-15.5 x 2.1 (m. <i>b</i> -m.)	_	15-19 x 2.5 (?)	_
Nemathybomes	29.0-50.7 x 2.6-4.7 (m. <i>b</i> -m.)	35-53 x 3-4 (?)	34-53 x 3-4 (?)	29.6-63.4 x 3-4 (?)
Actinopharynx	14.5-23.8·x 1.6-2.6 (m. <i>b</i> -m.) 14.5-25.9 x 3.6-5.7 (m. <i>p</i> -m.) 35.7-40.3 x 2.6-4.1 (m. <i>b</i> -m.) 14.5-22.8 x 2.1-3.1. (sp.)		24-26 x 5 (?) 31-41 x 3-4 (?)	31-52 x 4.2-5.6 (bas.)
Mesenterial filaments	18.6-25.9 x 1.6-3.1 (m. <i>b</i> -m.) 20.7-25.9 x 3.6-6.2 (m. <i>p</i> -m)			21-24 x 2.8 (bas.) 24-35 x 5.6-6.3 (m. <i>p</i> -m.) 31-49 x 4.2-5.6 (bas.)

TABLE 4: A comparison of the size ranges(µm) of cnidae in E. meridionalis and E. intermedia (sensu Carlgren)

m. b-m. = microbasic b-mastigophores m. p-m. = microbasic p-mastigophores bas. = basitrichs

- ?
- nematocyst type not stated
 nematocysts not recorded ____

(1927a) and fig. 1 of Carlgren (1959)) there should be such similarity between the sizes of nematocysts in the nemathybomes and other tissues of his specimens. However, the nemathybomes have variable distributions (see Carlgren, 1899, 1959) and it is noteworthy that the retractor and parietal muscles described by Carlgren (1927a, 1959) are quite different from those of *E. meridionalis*.

It is concluded that in view of the poor description of the single specimen of *E. intermedia*, Carlgren could hardly have identified his material with this nominal species with any certainty. On the other hand, despite a similarity between the nemathybome and other nematocysts of some of his specimens and those of *E. meridionalis*, there seems to be too much variation in his subsequent descriptions to be sure of the conspecificity of all of his specimens with the latter species. Indeed, the present confusion regarding *E. intermedia* is perhaps best summarized by Carlgren himself (1959): "The identification of the individuals here mentioned is rather uncertain as the single type specimen is imperfectly described . . . I identified (1927a) some individuals from Tierra del Fuego, South Georgia and Graham Land with *intermedia*. They may not be referable to this species because the nematocysts of the nemethybomes are shorter than in our specimens, but the number of tentacles is greater."

DISCUSSION

The genus-group name *Edwardsia* de Quatrefages, 1841, currently used for the genus of actiniarians dealt with in this paper, is preoccupied by *Edwardsia* O. G. Costa, 1834 (Crustacea): this homonymy invalidates the family-group name Edwardsiidae Andres, 1881. A request (Williams, 1979) has been made to the International Commission on Zoological Nomenclature for suppression of the name *Edwardsia* O. G. Costa and conservation of the names *Edwardsia* de Quatrefages and Edwardsiidae Andres. A brief outline of this request appears in appendix I.

The species *E. meridionalis* sp. nov. now described does not fit the generic definition of *Edwardsia* by Carlgren (1949), by virtue of its having the inner tentacles longer than the outer. Stephenson (1935, p.34) had already suggested that it may be advisable to place any species of edwardsiid possessing nemathybomes and having inner tentacles longer than the outer in a new genus. The only major difference between Carlgren's (1949) generic definition and that of Manuel (1977) is the omission by the latter author of any reference to the relative lengths of inner and outer tentacles. However, the present description of *E. meridionalis* and the description of *E. sipunculoides* by Verrill (1866), both with inner tentacles longer than the outer, provide justification for Manuel's (1977) amendment of Carlgren's (1949) generic definition. This makes unnecessary the proposal of a new genus to accommodate edwardsiid species with the inner tentacles longer than the outer and possessing nemethybomes, as suggested by Stephenson (1935).

Carlgren (1921) suggested that all members of the genus *Edwardsia* might have a perforate physa, although he did not include this feature in his generic definition. It is now known, however, that some *Edwardsia* species (e.g., *E. beautempsii* (see Manuel, 1977) and *E. meridionalis*) do have an imperforate physa.

It is interesting that anemones of the genus *Edwardsia* have been found so infrequently in Antarctic and Subantarctic seas. None was identified by Carlgren (1903, 1914, 1928, 1930, 1939), Carlgren and Stephenson (1929), Clubb (1902, 1908), Grebelny (1975), Mann (1948), Pax (1922, 1924a, 1926), Roule (1909) or Stephenson (1918), although some of the anemones examined by these authors were collected from McMurdo Sound where *E. meridionalis* is to be found. In some instances at least, the collecting gear used probably took only larger species: for instance, the sizes of the preserved specimens of

trawled anemones recorded by Stephenson (1918), which would have been even larger in life, are all much greater than the size of living specimens of *E. meridionalis*. Specimens assigned to *E. intermedia* by Carlgren (1899, 1927a, 1959) have already been discussed; the distribution of *E. meridionalis* will possibly become clearer when the true identity of Carlgren's material is determined. Carlgren's (1928) discussion of the distribution of *E. intermedia* may then have to be reconsidered.

Appendix II comprises a list of the names of all presently accepted *Edwardsia* species with notes on their synonyms and their geographical distributions. Appendix III is a list of nominal *Edwardsia* species here regarded as invalid.

ACKNOWLEDGEMENTS

I am grateful to Dr J. K. Lowry for providing me with fixed specimens of *E. meridionalis* and to Mr J. S. Oliver for diving for the living specimens. My thanks are also due to Dr P. F. S. Cornelius, Mr R. L. Manuel, Dr Lowry and Mr Oliver for valuable comments on the manuscript. Mr Manuel kindly took the photographs and prepared the sections. I am grateful also to Mrs S. C. Williams for undertaking the typing of the manuscript.

APPENDIX I

THE USAGE OF THE NAME EDWARDSIA DE QUATREFAGES, 1841

The problems relating to the homonymy between the generic names *Edwardsia* O. G. Costa, 1834 and *Edwardsia* de Quatrefages, 1841 can be summarized as follows.

The genus-group name *Edwardsia* has been proposed in five separate publications for different taxa, and replacement names have been proposed for the four junior homonyms (see Neave, 1939). The senior homonym, *Edwardsia* O. G. Costa, 1834 was long ago synonymized with *Sapphirina* Thompson, 1829, applied to a poecilostomatoid copepod (*e.g.* Giesbrecht, 1892). However, the oldest junior homonym, *Edwardsia* de Quatrefages, 1841, has been used regularly up to the present time and, furthermore, it is the name of the type-genus of the family Edwardsiidae Andres, 1881. The replacement name once proposed for *Edwardsia* de Quatrefages is *Milnea* Reichenbach *in* Wright, 1866 but it has apparently not been used since Wright's paper appeared and is regarded as an unavailable name (Williams, 1979).

Thus the little-used and now synonymized *Edwardsia* O. G. Costa threatens the established usage of *Edwardsia* de Quatrefages. Confusion would be caused by the use of a replacement name for *Edwardsia* de Quatrefages since the widely used actinian genus-group name *Edwardsia* would fall out of use. The family-group name Edwardsii de Quatrefages, 1881 is invalid since the name of its nominal type-genus, *Edwardsia* de Quatrefages, 1841, is a junior homonym. A request (Williams, 1979) has therefore been made to the International Commission on Zoological Nomenclature for suppression of the genus-group name *Edwardsia* O. G. Costa, 1834 and conservation of *Edwardsia* de Quatrefages, 1841 and also of the family-group name Edwardsiidae Andres, 1881.

The solution to these problems is dependent upon the publication of an Opinion by the Commission, and in the meantime the accepted usages of the names *Edwardsia* de Quatrefages and Edwardsiidae Andres have been followed in this paper.

R. B. WILLIAMS

APPENDIX II

CURRENTLY ACCEPTED EDWARDSIA SPECIES, THEIR SYNONYMS AND DISTRIBUTIONS

Of the nominal species of *Edwardsia* which were found in the literature, many are at present considered to be invalid (see appendix III). The remaining *nomina clara* (sensu Smith, 1963) are listed below with *E. meridionalis* sp. nov. The question of whether some of these *nomina clara* are valid names or not can probably only be decided after examination of type material, if available, or live specimens but is beyond the scope of the present paper.

- *Edwardsia beautempsii* de Quatrefages, 1842. This is the type species by subsequent designation (Carlgren, 1949), since no nominal species were included at the time the genus was established. Distribution: northern France.
- E. timida de Quatrefages, 1842. Junior subjective synonyms: E. harassi de Quatrefages, 1842 (q.v.); Edwardsiella harassii Andres (1883); ?Fagesia (≡ Milneedwardsia) dixonii (Carlgren, 1921) (see Manuel, 1977); E. callianthus Rawlinson, 1935 (q.v.); non E. timida (sensu Walton and Rees, 1913) (see Stephenson, 1935). Junior objective synonym: Edwardsiella timida Andres (1883). Distribution: northern France, north Wales, eastern Ireland.
- *E. tuberculata* Düben and Koren, 1847. Distribution: western Scandinavia (Denmark, Sweden, Norway) and southern Iceland.
- E. sipunculoides (Stimpson, 1853). Synonyms: Actinia sipunculoides Stimpson, 1853; Edwardsiella sipunculoides — Andres (1883). Distribution: Alaska and N.E. North America.
- E. sulcata Verrill, 1866. Distribution: eastern United States.
- *E. claparedii* (Panceri, 1869). Synonyms: *Halcampa claparedii* Panceri, 1869; *E. timida* (*sensu* Walton and Rees, 1913) (see Stephenson, 1935); *E. callimorpha* (*sensu* Stephenson, 1935); *non E.* (*Scolanthus*) *callimorpha* (Gosse, 1853) (see Manuel, in preparation). Distribution: southern Italy, northern France, southern and western England, southern Ireland.
- E. elegans Verrill, 1869. Distribution: N.E. North America.
- *E. pudica* Klunzinger, 1877. Junior subjective synonym: *E. adenensis* Faurot, 1895 (q.v.). Junior objective synonym: *Edwardsiella pudica* — Andres (1883). Distribution: Zanzibar, Gulf of Aden, Red Sea, southern India.
- *E. andresi* Danielssen, 1890. Distribution: Denmark, Norway to Spitzbergen, Iceland, western Greenland.
- E. fusca Danielssen, 1890. Distribution: southern Barents Sea.
- E. vitrea (Danielssen, 1890). Synonym: Edwardsioides vitrea Danielssen, 1890. Distribution: eastern Greenland, Spitzbergen.
- *E. neozelanica* Farquhar, 1898. Synonyms: *E. elegans* Farquhar, 1898 ($\equiv E.$ tricolor Stuckey, 1909) (*q.v.*). Distribution: New Zealand.
- *E. californica* (McMurrich, 1913). Synonym: *Edwardsiella californica* McMurrich, 1913. Distribution: south-western United States.
- E. tinctrix Annandale, 1915. Distribution: north-eastern and western India.
- *E. arctica* Carlgren, 1921. Distribution: Arctic (eastern Greenland to Kara Sea) and Sea of Japan (?).
- E. danica Carlgren, 1921. Distribution: Baltic Sea, Denmark, Heligoland.
- E. finmarchica Carlgren, 1921. Distribution: northern Norway.
- E. islandica Carlgren, 1921. Distribution: Iceland.
- *E. longicornis* Carlgren, 1921. The cnidom and certain other features of this species and *E. beautempsii* de Quatrefages, 1842 are very similar and the two species may prove to

be identical (see Manuel, 1977). Distribution: Denmark.

- E. vegae Carlgren, 1921. Distribution: Arctic Sea of Siberia.
- E. kameruniensis Carlgren, 1927b. Distribution: Cameroun.
- *E. carneola* (Verrill, 1928). Synonym: *Edwardsiella carneola* Verrill, 1928. Distribution: Kauai (Hawaii).
- *E. delapiae* Carlgren and Stephenson, 1928. Although this species was accepted as valid by Manuel (1975), he later considered that it was in part synonymous with *E. timida* de Quatrefages, 1842 (see Manuel, 1977). Certain aspects of the cnidom, anatomy and coloration agree with *E. carlgreni* nom. nov. ($\equiv E. pallida$ Carlgren, 1921). Should *E. delapiae* and *E. carlgreni* prove to be synonyms, the former name would have priority over *E. carlgreni* as the replacement name for *E. pallida*. See also *E. tecta* Haddon, an older possible synonym (appendix III). Distribution: southern Ireland.
- E. armata Carlgren, 1931. Distribution: Fiji.
- E. bocki Carlgren, 1931. Distribution: Fiji.
- E. duodecimtentaculata Carlgren, 1931. Distribution: Fiji.
- E. gilbertensis Carlgren, 1931. Distribution: Gilbert Islands, Great Barrier Reef.
- E. japonica Carlgren, 1931. Distribution: eastern Japan.
- E. maroccana Carlgren, 1931. Distribution: Morocco.
- E. octoradiata Carlgren, 1931. Distribution: Japan.
- E. capensis Carlgren, 1938. Distribution: southern South Africa.
- E. sanctaehelenae Carlgren, 1941. Distribution: Saint Helena.
- E. norvegica Carlgren, 1942. Distribution: Norway.
- E. annamensis Carlgren, 1943. Distribution: Cambodia.
- *E. stephensoni* Carlgren; 1950b. Certain aspects of this species agree with *E. bocki* Carlgren, 1931 and the two species may be synonymous. Distribution: Great Barrier Reef.
- E. vivipara Carlgren, 1950c. Distribution: southern Australia.
- E. jonesii Seshaiya and Cuttress, 1969. Distribution: southern India.
- E. ivelli Manuel, 1975. Distribution: southern England.
- *E. carlgreni* nom. nov. Senior objective synonym: *E. pallida* Carlgren, 1921 (q.v.). Distribution: Sweden.
- *E. meridionalis* sp. nov. Synonym:? *E. intermedia* (pro parte (?) sensu Carlgren, 1899, 1927a, 1959); non *E. intermedia* McMurrich, 1893 (q.v.). Distribution: Ross Sea and South America (?).

APPENDIX III

INVALID NOMINAL EDWARDSIA SPECIES

The 39 nomina clara found amongst the published descriptions of nominal *Edwardsia* species have already been compared with *E. meridionalis*. The remaining nominal species comprise *nomina nuda*, *nomina dubia*, synonyms and homonyms considered to be invalid for the reasons shown below. However, if more detailed descriptions or type specimens applicable to these names could be found, some of them might be raised to the status of *nomina clara*.

(1) Nomina nuda

E. fischeri Chevreux and de Guerne, 1887. This species has apparently never been described (see Fischer, 1887, p.432 and 1890, p.311). Although Fischer (1887, 1890) attributed the name to Chevreux and de Guerne, no other reference to *E. fischeri* was found in the literature.

E. lucifuga Fischer 1887. Given by Fischer (1887, p.432) in a geographical distribution list but the name was not made available until the next year (Fischer, 1888).

(2) Nomina dubia

E. clavata (Rathke, 1843). This species (\equiv *Actinia clavata* Rathke, 1843) was considered to be a senior synonym of *E. tuberculata* Düben and Koren by Andres (1883) and Carlgren (1893). Later, however, Carlgren (1921) rejected it as a *nomen dubium*, retaining *E. tuberculata* as a potentially valid name. Apparently Rathke (1843) did not record the presence of nemathybomes so the species may not be an *Edwardsia*. *E. clavata* (Rathke, 1843) is therefore not regarded as a secondary homonym of *E. clavata* Stimpson, 1855.

E. brevicornis Stimpson, 1855. This species cannot be identified with or differentiated from other *Edwardsia* species. Indeed, Verrill at first (1865) considered it to be a *Halcampa* Gosse, 1858a. (He mis-spelt the name as *Halocampa*.) Carlgren (1949) doubtfully included this species in the genus *Haloclava* Verrill, 1899, but Verrill had already himself (1899) suggested that the species belonged to *Eloactis* Andres, 1883.

E. clavata Stimpson, 1855. The description of this species is also inadequate to be certain of the genus to which it belongs. Verrill (1865) considered that it should be referred to the genus *Phellia* Gosse, 1858b. However, the species was transferred to the genus *Telmatactis* Gravier, 1916 by Carlgren (1949). It is not regarded here as a homonym of *E. clavata* (Rathke, 1843) (see above) so it does not require a replacement name at present.

E. collaris Stimpson, 1855. The same argument applies to this species as to *E. clavata* Stimpson. Again, Verrill (1865) considered it to be a *Phellia*, but Carlgren (1949) provisionally referred it to *Telmatactis* Gravier, 1916.

 \cdot *E. cretata* Stimpson, 1855. The description is inadequate to identify or differentiate this species from other *Edwardsia* species and it is also doubtful whether it is an *Edwardsia*. Carlgren (1949), with some doubt, admitted the species to the genus *Paraedwardsia* Carlgren, 1905.

E. rubricollum Stimpson, 1855. This is probably not an *Edwardsia* species, since it was described as having a tuberculate margin and being attached to stones. Verrill (1865) defined a new genus *Ammonactis* for it; Fischer (1890) cast doubt on its validity, although Andres (1883) had accepted it without comment. Carlgren (1949) did not list *Ammonactis* Verrill, 1865 as an accepted genus of anemones or as a synonym of one.

E. allmanni McIntosh, 1865. Despite the subsequent publication of a coloured figure (McIntosh, 1875), this description is not adequate to identify this species with or differentiate it from any other (see Stephenson, 1935 and Manuel, 1975).

E. goodsiri McIntosh, 1865. The same argument and references apply to this species as to the foregoing.

E. grubii (A. Costa, 1869). This species, described originally as a sipunculid *Urophysalus grubii* A. Costa, was considered to be synonymous with *E. claparedii* (Panceri) by Andres (1883). However, although definitely an *Edwardsia*, it is not possible from the original description to allocate with certainty the anemone to any known species.

E. arenosa Klunzinger, 1877. Andres (1883) thought that this species might be a juvenile cerianthid, with which I would agree, but the description was brief and based only upon one specimen.

E. coriacea Moseley, 1877. Although the coloration of the single specimen found is well described, in the absence of any other remarkable physical features in the description, the species definition is inadequate. The coloration is, however, quite different from that of *E. meridionalis*.

E. flaccida Marion, 1882. This species was extremely briefly described and no useful diagnostic features were given.

E. rigida Marion, 1882. As for E. flaccida Marion.

E. scabra Marion, 1882. As for E. flaccida Marion.

E. grubii Andres, 1883. This species was poorly described and may not be an *Edwardsia*. Pax & Müller (1962) failed to rediscover it in the Adriatic Sea. Its name is here replaced by *E. perdita* nom. nov. (see p.351).

E. octoplax (Sluiter, 1888). Originally described as a gephyrean worm (*Diphtera octoplax*) by Sluiter (1888), the species was later recognised as an *Edwardsia* (Sluiter, 1889). The nemathybomes appear to occur in tightly packed groups and to possess one type of nematocyst (Sluiter, 1888, plate I). Not enough detail is given to confidently assign this species, however. The trivial name appears as both *oktoplax* and *octoplax* in the original description, but the latter spelling is adopted here.

E. tecta Haddon, 1889. The species is of uncertain status but if it proves to be the young of *E. delapiae* Carlgren and Stephenson, 1928, as suspected by Stephenson (1935), the name will be a senior synonym of *E. delapiae* (*q.v.* in appendix II).

E. costata Danielssen, 1890. This species was described as having papillae upon its eight ribs from the capitulum down to the physa. Although almost certainly an edwardsiid species, it is difficult to be certain to which genus it belongs.

E. intermedia McMurrich, 1893. The single type specimen was incompletely described and probably poorly preserved since the nemathybomes contained no nematocysts. This species has already been discussed in detail (pp. 342-344).

E. ignota Stuckey, 1909. The species, though poorly described, was said to have a naked scapus and hence may not be an *Edwardsia*.

E. mammillata Bourne, 1916. No useful diagnostic features were given for this species.

E. rekaiyae Bourne, 1916. As for E. mammillata Bourne.

E. rugosa Bourne, 1916. As for *E. mammillata* Bourne. The single type specimen was largely decomposed.

E. vermiformis Bourne, 1916. As for E. rugosa Bourne.

E. willeyana Bourne, 1916. As for *E. mammillata* Bourne.

E. incerta Carlgren, 1921. This species was described from a single imperfect and badly preserved specimen. The large scattered nemathybomes, however, distinguish the species from *E. meridionalis*.

(3) Synonyms

(a) Species-group synonyms.

É. harassi de Quatrefages, 1842. A junior subjective synonym of *E. timida* de Quatrefages, 1842 (see Dixon, 1886).

E. farinacea Verrill, 1869. A junior subjective synonym of *E. duodecimcirrata* Sars, 1851 (*q.v.*) (Andres, 1883; Carlgren, 1893, 1949) and a senior subjective synonym of *E. lutkenii* Andres, 1883 (*q.v.*) (Carlgren, 1893).

E. grubii Andres, 1883. A senior objective synonym of its replacement name *E. perdita* nom. nov. (see p.351).

E. lutkenii Andres, 1883. A junior subjective synonym of *E. duodecimcirrata* Sars, 1851 (*q.v.*) and of *E. farinacea* Verrill, 1869 (*q.v.*) (Carlgren, 1893).

E. ader: Faurot, 1895. A junior subjective synonym of *E. pudica* Klunzinger, 1877 (see Carlgren, 1949).

E. elegans Farquhar, 1898. A senior objective synonym of its replacement name *E. tricolor* Stuckey, 1909 (see Stuckey, 1909) and, according to Carlgren (1924), a subjective synonym of *E. neozelanica* Farquhar, 1898.

E. leidyi Verrill, 1898. A junior subjective synonym of *E. lineata* Verrill, 1873 (q.v.) (see Crowell, 1976).

E. tricolor Stuckey, 1909. A junior subjective synonym of E. neozelanica Farquhar,

1898 and a junior objective synonym of *E. elegans* Farquhar, 1898 (see Carlgren, 1924).

E. pallida Carlgren, 1921. A senior objective synonym of its replacement name *E. carlgreni* nom. nov. (see p.351 and appendix II).

E. callianthus Rawlinson, 1935. A junior subjective synonym of *E. timida* de Quatrefages, 1842 (see Manuel, 1977) and also, therefore, of *E. harassi* de Quatrefages, 1842 (q.v.).

(b) Nominal *Edwardsia* species transferred to other genera.

E. vestita Forbes, 1843. A junior subjective synonym of *Pachycerianthus solitarius* (Rapp, 1829) (see Andres, 1883; Pax and Müller, 1962).

E. sarsii Düben and Koren, 1847. Transferred to the genus *Paraedwardsia* Carlgren, 1905 (see Carlgren, 1921, 1949).

E. duodecimcirrata Sars, 1851. Transferred to the genus *Halcampa* Gosse, 1858a (see Andres, 1883 and Carlgren, 1893; see also its junior subjective synonyms *E. farinacea* Verrill and *E. lutkenii* Andres).

E. callimorpha (Gosse, 1853). Reinstated in the genus *Scolanthus* Gosse, 1853 (see p.327), but *E. callimorpha* (sensu Stephenson, 1935) is synonymous with *E. claparedii* (q.v.), being a misidentification.

E. sphaeroides (Holdsworth, 1855). Originally described as *Scolanthus sphaeroides* Holdsworth, and at first transferred to the genus *Edwardsia* by Gosse (1855b). Later (Gosse, 1860) was regarded as a synonym of *Sagartia troglodytes* (Price *in* Johnston, 1847), a view shared by Stephenson (1935).

E. carnea Gosse, 1856. Transferred first to the genus *Edwardsiella* by Andres (1883) and later to *Milneedwardsia* Carlgren, 1893 (see Stephenson, 1935), which name being preoccupied, was replaced by *Fagesia* Delphy, 1938. However, as Crowell (1976) has pointed out, the name *Fagesia* is also preoccupied and a further replacement name is required. Meanwhile, *Fagesia* remains in use (*sensu* Carlgren, 1949). The *E. carnea* of Appellöf (1891) was, according to Carlgren (1921), a misidentification of *Paraedwardsia sarsii*, (Düben and Koren, 1847).

E. microps (Gosse, 1858b). This species (\equiv *Halcampa microps* Gosse) was regarded by Andres (1883) as an immature *Edwardsia*. Now known to be the young of *Fagesia carnea* (Gosse, 1856) (see Stephenson, 1935).

E. lineata Verrill, 1873. Currently known as *Fagesia lineata* (See Carlgren, 1949), but see note on *E. carnea* above.

E. kerguelensis Studer, 1878. Regarded as an *Edwardsiella* by Andres (1883) and later transferred to the genus *Halianthella* Kwietniewski, 1896 (see Carlgren, 1949).

E. pallida Verrill, 1879. Transferred to the genus *Drillactis* Verrill, 1922 (see Verrill, 1922).

E. janthina Andres, 1881. Andres (1883) reduced this nominal species to a variety of *E. claparedii* (Panceri, 1869). However, because of its external appearance and its natural habitat in holes in rocks (see Andres, 1883, plate 11), it is here transferred to the genus *Fagesia* Delphy, 1938. Further research may show *F. janthina* (Andres) to be synonymous with *F. carnea* (Gosse).

E. lucifuga Fischer, 1888. Transferred to *Isoedwardsia* Carlgren, 1921 (see Carlgren, 1949) but now regarded as a junior subjective synonym of *Scolanthus callimorphus* Gosse, 1853 (see p.327).

E. horstii Pax, 1924b. Carlgren (1931) examined the type material and found it to consist of specimens of both *Capneopsis solidago* Duchassaing and Michelotti, 1866 and *Isoedwardsia curacaoensis* Pax, 1924b. Hence, discounting the previously described *C. solidago*, *E. horstii* and *I. curacaoensis* are simultaneously published synonyms for the same taxon: since this taxon is a species of *Scolanthus* Gosse, 1853, the valid name adopted here is *S. curacaoensis* (Pax, 1924b).

E. leucomelos Parry, 1951. Transferred to the genus *Drillactis* Verrill, 1922 (see Carlgren, 1954). (Carlgren mis-spelt the trivial name as *leucomeles*.)

(4) Homonyms

E. grubii Andres, 1883 is a junior secondary homonym of *E. grubii* (A. Costa, 1869). The replacement name *E. perdita* nom. nov. is proposed for *E. grubii* Andres since there seem to be no available synonyms. The new trivial name refers to the apparent absence of records of this nominal species since it was first described by Grube (1864, p.107) as an un-named species.

E. elegans Farquhar, 1898 is a junior primary homonym of *E. elegans* Verrill, 1869. Stuckey (1909) proposed the replacement name *E. tricolor*, which is now rejected in favour of *E. neozelanica* Farquhar, 1898, since Carlgren (1924) considered *E. elegans* Farquhar and *E. neozelanica* Farquhar to be synonymous. If future work should show these two nominal species to be separate, then the name *E. tricolor* would be reinstated.

E. pallida Carlgren, 1921 is a junior primary homonym of *E.* pallida Verrill, 1879 (\equiv Drillactis pallida (Verrill, 1879)). The replacement name *E.* carlgreni nom. nov. is proposed for *E.* pallida Carlgren since there appear to be no available synonyms.

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Manuscript accepted for publication 12 July, 1979.