A Comparative Study of *Metridium senile* (L.) var. *dianthus* (Ellis) and a Dwarf Variety of this Species occurring in the River Mersey, with a discussion on the Systematic Position of the Genus Metridium.

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With 5 Figures in the Text.

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INTRODUCTION.

The anemone at present under consideration resembles *M. senile* (L.) var. *dianthus* (Ellis) in many respects but shows certain differences. It was for a time provisionally regarded as *M. senile*, but the body wall is thinner than in this species, sexual maturity is attained at a very small size and the disc is rarely distinctly lobed. The subsequent discovery of an abundance of penicilli in the acontia led one to think that the Dingle anemone was perhaps a Sagartia and not a Metridium. Living specimens were then sent to Professor Stephenson who identified them as one of the small local atypical forms of *M. senile* which occur in the inter-tidal regions of many parts of the British coasts. It is not known whether all these forms are simply varieties or whether on further investigation some of them might be justly ranked as species. The present research

was undertaken with a view to solving this problem in the case of the Dingle anemone.

All sizes and all colour varieties of *M. senile* were obtained either from Plymouth or Port Erin for comparison with the Dingle form. Observations have been made on the external features and the stinging cells of specimens from these three localities along with an investigation of the anatomy of the Dingle form.

THE DINGLE ANEMONE.

HABITAT.

The anemone occurs on the river side of the revetment to the north of the oil jetty, Dingle, River Mersey (**1**, Fig. 1). Many individuals are attached to a mooring chain and other large colonies occur on the adjacent rocks. Only at extreme low water can one be sure of collecting specimens, since average tides fail to expose them.

The revetment is a low bank which lies parallel and close to the shore. It consists of large loose stones, rough with barnacles and covered with a thick deposit of fine mud. The water here is brackish and particularly foul because of the abundance of silt, the presence of an oil jetty, and a sewer in the vicinity. Often, when collecting, the water was seen to be covered with a film of oil. The average salinity of the river at Dingle is recorded by Fraser (unpublished records, 1931) as $13°/_{oo}$ at Low Water and $20°/_{oo}$ at High Water and the pH as about 7·9.

Large colonies of the more typical *M. senile* are found about three miles down the river on a wooden jetty situated at the north end of the Princes Landing Stage. Here, Fraser gives the average salinity as somewhat higher than at Dingle ($23-28°/_{oo}$ in summer and $21-27°/_{oo}$ in winter), but the pH value as about the same. These latter colonies are not specially dealt with in this paper.

COLOUR VARIETIES, SIZE, AND HABITS.

There are four colour varieties of the Dingle anemone, salmon pink, white, olive-brown, and grey; the latter two are rare. All the individuals are small; the base of the largest one collected measured only $2·5 \times 3·5$ cm. and the diameter of the expanded disc rarely exceeded 2·5 cm.

Reproduction occurs by basal laceration and by the deposition of ova. Both these methods are recorded for *M. senile* (**2** and **3**), and its closely allied American forms (**4**). Laceration takes place in the ordinary way by tearing. Figure 1 shows a Dingle specimen with buds produced by this method in the laboratory between 17.9.32 and 22.12.32. It was given frequent changes of sea-water and fed with portions of Mytilus which were
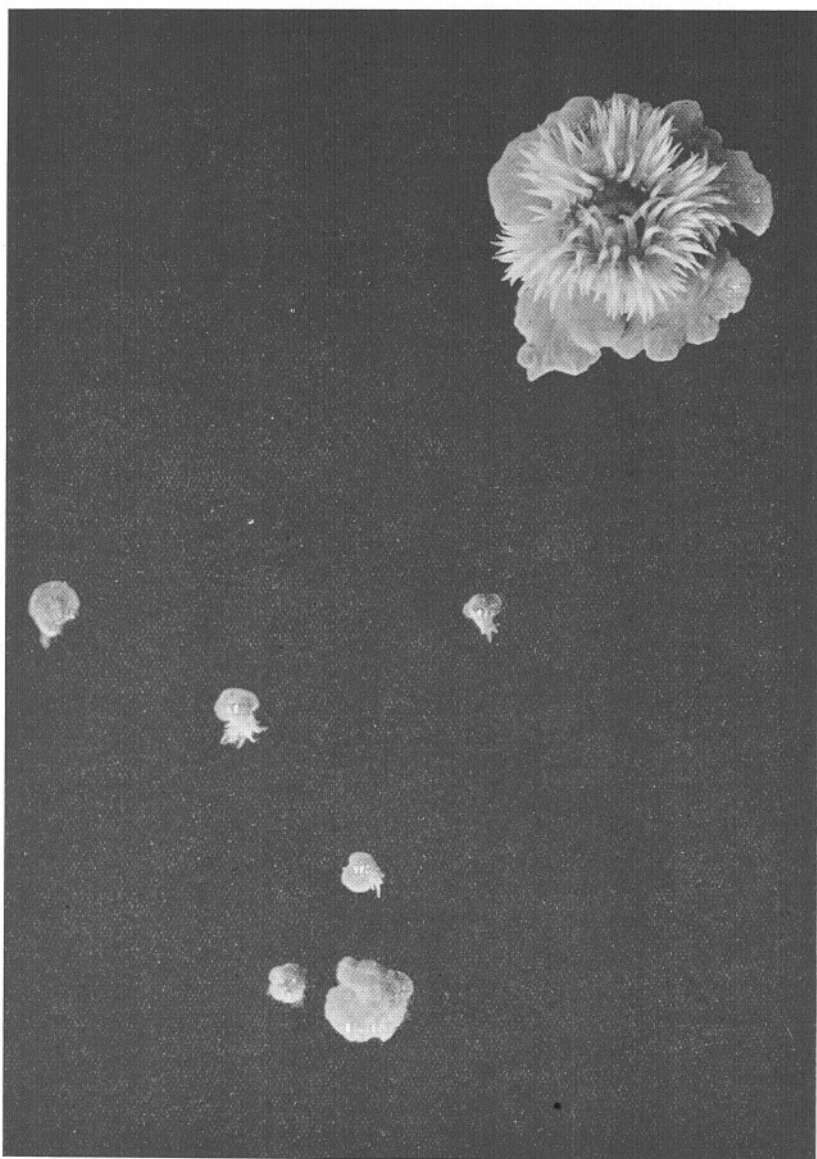
Fig. 1.—A Dingle anemone with buds produced by basal laceration. × 2.
Photograph by P. Bond.

ingested, and with Nitzschia culture. Two individuals kept in captivity by Professor Orton from 5.6.30 to 5.11.30 together produced 34 buds. In this case the adults were not fed, but they were kept clean and the water was changed frequently. They were perfectly healthy.

Laceration appears to be of frequent occurrence in the Dingle anemones in their natural habitat; they often have a very irregular and sometimes torn basal outline. It has been shown in Sagartia and other anemones that the roughness and smoothness of the substratum has little or no effect on the rate of reproduction by this method (2). The observations of Torrey (5) on $M.$ $fimbriatum$ Verrill, suggest that one might possibly attribute the frequency of this process to the uncongenial habitat at Dingle. He concluded from his experiments that the mode of reproduction may be influenced by the environment. Only on one occasion did he observe basal laceration in the natural habitat, all other examples occurred in anemones which had been kept for several months in aquaria where the conditions were not so favourable. Wider observations may however show that lacerations are commoner in the field than is here suggested.

Basal buds have been seen in the Dingle anemones; they are also recorded in $M.$ $senile$ (3) and $M.$ $fimbriatum$ (5). They are probably incompletely lacerated portions of the base which have already developed tentacles, since true budding is of doubtful occurrence among the Actiniaria (2). No œsophageal buds such as are described in $M.$ $fimbriatum$ have been seen in the Dingle form.

Sexually mature individuals may be found in June, but the duration of the breeding season is unknown. The few available records of the spawning of $M.$ $senile$ give its breeding season from March to September although they also suggest a variation in the period according to the locality. The Millport specimens breed from March to June (6), whereas the Plymouth records (7) are from August to September. Two spawning females of the Dingle anemone were observed by Professor Orton in June, 1932. The eggs ranged from $110–130\mu$ in diameter. Their size differs somewhat from the measurements of the eggs of $M.$ $marginatum$ (8) and $M.$ $senile$ (9), but the few observations on the eggs of the latter indicate a considerable amount of variation in their size. Gemmill (9) records an average diameter of 0·1 mm., but 105 eggs of a large brown specimen from Plymouth which spawned overnight in the laboratory at Liverpool on 11.11.32 had an average diameter of $173·6\mu$.

Sexual maturity at a small size is one of the most interesting features of the Dingle anemone. Observations on the smallest size at which $M.$ $senile$ var. $dianthus$ is mature do not appear to have been made apart from Elmhirst's record. I am indebted to him for his information about the Millport specimens. Spawning does not take place, as far as he can recall, until the animals are approximately 2″ in height when expanded.

They are therefore at least twice as large as some of the ripe Dingle anemones.

When kept in finger bowls, the Dingle specimens frequently creep up the sides of the vessel until they are partly exposed to the air, a habit which they share with *M. senile* (3). Both young and adults possess the capacity of floating upside down beneath the surface film, although this position was only observed when the water in the bowls required renewal. In each case the animal crept up the side of the bowl to the water level, slowly released its hold and finally floated off. Sometimes a delicate horny, brown membrane covered the base. The base of such individuals frequently has a silvery appearance which one may possibly attribute to the enclosure of air between the membrane and the true base. This observation recalls the interesting modification met with in the floating Minyads, which have a hollow base containing a horny float from which the anemone is suspended head downwards.

A COMPARISON OF *M. SENILE* (L.) VAR. *DIANTHUS* (ELLIS) WITH THE DINGLE ANEMONE.

(a) The external features and anatomy.

Anatomical investigations have been made to determine the characters of the Dingle anemone for comparison with those of *M. senile*. Only the salmon-coloured anemones were used. Dissections, and hand sections of material fixed in either formalin or Bouin's fluid and frozen in a solution of gum arabic were made to study the grosser anatomical features. Serial sections of material embedded in paraffin wax and stained in borax-carmine and picro-indigo-carmine were used to study the finer characters.

The results of these investigations and a careful comparison of the external features of the Dingle anemone with the accepted descriptions of *M. senile* (3, 10, 11, and 12) indicate a very close resemblance between these two forms, but also certain differences. The general appearance of the Dingle anemone differs in some respects from the typical adult *M. senile* ; the column is often short, although it sometimes forms quite a tall pillar ; the base is broad, spreading, with an irregular outline as in some Sagartias and a diameter usually greater than the height of the column. The scapus wall is thinner and more translucent than in the typical form. Maybe, as has been suggested by Fraser (unpublished records, 1931), its different texture is due to the low salinity of the water at Dingle. In the number of tentacles and the frequent absence of clear disc lobes, the Dingle anemone resembles the young of *M. senile* rather than the adult. Individually, the above features may not be very significant, but together they give the living anemone quite a different facies from the type form. The same colour varieties and colour pattern

are met with in both anemones. They are identical in the structure of their mesenteries and cinclides and in the form and distribution of the musculature of the tentacles, disc, and scapus. They both exhibit fluctuations in the number of their perfect mesenteries. The European M. senile and the American species of Metridium are often hexamerous, but specimens of the former are recorded with 6–11 pairs of perfect mesenteries and of the latter with 4–15 pairs. In thirty-three examples of the Dingle anemone their numbers were as follows :—

No. of pairs of perfect mesenteries.	11	10½	10	9	8½	8	7½,½	7	6½	6	5½	5	4
No. of individuals	2	1	1	1	3	8	1	5	1	3	2	4	1

The sections of the specimens with five and ten pairs were incomplete, so that it is possible that they possessed more than this number.

A detailed study of the variation in the number of perfect mesenteries in the European M. senile does not appear to have been made, but this aspect of the American representatives of the genus has been the subject of various papers. A brief consideration of these is not irrelevant here, more especially as M. fimbriatum Verrill and M. marginatum Milne-Edwards are regarded as synonymous with the European M. senile (L.) var. dianthus (Ellis), (5) ; absolute agreement between them is, however, not yet certain (17).

Torrey (4), after working on M. fimbriatum, concluded that basal fragmentation was especially interesting as a factor affecting the variation in the number of mesenteries and siphonoglyphs. Experiments have shown that monoglyphic and diglyphic polyps can each give rise asexually to both kinds of buds and that the number of siphonoglyphs depends upon whether or not a detached fragment contains a portion of the parent directive system (13). In the majority of regenerating fragments, a pair of directive mesenteries is developed from the torn part of the body wall. If a portion of the parent directive system is also present, then a diglyphic polyp with two pairs of directive mesenteries is produced, if not, a mono-glyphic form with one pair of directive mesenteries. Hahn and Torrey's experiments demonstrate that there is a definite, but not absolutely strict correlation between the mode of reproduction and the morphology of the polyp. It is considered that sexual reproduction more frequently gives rise to regular diglyphic individuals and laceration to irregular monoglyphic ones. It is probable, therefore, that the pre-dominance of forms with an irregular number of mesenteries among the thirty-three specimens specially examined from Dingle may be attributed to the asexual mode of reproduction.

Perfect agreement has been demonstrated regarding the number of

siphonoglyphs and the number of pairs of directive mesenteries (**4**) and (**10**). The variation in their number has not been particularly studied in the Dingle anemone, but twenty specimens which were examined proved to be monoglyphic with one pair of directives. It is interesting to note the variation in the percentages of monoglyphic and diglyphic polyps from various American localities (**13**). The different values may possibly be attributed in some measure to the environment. Unfortunately, the habitat is not described for all the localities which have been studied, but in each there is a greater percentage of the monoglyphic type. Assuming that basal fragmentation is correlated with an unfavourable environment, then one would expect a predominance of monoglyphic specimens at Dingle, since the chances of a detached fragment containing a portion of the parent directive system are fewer than it not containing a piece. It would be interesting to compare the percentages of monoglyphic and diglyphic polyps at Plymouth, Port Erin, and Liverpool.

The arrangement of the imperfect mesenteries in the genus Metridium is also very variable (**14**). In some of the Dingle anemones there were only two cycles of imperfect mesenteries with well-developed retractor muscles and mesenterial filaments : three such cycles are present in the young *M. senile* (**11**). This character is probably of little importance in comparing these anemones since it varies with the age of the individual.

Single unpaired mesenteries occur in the Dingle anemones ; a similar condition is recorded for *M. senile* (**10**) and *M. marginatum* (**14**). In all these forms one sometimes finds a union of the free edges of two adjacent mesenteries belonging to different mesentery pairs. Irregular specimens of *M. marginatum* and certain of the Dingle anemones agree in their tendency to concentrate the non-directive perfect mesenteries at one end of the actinopharynx.

The majority of the mesenterial filaments in the upper part of the column of the Dingle anemone have a typical trefoil appearance when viewed in transverse section. Their shape agrees fairly closely with the filament of *M. senile* (**11**, Fig. 20), but the lobes are frequently more distinct and the reticulate region better developed. Occasionally a 4 or 5-lobed appearance is presented. One may agree with E. M. Stephenson (**11**) that the specific value of the shape of the mesenterial filaments when viewed in transverse section is not yet fully understood, as a sufficient number of individuals of any one species has not been investigated.

The genus Metridium has in the past been defined as having the gonads on the imperfect mesenteries. Carlgren (**10**) and Professor Stephenson (letter to the author, 8.2.33) record examples in which gonads were present on some of the perfect mesenteries also, the former author stating

that when there are more than six pairs of perfect mesenteries, gonads
may occur on the additional ones.   The Dingle anemones with an irregular
number of perfect mesenteries may have gonads developed on some of
them.   A fertile specimen with only six pairs of perfect mesenteries was
not found.

The inferences of importance which may be drawn from the above
discussion of the mesenteries and their associated structures are :—

1. The number of perfect mesenteries present in the European *M.
senile* and in the American species of Metridium is variable.   A
knowledge of the number of perfect mesenteries present in a particular
individual cannot therefore be used as a reliable character for its
identification.

2. Environment may influence habit, and cause changes in the mor-
phology of the genus Metridium.   Uncongenial surroundings possibly
stimulate reproduction by basal laceration whereby polyps with an
irregular number of perfect mesenteries and a varying number of siphono-
glyphs are produced, although an irregular number of mesenteries is more
frequently associated with the monoglyphic than with the diglyphic
condition.

3. There is a definite, but not absolutely strict correlation between
the mode of reproduction and the morphology of the individual.   Egg
embryos as a rule give rise to regular polyps while reproduction by
basal laceration is the principal contributory factor to the production
of irregular ones.

4. In the typical adult *M. senile* the perfect mesenteries are sterile
and the gonads occur on the imperfect mesenteries.   When more than six
pairs of perfect mesenteries are present, some of them may develop
gonads.

(b) *The Nematocysts.*

The nematocysts of the Dingle anemone are one of its most interesting
features.   It possesses all the characters of the Metridiidæ (**15**), but it has
an abundance of both spirulæ and penicilli in its acontia, a character which,
according to the latest classification (**16**), immediately removes it from this
family.   Special care was taken when removing the acontia to prevent
them from touching any other tissues.   The acontia were cut off with
clean instruments as soon as they were extruded through the cinclides or
mouth so that there was no possibility of contact with cut tissues.
Portions were then finely teased in sea-water, mounted either unstained
or stained in 1% acid fuchsin, and examined with a 1/12th objective.   A
pure sample of the acontia cannot however be guaranteed since sooner
or later in their ordinary life they are bound to be contaminated with
the nematocysts from the mesenterial filaments and the ectoderm.

The acontia of at least thirty individuals have been investigated. They all contained both types of nematocyst. The spirulæ were most abundant, but the penicilli were always plentiful and one was sure of finding them in any preparation of a fragment of an acontium. The two types are quite distinct when they are exploded. The spirulæ are identical with those described for *M. senile* (**16**, Fig. 1). The penicilli (Fig. 2) are of the bottle-brush type. The majority have a blunt tip, but I suspect that a few may have a short, fine, terminal thread. The average size, length and breadth of the spirula and penicillus capsules is given in Table I. Their size shows only minor fluctuations between anemones of approximately equal sizes.

A very careful search was then made for penicilli in the acontia of *M. senile* var. *dianthus* from Plymouth, Port Erin, and the Princes Landing Stage, Liverpool. They were found to be universally present in quite considerable numbers in all the small specimens which were examined from each of these localities (see Table I), although they were not so abundant as in the Dingle anemones. They occur in the white, grey, orange, and brown colour varieties. In large specimens they are sparse and sometimes absent. Since these results were obtained, Carlgren (**17**, 1933) has recently recorded the presence of a few penicilli in young specimens but has failed to find them in the adults.

The spirulæ and the penicilli from the acontia of the Dingle anemone have much the same range in size as in *M. senile* (see Figs. 4 and 5, pp. 911–2). The spirulæ of the former do not, however, attain such a large size as those of the latter and their modal value is lower. It is possible that this discrepancy is explained by a difference in the size of the Dingle anemones from which the cells were taken compared with those studied from the other localities, since smaller spirulæ (**16**) and smaller penicilli (see Table I) occur in the young than in the adults of the typical *M. senile*. The anemones from which the data were obtained for Figures 4 and 5 were all small, but their shape is so variable that only their approximate size can be measured. The penicilli do not show any appreciable difference in either their range in size or their modal value (see Fig. 5), which suggests that possibly some other factor is contributory to the smaller size of the spirulæ. Maybe it varies slightly in different localities, possibly with salinity and perhaps in the case of the Dingle anemone, the dwarfing of the body is reflected to some degree in the individual cells.

Three very large specimens, a brown one from Plymouth and an orange and a white one from Port Erin, all showed a relative scarcity of penicilli compared with their numbers in the small individuals. After several days' continued search only six were found in the Plymouth anemone. They were similar in size and shape to those of the scapus ectoderm but their capsules were only approximately half the length of the penicillus
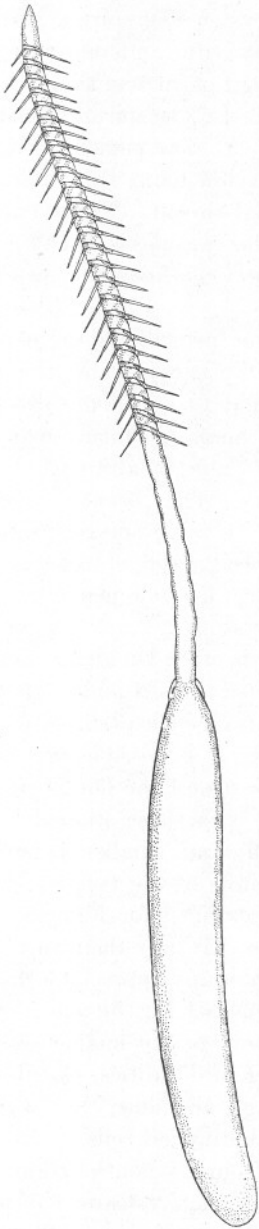
FIG. 2.—A penicillus from an
acontium of a typical *M. senile*
× 1800.

FIG. 3.—A penicillus from
the ectoderm of a typical
M. senile × 1600.

capsules found in the acontia of the other small individuals which had been examined. Their scarcity, together with their resemblance to those of the scapus, led one to conclude that penicilli were absent from the acontia, but that a few stray cells, probably from the ectoderm, had adhered to the acontia after or during their extrusion. Penicilli were also absent from the acontia of the white specimen from Port Erin, but a few of the usual type and size were found in the orange-coloured one (see Table I). The
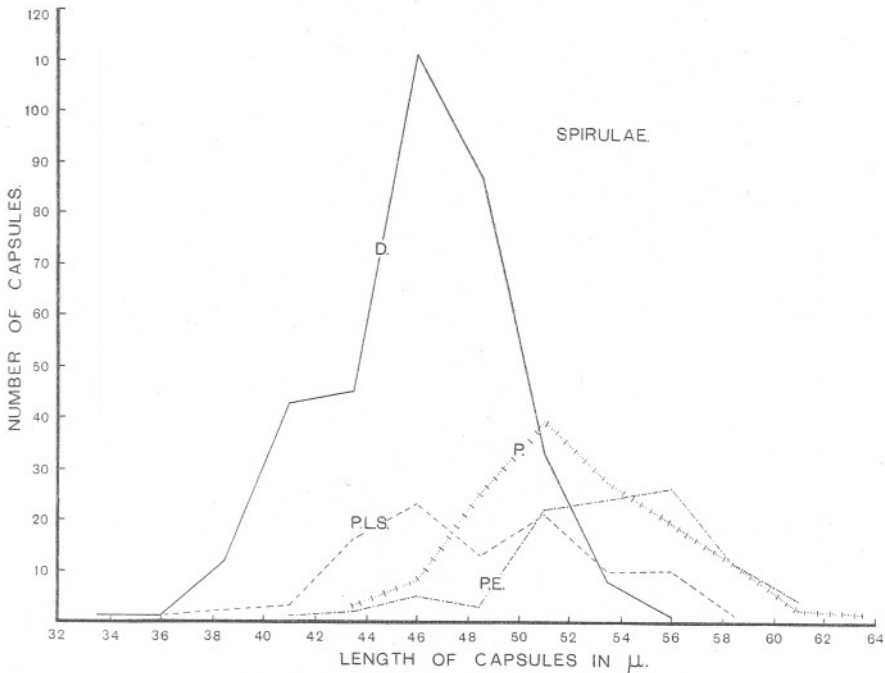

FIG. 4.—Graphs showing the variation in length of the spirula capsules, exploded and measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile* from the Princes Landing Stage (Liverpool), Plymouth and Port Erin.

D.	340 cells from the Dingle specimens in Table I.
P.L.S.	100 cells from the Princes Landing Stage specimens in Table I.
P.	132 cells from the small Plymouth specimens in Table I.
P.E.	100 cells from the small Port Erin specimens in Table I.

acontia of eight additional Plymouth specimens with a column height ranging from 3·5–6·5 cm. showed the same scarcity of penicilli.

The particular function of the penicilli is unknown and the reduction in their number in large specimens is as yet inexplicable. In some Cœlenterates (**18**), the developing nematocysts are migratory. It is possible they are so in *M. senile* and that there is a difference between their migratory powers in the young and the adults. One would expect to find wandering cells in the young rather than in the old individuals.

A comparative study of the types of cnidæ occurring in the ectoderm of
the scapus has shown that these cells also are structurally similar and
comparable in size in the Dingle anemone and *M. senile* (see Table I).
Both spirulæ and penicilli are present. The spirula capsules are smaller
than those found in the acontia. The spiral is uniform in width, limited
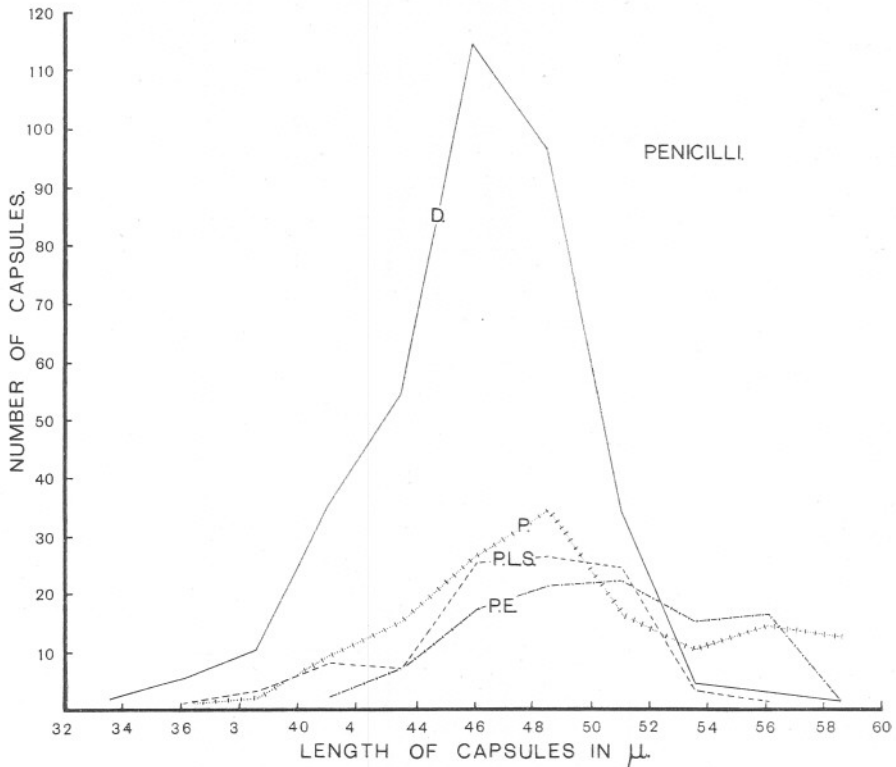to a short distance at the base of the thread and has three to four turns,

Fig. 5.—Graphs showing the variation in length of the penicillus capsules, exploded and
measured to the nearest 0·5μ, from the acontia of the Dingle anemone and *M. senile*
from the Princes Landing Stage (Liverpool), Plymouth and Port Erin. The cells
were taken from the same anemones as gave the data for Fig. 4.

    D.   354 cells from the Dingle specimens.
    P.L.S.   100 cells from the Princes Landing Stage specimens.
    P.   140 cells from the Plymouth specimens.
    P.E.   101 cells from the Port Erin specimens.

whereas the spiral of the acontia spirulæ is much more extensive with
about twenty turns and considerably expanded towards its distal end
(**16**, Fig. 1). There are at least two distinct kinds of penicilli, a small one
with a rather globular capsule and a distinct wisp-like terminal thread
and a larger variety (Fig. 3) similar to, but smaller than those found in the
acontia and with an elongated oval capsule. The latter are very much

TABLE I.

MEASUREMENTS OF THE SPIRULA (SP.) AND THE PENICILLUS CAPSULES (PEN.) OCCURRING IN THE ACONTIA AND THE SCAPUS ECTODERM OF THE DINGLE ANEMONE AND *M. senile.*

(The measurements were made on living cells exploded in sea-water and unstained except the ectoderm cells which were stained with 1% acid fuchsin.)

Locality.	No.** of specimens examined.	Approximate diameter in cm. Base	Disc	No. of cells measured.			Range in size of the cells in μ.	Average size of the cells in μ.
Dingle	5	1·2	1	Ectoderm	Pen.	95	11–20·5 × 3–4·5	16·2 × 3·6
				Acontia	Sp.	100	38·5–55·5 × 3–4·5	47·9 × 3·6
				,,	Pen.	100	34·5–54 × 3·5–6	47·1 × 5
	8 (1 g.)	0·6	0·8	Acontia	Sp.	156	33–50·5 × 3–4·5	44·6 × 3·6
				,,	Pen.	160	32–51 × 3–6	44·9 × 4·9
	4	1	1	Acontia	Sp.	80	38–53·5	46·8
				,,	Pen.	80	39–58	47·1
	1		0·5	Ectoderm	Sp.	20	9·5–13 × 1·5–3·5	11·3 × 2·4
				,,	Pen.	21	13–19·5 × 3–4·5	16·3 × 3·4
	1		1	Ectoderm	Sp.	20	10–15 × 2·5–3·5	12·3 × 2·8
				,,	Pen.	20	16–20 × 3·5–4	18 × 3·7
				Ectoderm	Sp.	20*	9·5–13·5 × 2–3·5	12·5 × 2·7
				,,	Pen.	20*	13–21 × 3·5–5·5	18·8 × 4·3
Princes Landing Stage	5 (br. and p.)	1·4	1·1	Acontia	Sp.	100	35·5–59 × 3–5·5	47 × 3·8
				,,	Pen.	94	36·5–53 × 4–6·5	47·3 × 5·3
Plymouth	1† (br.)		12·5	Ectoderm	Sp.	20	11–19·5 × 1·5–4	15·9 × 2·6
				,,	Pen.	21	20–27 × 2·5–4·5	24·4 × 3·4
				Acontia	Sp.	23	57–69·5 × 3–4·5	63·4 × 3·4
				,,	Pen.	0	Absent	
	1 (n.r.)		0·4	Ectoderm	Sp.	12	9–13·5 × 1·5–3	11·7 × 2·2
				,,	Pen.	16	13·5–18·5 × 3–4	16 × 3·4
				Acontia	Sp.	13	42–53 × 3–4	48 × 3·6
				,,	Pen.	21	40–48 × 4–5·5	43·4 × 4·8
	3	0·5	0·8	Ectoderm	Pen.	31	10·5–25·5 × 3–5	17·2 × 3·5
				Acontia	Sp.	60	44–59 × 3–4·5	51·3 × 3·8
				,,	Pen.	60	42–59 × 4–6	49·9 × 4·9
	4 (br. p. w. and n.r.)	0·5	0·7	Acontia	Sp.	59	45·5–64·5 × 3–5	53·6 × 3·7
				,,	Pen.	73	38–59·5 × 4–6·5	48·3 × 5
	1† (n.r.)		2·7	Ectoderm	Sp.	20	9·5–16 × 1·5–3	14·1 × 2·5
				,,	Pen.	16	16–22 × 3–4	20 × 3·4
Port Erin	5 (o. and w.)	1·4	1·4	Acontia	Sp.	100	35–62 × 2·5–4·5	53·3 × 3·5
				,,	Pen.	101	41–57·5 × 3–6·5	50·1 × 4·8
	1† (o.)		10	Acontia	Pen.	16	53–62 × 4·5–6	57·3 × 5·2

* These cells were unexploded and unstained.

† The stinging cells from these specimens are not used in Figs. 4 and 5.

** Colour pink, unless noted as :—

br.=brown, g.=grey, o.=orange, w.=white, n.r.=not recorded.

more abundant than the former ; they sometimes show a terminal thread. All the measurements refer to the larger kind. Their size varies but little between different individuals of about the same size, but like the stinging cells of the acontia they are slightly larger in old specimens than in young ones.

To summarise the observations on the nematocysts one may say :—

i. the spirulæ and penicilli from the acontia and the scapus ectoderm of the Dingle anemone are identical in form and comparable in size with those found in *M. senile.*

ii. both spirulæ and penicilli are present in abundance in the acontia of typical small *M. senile* from various localities, but they are sparse and sometimes absent from large and medium-sized individuals.

iii. the acontia of the largest and the smallest specimens of the Dingle anemone contain an abundance of spirulæ and penicilli ; some of the anemones were sexually mature.

The Dingle Anemone as a New Species or a Variety of *M. senile.*

The close correspondence between the habits, the methods of reproduction, the anatomy, the types and sizes of the stinging cells from the ectoderm and the acontia, as noted in the foregoing sections, gives quite sufficient evidence for regarding the Dingle anemone as *M. senile.* It nevertheless exhibits certain features which at present justify its recognition as a dwarf variety. The small size of all the individuals composing the colony and their attainment of sexual maturity while small support this suggestion. The fertile specimens also exhibit the following characters of the young of the ordinary type ; the general appearance of their tentacles, the abundance of penicilli in their acontia and the absence of clear disc lobes. Much of the interest of these characters would be lost should further researches prove that the typical form is sexually mature at a smaller size than is thought at present.

Gosse (3) observed young specimens of Metridium between the tide-marks and suggested that with advancing age they move offshore to deeper waters. Perhaps the Dingle anemones migrate, but actual proof of this habit is difficult to ascertain. Their dwarf form is possibly associated with the separate or combined effects of the following factors ; their intertidal position, the low salinity and the pollution of the water.

One small fertile specimen was sent to the Laboratory, Plymouth, where it was fed with plankton. It did not show any appreciable change in size after living there for seven months. A subject for further experiment is to determine whether the Dingle anemones are permanently

dwarfed, or whether if transferred to other more favourable environments they would grow to the average size and develop all the characters of the type species.

THE SYSTEMATIC POSITION OF THE GENUS METRIDIUM.

Some of the principal changes in the systematic position of Metridium are shown below :—

Fam. SAGARTIADÆ Gosse (**3**, 1860), including the genera Actinoloba (=Metridium) Sagartia, Phellia, Adamsia, Gregoria, and Discosoma.

Fam. SAGARTIDÆ (Hertwig, 1882).

Sub. fam. Metridinæ, Carlgren (**10**, 1893), including the genera Metridium, Adamsia, Aiptasia, Stelidiactis, and Calliactis.

Fam. METRIDIIDÆ Stephenson (**15**, 1920), including the genera Metridium, Calliactis, Adamsia, Aiptasia, Aiptasiomorpha, Heteractis, and Bartholomea.

Fam. METRIDIIDÆ Stephenson (**16**, 1929), including the genera Metridium, Calliactis, Adamsia, Hormathia, Actinauge, Paraphellia, Leptoteichus, Chondrodactis, etc. (and the remaining genera included in the Metridiidæ and Chondractiniidæ **15**, 1920, with the Aiptasiids and Sagartiomorphe removed).

In 1860 it was classed with the Sagartias in the family Sagartiadæ (**3**). Many years afterwards Carlgren (**10**) placed it in his new sub-family, the Metridinæ. Stephenson (**15**) renamed the sub-family Metridinæ the Metridiidæ, and raised it to the rank of a full family on a level with the Sagartiidæ. Later, as the result of much work on the nematocysts of anemones with acontia, he revised the members and the characters of these two families (**16**, 1929), and in addition to the characters given in his earlier classification he provisionally distinguished the Sagartiidæ as forms with an abundance of spirulæ and penicilli in the acontia and the Metridiidæ as forms possessing spirulæ only. The resemblances and differences between the Sagartiidæ and the Metridiidæ (**16**) strongly suggest a reconsideration of the systematic position of the genus Metridium, as both spirulæ and penicilli have recently been found in the acontia of the young of the typical *M. senile.*

The general systematic value of the presence or absence of cinclides and the position of the gonads has already been queried (**12**). If the type of stinging cell found in the acontia is to remain a family character, then Metridium must be removed from the family Metridiidæ provided that further researches on *young* and *adult* specimens of Adamsia, Calliactis and the other genera included in the family prove the absence of penicilli

from their acontia. There seem to be only two alternative positions for it, either it must once more be classed with the Sagartias in the Sagartiidæ or else it must be placed in a family by itself as recently suggested by Carlgren (**17**, 1933). There are points in favour of both these suggestions.

Since the discovery of both spirulæ and penicilli in the acontia of *M. senile* and the Dingle variety, there exists no constant difference between the Sagartiidæ and the Metridiidæ. This is the principal evidence in favour of placing Metridium with the Sagartias. Such a grouping would probably be quite satisfactory for the young individuals of *M. senile*, but the presence of a distinct collar and the possible absence of penicilli from the acontia of the adults directly oppose this classification. It is noteworthy that one of the family characters quoted in the past for the Sagartiadæ (**3**), which contained the genus Metridium, is the presence in the acontia of cnidæ with a short densely armed wire. They are obviously penicilli.

If the genus is placed in a family by itself the characters of such a family cannot be anything but indefinite because certain of the features exhibited by the young and adults are different, moreover, the form of the body, the number of perfect mesenteries and the position of the gonads are variable characters. There is, however, a more marked tendency towards the sterility of the primary mesenteries and to hexamerism in the genus Metridium than in the Sagartias.

A consideration of these characters and the above-mentioned objections to placing the genus with the Sagartiidæ, together with the further evidence of the presence of penicilli in the acontia of both *M. senile* var. *dianthus* and the Dingle variety, favours Carlgren's suggestion of restricting the Metridiidæ to the genus Metridium. The remaining genera of the present Metridiidæ may then be referred to the Chondractiniidæ (now the Hormathiidæ, **19**), as suggested by Professor Stephenson (letter to the author, 4. 4. 34). The evidence obtained from the stinging cells of the acontia and the general trend of certain characters of the genus along a path distinct from the Sagartias support these suggestions. The types of stinging cells in the acontia would not alone be a useful diagnostic character for the revised Metridiidæ, since the number of types present varies with the age of the individual. In conjunction, however, with the unique form of the spirulæ from the acontia, and the characters already described for the genus (**15**), one would have ample features on which to base a description of a family which contained the genus Metridium as its sole representative.

Unfortunately, living specimens of *M. marginatum*, Milne-Edwards, *M. fimbriatum*, Verrill, and *M. senile* var. *pallidum* (Holdsworth) have not been available for an investigation of their stinging cells, but Carlgren (**17**, 1933) has now recorded the presence of penicilli in one small

Metridium sp. and one large specimen of *M. fimbriatum*. It is highly probable therefore that all these forms would fit in with the revised Metridiidæ since the var. *pallidum* is not very different from the ordinary type and, as previously noted, certain authors regard the American species and the European *M. senile* as synonymous.

The following conclusion may be drawn from the foregoing discussion. The variation which is met with in the genus Metridium and the difficulties which present themselves in connexion with its systematic position show that the genus is transitional between the Sagartiidæ and the Metridiidæ as defined in 1929. Its affinities with the Aiptasiidæ have also been mentioned by Carlgren (**17**). Some specimens of Metridium exhibit characters which suggest a trend towards the Sagartias, but others possess features which are different from those of this family, namely, hexamerism and the sterility of the perfect mesenteries. An intensive study, nevertheless, shows that they are all referable to the one genus. The Sagartian trend of the genus is further emphasised by certain characters of the Dingle anemone. In many ways it is true to type, but in addition to the frequent occurrence of more than six pairs of perfect mesenteries, both young and adults possess an abundance of penicilli in their acontia. The latter is a feature of the Sagartias and one which at present distinguishes the adults of the Dingle form from the adults of the typical *M. senile*. The asexually produced polyps of the latter often show the Sagartian feature of more than six pairs of perfect mesenteries, some of which may bear gonads. The deviation from hexamerism is not entirely due to the mode of reproduction (see p. 906) and moreover, other anemones, e.g. Aiptasia, which reproduce by basal laceration, always give rise to daughter polyps which are diglyphic and hexamerous irrespective of the size and constitution of the original fragment (**4**). In the latter species hexamerism seems to be a stable character, whereas in Metridium the inherent tendencies to this primitive condition are not so pronounced.

The presence of acontial penicilli appears to be a constant character of the Dingle anemone and should future investigation show that irregular polyps normally arise by sexual reproduction then such a form of Metridium would be almost as near to the genus Sagartia as to the genus Metridium ; the presence of a distinct collar in the latter does, however, distinguish the two genera. A large amount of experimental work involving the rearing of egg embryos would be necessary to prove this point. Until more is known about the morphology of egg embryos the true state of affairs within the genus cannot be estimated.

SUMMARY.

1. A special study has been made of a small Metridium-like anemone found at Dingle, Liverpool, in comparison with the typical form of *Metridium senile* (L.) var. *dianthus* (Ellis).

2. Penicilli, formerly believed to be absent from the acontia of typical *M. senile*, have been discovered in abundance in the young, but rarely in the adults. In young and sexually mature specimens of the Dingle anemone they are also abundant.

3. There is close agreement between the anatomy of the Dingle form and the typical *M. senile*.

4. A considerable amount of variation occurs in the Dingle anemone, as in *M. senile* var. *dianthus* and *M. marginatum*, Milne-Edwards.

5. The resemblances and differences between the Dingle form and *M. senile* indicate that the former is a dwarf variety of the latter.

6. The discovery of an abundance of penicilli in the acontia of young typical *M. senile* and mature specimens of the Dingle variety, in conjunction with the great amount of variation in the genus Metridium, suggests that a reconsideration of the systematic position of the genus is necessary and would justify either the restriction of the family Metridiidæ to the single genus Metridium, or else the fusion of the Metridiidæ with the Sagartiidæ. The sum of the evidence appears to lie in favour of placing the genus in a family by itself.

ACKNOWLEDGEMENTS.

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