

**Systematic Implications of *Euphysa ruthae* n. sp.
(Athecata: Corymorphidae), a Psammophilic
Solitary Hydroid with Unusual Morphogenesis¹**

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Abstract. *Euphysa ruthae* n. sp. is described from the San Juan Island region, Washington, U.S.A. It is found commonly in infralittoral coarse sands at several locales, its size and field distribution suggesting that it is a member of the mesopsammic meiofauna. As is characteristic for *Euphysa* hydroids, *E. ruthae* is solitary and possesses an elongated hydrocaulus with a mucoid sheath, moniliform aboral tentacles, and basal papillae. *E. ruthae* shares the unusual property of polarity reversal in bud formation with three other species of *Euphysa*. The buds of *E. ruthae* are unique in that they combine morphogenetic features of gonophores with those of asexual bud formation. Bud morphogenesis has similarities to actinula morphogenesis in the closely related Tubularoidea. Each basal papilla contains a simple, terminal statocyst that apparently is homologous with that of *Corymorpha palma*, suggesting a synapomorphy that links the genera *Euphysa*, *Corymorpha*, and perhaps *Vannucia*. Comparison with other interstitial hydroids suggests that certain features may have special adaptive value.

The genus *Euphysa* (= *Heteractis*) is generally accepted as being among the primitive, capitate, athecate hydroids and has been aligned with the Corymorphidae (Kramp, 1949; Rees, 1958). Kramp (1949) considered the *Euphysa* group of hydroids to be derived from Corynidae, but Rees (1957) considered it to include some of the most primitive hydroids. Kramp (1949) accepted five species of hydroids that may be unified in the genus *Euphysa* on

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the basis of aboral moniliform tentacles and oral moniliform or capitate tentacles. *Euphysa aurata* has received frequent attention (Broch, 1937; Rees, 1937, 1938; Kramp, 1949; Werner, 1959; Brinckmann-Voss, 1970) but there is little detailed knowledge of it and only sparse notes on the other species. Three species of *Euphysa* provide evidence of polarity reversal in their asexual reproduction; *E. farcta* and *E. peregrina* in their fragmentation of the hydrocaulus and *E. aurata* in its formation of lateral buds on the hydranth. *Euphysa* species have in common with several *Corymorpha* species the presence of papillae about the hydrocaulus which give rise to filamentous anchoring threads. The cnidom of *E. aurata* is the only *Euphysa* previously characterized.

A new species of *Euphysa* from the San Juan Island region of the state of Washington, described here, appears to be closely related to *E. aurata*. The detailed observations on its anatomy and extraordinary mode of reproduction may offer further insights into the relationships of the euphysines and lower corymorphids. The new species will be of interest in our attempts to understand the relationships and adaptations of the heterogeneous group of small, solitary, epi-, or mesopsammic hydroids.

MATERIALS AND METHODS

Several hundred specimens were obtained during August 1979 and July 1981 from various sand samples on and about Minnesota Reef near Friday Harbor, San Juan Island. Sand samples were collected between -0.3 and -0.9 m on the "reef" by walking to the sites and also by divers at 10-15 m depth adjacent to the "reef." A few specimens were obtained from poorly-sorted sand in front of the main laboratory at the Friday Harbor Laboratory and from well-sorted infralittoral and sublittoral sands from Cattle Point, San Juan Island. Sand samples were collected with a trowel to a depth of 5-10 cm, placed in buckets or plastic Whirl-Paks, and returned to the laboratory. Sand samples were maintained at 9-11°C and usually sorted within a few days but could be maintained for several weeks without observable adverse effects on the hydroids. Specimens were separated from the sand by swirling a subsample of sand in a bucket with seawater and quickly decanting the water through a 63- μ m mesh sieve. Dozens of animals were observed alive with a dissecting microscope and in squeeze preparations (live specimens in a drop of water under pressure of a coverslip) with the compound microscope. For preservation and histological studies, specimens were anaesthetized briefly (2-5 min) in 7.5% MgCl₂, fixed in Hollande's cupri-picri-formal-acetic fixative, and embedded in polyester wax (Steedman, 1960). Transverse and longitudinal sections were cut at 5 and 9 μ m and stained with Heidenhain's azan or Heidenhain's iron hematoxylin methods (Galigher & Kozloff, 1971).

Numerous specimens were kept alive in embryological culture dishes and were observed daily. Most were kept at ambient sea-water temperature (11-12°C), but some were maintained at ambient room temperature (20-24°C). Some were fed *Artemia* nauplii and planktonic copepods; others were maintained in dishes submerged in running seawater.

SYSTEMATIC ACCOUNT

Euphysa ruthae n. sp.
(Figs. 1-20)

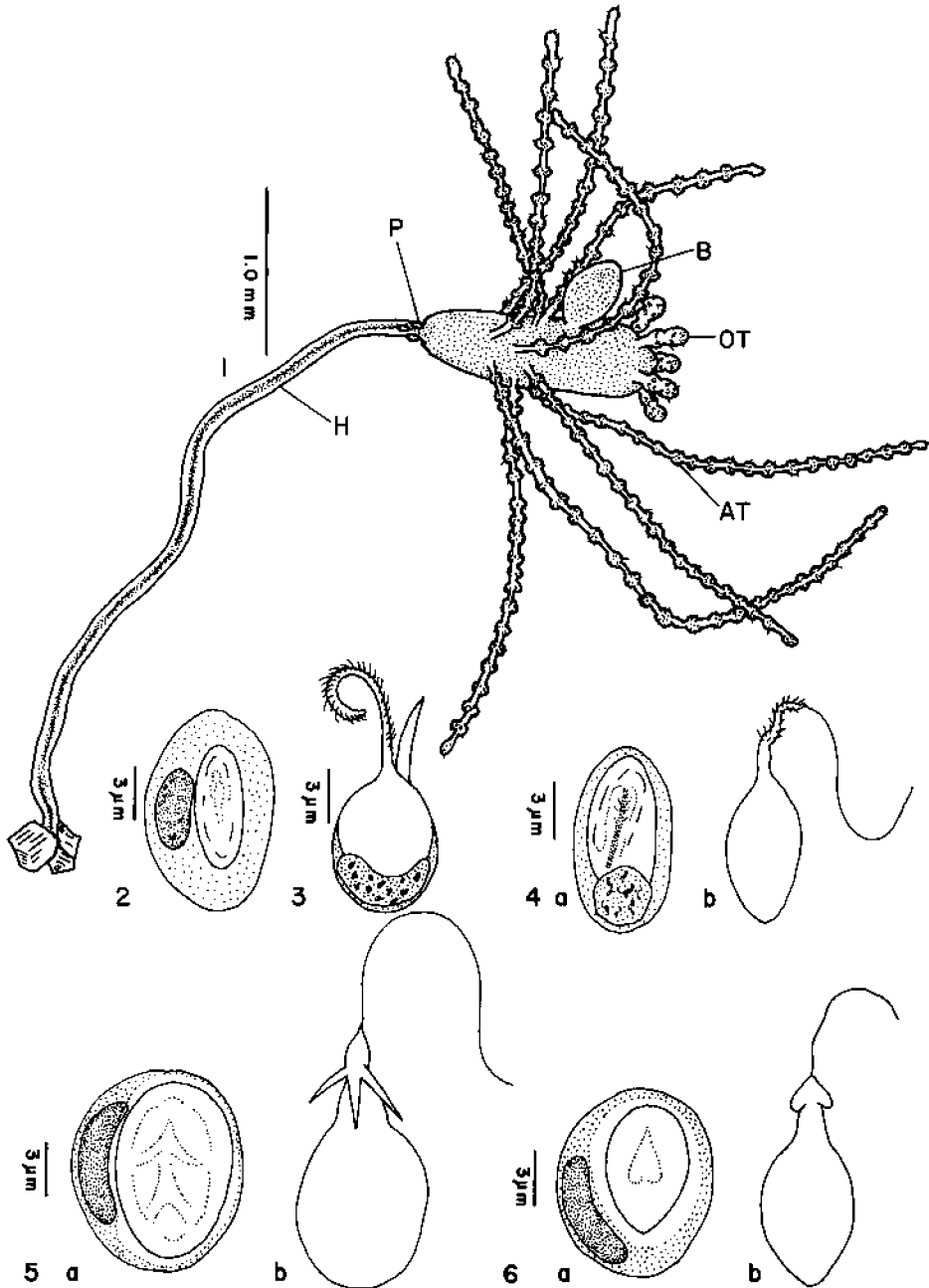
Species diagnosis. Solitary, to 40 mm in length, hydranth to 1.5 mm in length, remainder is extended hydrocaular length; up to seven oral tentacles, forming single whorl, capitate and moniliform with two nematocyst annuli; 4-12 aboral tentacles, in three alternating whorls, moniliform; hydranth demarcated from hydrocaulus by shelf-like constriction; hydrocaulus highly extensible, with mucoid sheath; 5-14 papillae with gastrodermal cores encircle hydrocaulus just below hydranth, each papilla with a terminal statocyst; buds borne between the aboral and oral tentacles, oral end attached to parent; coelenteron undivided. Cnidom: stenoteles, microbasic p-mastigophores, desmonemes; nematocysts in epidermis and gastrodermis of hydrocaulus. Sexual individuals unknown.

Type specimens. Holotype (USNM 60407) is deposited in the Department of Invertebrate Zoology at the U.S. Museum of Natural History, Smithsonian Institution, Washington, D.C. Three paratypes, USNM 60408 (a longitudinally serially sectioned animal stained with Heidenhain's azan), and USNM 60408 (two intact animals).

Type locality. Sand at -0.9-0 m at the northwest end of a rocky outcrop, known locally as Minnesota Reef (Lat. 48°31'42"N; Long. 122°59'15"W).

Etymology. The specific designation honors Ms. Ruth Illg, who facilitated, participated in, and generally enlivened the field work.

General description. Healthy specimens have a rosy internal coloration typical of many small gymnoblastic hydroids, with the hypostome and basal region being conspicuously white. The tentacles and hydrocaulus are translucent and colorless. The living, extended hydranth (Fig. 1) is elongate; from mucoid sheath to hypostome its length is between 0.35 mm for a newly released bud to 1.45 mm for the largest specimen observed. The diameter of extended specimens is relatively uniform, between 0.25 and 0.32 mm. A thin and highly extensible hydrocaulus frequently reaches lengths of 30-40 mm, which may contract to about 1-3 mm. Three to seven oral tentacles (Figs. 1, 8) have been recorded, but five or six occur most frequently. They are loosely arranged as a single whorl just below a small, extensible hypostome and are about 0.35 mm long when extended. The oral tentacles may be considered capitate, in that the terminal cluster of nematocytes is quite prominent and relatively larger than that of the aboral tentacles. In addition, the oral tentacles are moniliform (Figs. 1, 9), usually possessing two annuli of nematocytes that are more or less conspicuous in accordance with the overall size of the hydroid. The aboral tentacles (Figs. 1, 7, 8) normally reach lengths of 2.5-3.0 mm, rarely, 3.5 mm, and are arranged in three alternating whorls. Each tentacle is moniliform, having about 15-25 annuli and a terminal knob not larger than these annuli (Figs. 11, 12). The number of aboral tentacles is 9-12 for large specimens and usually, three or four on newly released buds. By the time six or seven tentacles are present, the alternating nature of the three



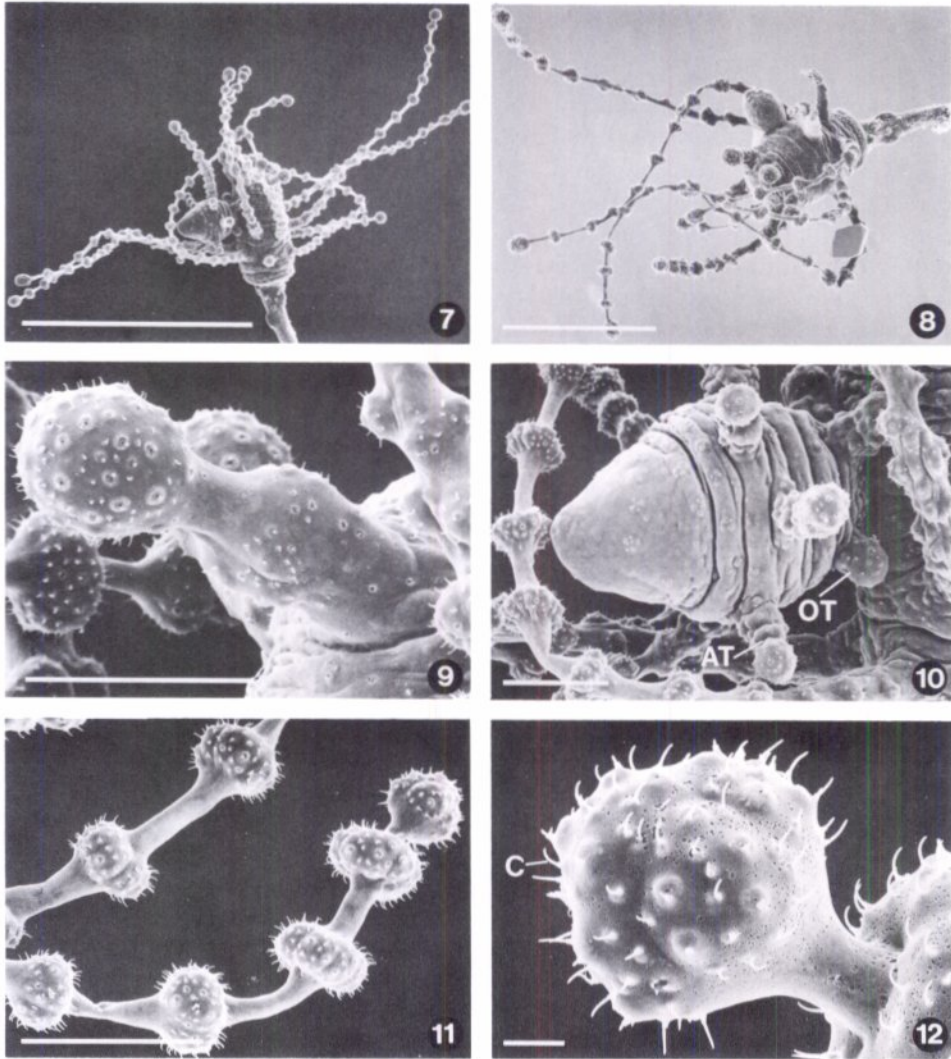
FIGS. 1-6. *Euphysa ruthae* n. sp. Fig. 1. Line drawing from live, extended adult. AT, aboral tentacle; B, bud; H, hydrocaulus; OT, oral tentacle; P, papilla. Figs. 2-6. Line drawings of nematocytes and nematocysts drawn from sectioned specimens. Fig. 2. Nematocyte from gastrodermis; nematocyst unidentified. Fig. 3. Desmoneme everted. Fig. 4. Microbasic mastigophore. a, nematocyte; b, everted. Fig. 5. Stenotele, type 1. a, nematocyte; b, everted. Fig. 6. Stenotele, type 2. a, nematocyte; b, everted.

whorls becomes obvious (Figs. 1, 7). The aboral and oral tentacles have a gastrodermal core consisting of a column of cells. The hydranth is demarcated from the hydrocaulus by a slight, shelf-like constriction (Fig. 7). Below this is the hydrocaulus which shows a single gastrovascular canal in squeeze preparations, and is loosely invested with a mucoid sheath. Just below the constriction, the hydrocaulus bears 5–14 irregularly distributed papillae (Fig. 1) directed distally. Each of these has a central cord of several gastrodermal cells of which the most distal is concave, the concavity enclosing a vesicle with a central cluster of granules. Although specimens kept in culture rarely form filamentous anchoring threads, those obtained with grains of substratum still attached had numerous filaments proximal to the papillae. Because specimens in culture eventually have more proximal papillae, the filaments probably are the attenuate remnants of papillae.

To date, *E. ruthae* has been observed to produce only non-sexual buds. Usually, these arise distal to the aboral tentacles but frequently they arise at the base of one and carry it away from the parent polyp (Fig. 7). This adult tentacle always is at an appropriate position relative to the bud's own aboral tentacles. The size of buds at comparable stages of development varies with the size of the parent. A bud arises as a small, spherical exfoliation of the parent body wall, such that it has a central region of rosy gastroderm from its beginning. As the bud enlarges, a white, relatively opaque region appears between the gastrodermis and epidermis. The rosy gastrodermal mass increases only slightly in size. The bud maintains a spherical shape, having the appearance of a typical gymnoblastic gonophore (Fig. 8). Although scores of these buds were observed immediately after collection and subsequent intervals, no gametes were ever observed or identified. After 2–3 weeks at ambient temperature (approximately 11–12°C), oral tentacles become apparent, followed shortly by the hydrocaulus. There are 4–6 oral tentacles formed about the attachment to the parent (Figs. 7, 10). Hydrocaulus formation is preceded by organizational activity at the distal portion of the bud. Specimens maintained at ambient room temperature (20–24°C) did not appear to be as healthy but they progressed comparably. As many as six relatively mature buds have been observed on a single polyp. These buds were arranged in two alternate whorls above the aboral tentacles.

Nematocysts occur over the entire hydranth surface but are restricted to the annuli and terminal knobs in the tentacles. The stenoteles are conspicuous. There are no nematocysts in the basal collar of the hydranth.

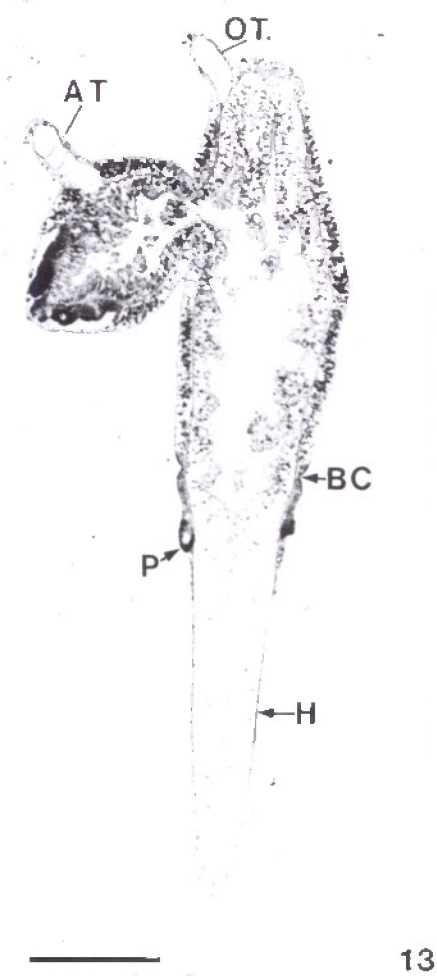
Histology. The epidermis primarily consists of epitheliomuscular cells, with basal muscle fibers oriented along the oral-aboral axis. The nuclei are ovoid to circular in profile, with a 5–7- μm major axis and usually a single prominent nucleolus (2 μm). Epidermis of the hypostomal region is relatively thin (10–15 μm) and contains very few scattered nematocysts (Fig. 15). The latter are microbasic p-mastigophores (5–7 μm long axis) and rare stenoteles (Figs. 4–6). Epidermis below the hypostome is 30–40 μm thick and contains many stenoteles [most are 7–8 μm (type 2) and about one-third are 10–12 μm (type 1) in their major dimensions] with fewer desmonemes (5 μm) and microbasic



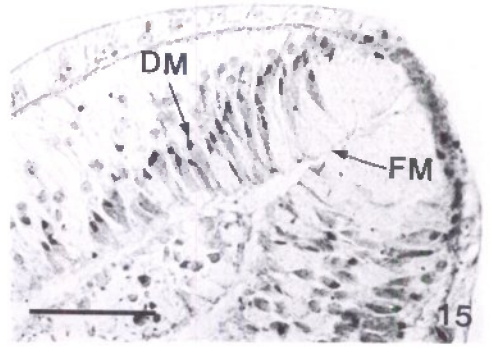
FIGS. 7-12. *Euphysa ruthae* n. sp. Fig. 7. Whole organism with maturing bud, note alternating whorls of aboral tentacles on parent, and long parental tentacle on bud. Scale bar represents 1,000 μm . Fig. 8. Anterior view of hydranth with a small bud. Scale bar represents 500 μm . Fig. 9. Moniliform, capitate oral tentacle; note the distinctly segregated ring of enidocils below the terminal bulb (second, more basal ring is indistinct). Scale bar represents 100 μm . Fig. 10. Enlargement of bud in Fig. 7; note oral tentacles and whorls of aboral tentacles. Scale bar represents 100 μm . AT, aboral tentacle; OT, oral tentacle. Fig. 11. Moniliform aboral tentacles; note distribution of nematocysts as shown by their enidocils. Scale bar represents 100 μm . Fig. 12. Terminal bulb of aboral tentacle. Scale bar represents 10 μm . C, enidocil.

p-mastigophores. Near the base of the hydranth is a distinct constriction (Fig. 13) from which the mucoid sheath extends. The epidermis of this region consists of a wide zone (about 100 μm) formed by a single cell type which is columnar (20 μm tall) and has dense cytoplasm that is azanophilous with a cyanophilous hue (Figs. 13, 14). The cells of the upper one-third of the zone, above the constriction, have strongly azanophilous minute granules at their apical surfaces. Generally, the nuclei of this zone are basal with two or more prominent nucleoli. A similar but more cyanophilous cell type forms the epidermis of the basal two-thirds and the papillae which arise there. Most papillae are just below the hydranth (Fig. 14). The epidermis of this basal zone and of the papillae contains basal longitudinal muscles, but not nematocysts. The epidermis of the hydrocaulus is squamous and vacuolate and contains basal longitudinal muscles (Fig. 20). The gastrodermis and epidermis contain bacilliform nematocysts which typically are about 7-9 μm long and 2 μm in diameter (Figs. 2, 20). Associated with each nematocyst is a lateral, reticulate-patterned nucleus that usually is larger in the epidermis. The nematocyst and nucleus are surrounded by a membrane, and these cells seem to lie randomly in the gastrodermis of the entire hydroid (Fig. 20) and epidermis of the hydrocaulus. They could not be well-characterized, although they often appear to be discharged and are the source of long, thin tubular strands lying in the gastrovascular cavity. Epidermis of the tentacle consists of annuli of nematocytes (Fig. 19) separated by squamous myoepithelial cells with basal, longitudinal muscles. The nematocysts are predominantly desmonemes (5 μm), with fewer stenoteles (types 1 and 2) and rare microbasic p-mastigophores. Generally, the epidermis of buds is a somewhat thinner extension of the parental hydranth epidermis and contains the same nematocysts. The hydranth and bud epidermis is separated from the gastrodermis by a conspicuous mesolamella. The mesolamella is not evident in the tentacles or hydrocaulus. A supporting lamella, which some workers (e.g., Kramp, 1949) describe as separating tentacular gastrodermis from the hydranth gastrodermis in some tubulariids, is lacking in this species. The mesolamella does form a constriction at the base of some oral tentacles but not at all for others.

The gastrodermis of the oral region usually is thrown into marked longitudinal ridges and troughs, the number of troughs roughly corresponding to the number of oral tentacles and projecting toward these. This region consists primarily of mucous cells, as is typical for hydroids and is richly flagellated. These cells contain a large mass of foamy, weakly cyanophilous product (foamy mucous cell) and roughly alternate with a slender, more basal, strongly cyanophilous region of fine granular material (dense mucous cell) (Fig. 15). Associated with the basal region of the latter is a prominent dense body (black with hematoxylin) that is brilliantly azanophilous with azocarmine (Fig. 15). This is either in, or associated with, the nuclei of these mucous cells. Below the oral region, the gastrodermis may continue to be ridged or relatively smooth and consists of typical, columnar digestive cells. There is no gastric diaphragm. Hydranth gastrodermis contains well-developed, basal, circular



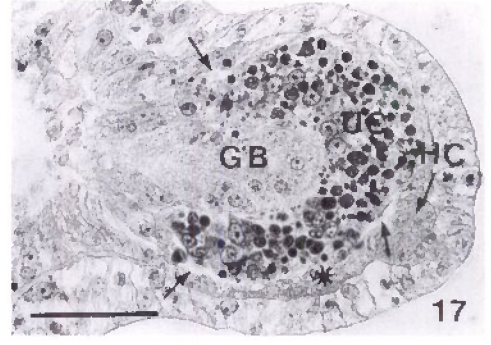
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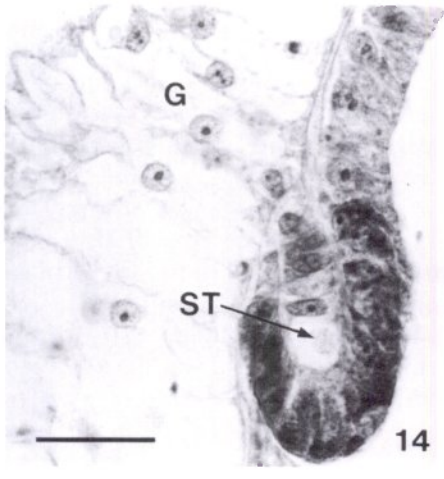
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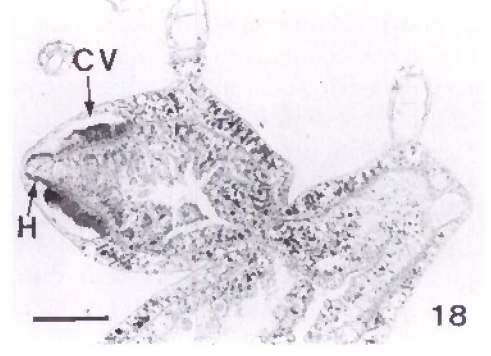
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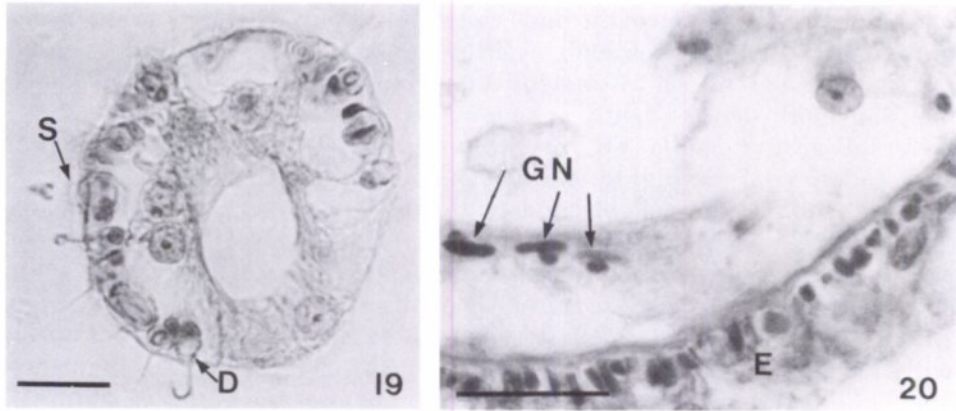
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FIGS. 19, 20. *Euphysa ruthae* n. sp. Fig. 19. Transverse section of single nematocyst ring of an aboral tentacle; note discharged and intact desmoneme side by side. Scale bar represents 20 μm . D, desmoneme; S, type 2 stenotele. Fig. 20. Transverse section of hydrocaulus showing several gastrodermal nematocytes (opacity due to hematoxylin). Scale bar represents 20 μm . E, epidermis; GN, gastrodermal nematocytes.

muscle fibers. Although there appear to be faint circular striations in the tentacles and hydrocaulus, their muscular nature could not be ascertained. The gastrodermis of the hydrocaulus consists of large cuboidal cells appearing devoid of cytoplasm and having a small marginal nucleus. These cells often have pseudopodia-like projections into the lumen. The gastrodermal core of the papillae consists of cells with relatively dense cytoplasm, in contrast to the vacuolate appearance of the tentacle gastrodermis. The basal two cells of this cord are elongated and project well into the hydranth gastrodermis. The proximal surface of the distal terminal cell is concave and partially surrounds a spherical cavity (10 μm) in which lies a simple statolith (5 μm) (Fig. 14).

Early bud formation is initiated by a proliferation of gastrodermal cells. These cells have a dense cytoplasm (Fig. 17) and appear to be nutritionally

FIGS. 13–18. *Euphysa ruthae* n. sp.; histological sections. Fig. 13. Longitudinal section of adult and mature bud. Scale bar represents 0.25 mm. AT, aboral tentacle; BC, basal constriction; H, hydrocaulus; OT, oral tentacle; P, papilla. Fig. 14. Longitudinal section of basal papilla and statocyst. Scale bar represents 25 μm . G, gastrodermis; ST, statolith. Fig. 15. Longitudinal section of hypostome showing two mucous cell types. Scale bar represents 25 μm . DM, dense mucous cell; FM, foamy mucous cell. Fig. 16. Transverse section with two early buds and aboral tentacles in tangential section. Scale bar represents 100 μm . Fig. 17. Longitudinal section of early bud; note the double-layered "heteromedusoid" structure enclosed with mesolamella. An inner cavity (arrows) separates the mass of undifferentiated cells (UC) from an outer epithelial layer (*). The hollow hydrocaulus (HC) rudiment appears in tangential section. Scale bar represents 50 μm . GB, bud gastrodermis. Fig. 18. Longitudinal section of mature bud; note densely-stained epidermis of basal collar and the surrounding cavity. Scale bar represents 100 μm . CV, cavity; H, hydrocaulus.

inactive until the outline of the bud is well-developed. This new gastrodermis forms a papillar projection with a narrow cavity contiguous with the gastric cavity of the parent. An assortment of ameboid cells (7–20 μm in major dimension) with dense slightly cyanophilous cytoplasm begins to aggregate about this gastric papilla (Fig. 16), which is separated from the gastrodermis and epidermis of the bud by mesolamella. These cells have large nuclei (9 μm) with numerous nucleoli, and in the cytoplasm there are many dense (black with hematoxylin) azanophilous granules 2–6 μm in diameter (Fig. 17). As this aggregate of cells increases, a schism appears such that there is a thin outer layer of cells apposed to the mesolamella of the distal bud surface (Figs. 16, 18). These contain very few dense granules and have smaller oval nuclei without conspicuous nucleoli. The thicker inner layer consists of large ameboid cells as described above. Thus, in effect or appearance, there is formed a "heteromedusoid entocodon" as in certain *Tubularia* species. Most of the growth of the bud up to the point of tentacle differentiation appears to be a function of increase in the inner (exumbrellar?) mass of undifferentiated cells and an enlargement of the schism between the "heteromedusoid" surfaces. The first differentiation of "entocodon" cells occurs at the site of the putative velar plate, where a short hollow cylinder forms (Fig. 17). This is the rudimentary hydrocaulus, and it does not break through the bud epidermis until tentacles have differentiated and the bud is nearing the point of liberation. As the gastric cavity of the bud enlarges, its gastrodermal cells begin taking on the more characteristic appearance of active nutritional cells. During this time, the putative exumbrellar surface of the "heteromedusoid" is undergoing differentiation and reorganization, eventually giving rise to the papillae and the basal collar of specialized epidermis just above the papillae (Figs. 13, 18). The epidermal cells of the papillae at this time have strong, mixed cyanophilous and azanophilous properties. The papillar gastrodermal core and statolith are present before the parental epidermis of the bud is penetrated by the hydrocaulus. In fact, the entire basal region of the new polyp is formed within the bud (Fig. 18). The distal epidermis of the bud becomes highly attenuated and (presumably) eventually ruptures at the site of the hydrocaulus (velar plate); it is reabsorbed into the epidermis above the basal collar of the new polyp. Before this happens, several aboral tentacles differentiate from parental bud tissue, followed shortly by the oral tentacles. Thus, in effect, the basal epidermis of the new hydranth is formed by the "heteromedusoid" undifferentiated cells and the upper region is formed by extension of parental differentiated cells. The source of the papillar gastrodermis is not clear, although we suspect that it is parental.

DISCUSSION

Euphysa ruthae occurs most abundantly in coarse sand that originates from high current areas and is relatively low in particulate, organic material. Usually, this sand is rich in typical interstitial fauna. Many specimens of *E. ruthae* appear at the surface of stored sediments within a few days, but there are still many that may be recovered from deep within the sediment weeks later;

TABLE I
Comparison of *Euphysa* hydroids (excluding *E. brunnea*)

	<i>E. aurata</i>	<i>E. farcta</i>	<i>E. peregrina</i>	<i>E. obvoluta</i>	<i>E. ruthae</i>
Oral tentacles					
Capitate	+	+	-	-	+
Moniliform	-	-	+	+	+
Number	3-9	6-8	10	20	3-7
Aboral tentacles					
Moniliform	+	+	+	+	+
Whorls	1	1	1	1	3
Number	6-40	8-16	14	28	4-12
Papillae	3-8	3-6	+	many	5-14
Hydranth length (mm)	4-8	5	3-4	32	0.5-1.5
Asexual buds hydrocaulus	+	+	+	?	-
Gonophores	Cluster ovoid	?	Styloid	Cluster ovoid	?
Medusae	Free	Free	Crypto-?	Crypto-	?
Hydranth buds	+	?	-	?	+

these do not appear qualitatively different from those at the surface. Thus, it appears that *E. ruthae* at least can be a facultative member of the mesopsammon. The papillae and hydrocaulus suggest that the polyp normally is well-rooted in the substratum.

Kramp (1949) included five species of hydroids in the genus *Heteractis* (Sars) which, under the unified nomenclature of hydroids and medusae (Rees, 1957), must be considered a junior homonym for *Euphysa* Forbes. In addition to *E. ruthae*, we include in the genus *Euphysa*: *E. aurata* Forbes, 1848, *E. brunnea* E. S. Russell, 1906, *E. farcta* Miles, 1937, *E. obvoluta* Kramp, 1933, and *E. peregrina* Murbach, 1899 (Table I). Although five species of *Euphysa* medusae are known (Kramp, 1961), only the hydroid of *E. aurata* is known. The remaining *Euphysa* hydroids have not been linked with any known medusae. Thus, the remaining discussion is concerned with the hydroids. Kramp (1949) believes that *E. brunnea* may be conspecific with *E. aurata*. *E. ruthae* is most similar to *E. aurata*. In particular, they share the quite unusual feature of producing reversed polarity buds on the hydranth. Although the appearance of *E. ruthae* is much like that depicted for *E. aurata* in the figures of Rees (1937, figs. 1-3; 1938, fig. 8) and Brinckmann-Voss (1970, fig. 12), some clear differences are indicated. Rees (1937, 1938) depicts a single whorl of aboral tentacles with a possible tendency to two whorls, while Brinckmann-Voss (1970) clearly shows a single whorl. Rees (1946, p. 105; 1957, p. 507) was quite aware of the potential significance of moniliform oral tentacles, but he and subsequent workers referred only to capitate oral tentacles in *E. aurata*. Because this account of *E. aurata* does not conflict with investigations of that species from western Norway (Broch, 1937), England (Rees, 1938; Werner, 1959), and the Mediterranean (Brinckmann-Voss, 1970), we may rea-

sonably suppose that *E. ruthae* is distinct in possessing moniliform, capitate oral tentacles and three alternating whorls of aboral tentacles. Further support for specific distinction of these species may be found in their cnidoms. Westblad (1947) compared the cnidoms of *Boreohydra simplex* and *E. aurata*, and reported "desmonemes," "stenoteles," and "atriches" (bastriches?) for the former and "atriches," "anisorhizes heterotriches," and "stenoteles" for *E. aurata*. Desmonemes dominate in the tentacles of *E. ruthae*; thus, their absence in *E. aurata* is quite significant. The cnidoms of the other *Euphysa* species are not known.

The cnidom of *E. ruthae* serves to further integrate *Euphysa* into the Tubularoidea, because the presence of microbasic mastigophores supports affinity with both the Corymorphidae and the Tubulariidae. Of species of Tubularoidea listed by Rees (1958), only *E. aurata* lacks desmonemes, while only one of these species is reported to have microbasic mastigophores. Rees (1958) erected the superfamily Moerisioidea for the Moerisiidae and transferred the latter from the Limnomedusae to the Athecata Capitata on the basis of "... many points of resemblance between the lower corymorphines and the Moerisiidae . . ." The greatest support is based on the close correspondence of the cnidoms and the presence of moniliform tentacles. The presence of desmonemes in *E. ruthae* offers strong corroboration for Rees' (1958) view. Although we are not aware of any account that describes nematocysts in the hydrocaulus of any "lower" corymorphids, Broch (1937) clearly figured (fig. 2c) two bacilliform nematocysts in the hydrocaular gastrodermis of *E. aurata*, but he stated that there were none in the hydrocaulus. The findings of Burnett (1960) and Burnett & Lentz (1960), which suggest that in *Hydra* nematoblasts may migrate from the gastrovascular cavity to the tentacles, should be kept in mind. However, it seems improbable that the bacilliform nematocysts of *E. ruthae* are immature. Not only were many discharged in squashes and in histological sections, they consistently have more curved and elongate capsules than do the microbasic mastigophores, the only other nematocyst of *E. ruthae* that they could possibly be related to. The two also differ in position of the nucleus. Similar gastrodermal bacilliform nematocysts are present in *E. peregrina* (unpublished observations).

Moniliform tentacles and single whorls of oral and aboral tentacles were considered to be "primitive" characteristics by Rees (1957), and he argues for the primitiveness of the euphysines within the Athecata Capitata. Thus, *E. peregrina* and *E. obvoluta* would be most plesiomorphic, or "primitive," in these features. Given the restricted taxonomic distribution of moniliform tentacles, it seems somewhat improbable that they are plesiomorphous with respect to filiform tentacles. Indeed, it is difficult to accept the postulate that the segregation of nematocysts into annuli and terminal knobs could be anything other than a derived condition. In fact, the euphysines and Moerisiidae may be more closely related than envisioned by Rees (1958, 1966). If moniliform tentacles are taken as a relatively apomorphic condition, one may, on the basis of Rees' (1958) comparisons, view these two groups as belonging to a common, terminal monophyletic taxon (perhaps they are sister groups),

as opposed to stem groups. However, the observations of Clausen (1967) suggest that there also is a tendency toward the moniliform condition among *Halammohydra* species, and these do not appear to be closely related to either group.

Basal papillae appear to be a consistent feature for species of *Euphysa*. Murbach (1899) mentioned a "... thickened collar-like portion studded with nettling organs ..." separating the hydranth from hydrocaulus in *E. peregrina*. Such a feature does not appear to occur in any other species of *Euphysa*. *Euphysa peregrina* also has scattered papillae on the hydrocaulus (unpublished observations), but we had too few sections available to determine if statocysts are present. Papillae on the upper hydrocaulus have been described from *Corymorpha* species, and Campbell (1968) demonstrated that the papillae of *Corymorpha palma* actively behave as anchoring filaments. The activity of each papilla apparently is linked to the presence of a terminal statocyst (Campbell, 1972) which is identical in structure and position to that found in *E. ruthae*. The papillae ("frustules") of *E. farcta* figured by Miles (1937) leave no doubt that these also contain identical statocysts, although he did not perceive them as statocysts. It seems reasonable that they may be found in other species of *Euphysa* and *Corymorpha* (see also *Vannucia forbesii* in Brinckmann-Voss, 1970) and, as such, form a fundamental synapomorphy for these genera. In this connection, we must note the remarkable similarity between these statocyst-bearing papillae and the basal projections (cavity diameter 15 μm) identified as gonophores in *Siphonohydra adriatica* by Salvini-Plawen (1966). Two other hydroid statocysts are known. In *Halammohydra*, they are oral to the basal tentacles (Clausen, 1967), while in *Otohydra*, they are aboral relative to the tentacles (Swedmark & Teissier, 1958). We have not encountered a description of the latter two statocysts that allows a critical comparison, but there are indications that the corymorphid form is much simpler. The medusae of this group do not have statocysts (Bouillon, 1968).

Rees (1957, p. 460) stated that in the primitive corymorphines "... there is no diaphragm in the hydranth and there are no stem canals ..." This is true for *E. ruthae*, and, among the euphysines, only *E. obvoluta*, a very large species, has multiple "stem canals." All euphysines have a hydrocaular mucoid sheath. The basal, shelf-like constriction of the hydranth in *E. ruthae* is accompanied by a relatively abrupt change in the gastrodermis, in addition to the band of nematocyst-free, specialized epidermis. However, this change in gastrodermis does not appear to be comparable to a diaphragm as, for example, in *Corymorpha nutans*.

Perhaps the most peculiar features of *E. ruthae* are the apparent conversion of a presumptive gonophore to a non-sexual bud, and the concomitant polarity reversal of this bud with respect to the parent polyp. Rees (1957) considers the bud formation of *E. aurata* to be the primitive site of gonophore formation, and it is in fact the site where euphysines and corymorphids form gonophores. The physical appearance and site of bud formation are similar in *E. aurata*

and *E. ruthae*. It would be instructive to know if the reversed buds of *E. aurata* also undergo a similar morphogenesis, even though *E. aurata* has a free medusa phase (Russell, 1953; Brinckmann-Voss, 1970). Although settlement of the hydroid planula and formation of the medusa may be interpreted to involve polarity reversal, such reversals in budding are unusual. It is quite striking to find polarity reversal of the non-sexual bud in *E. farcta* (see Miles, 1937), *E. peregrina* (see Murbach, 1899), *E. aurata* (see Brinckmann-Voss, 1970), and possibly in two species of Moerisiidae (Naumov, 1969). We are aware of only two other cases of such polarity reversal; both are forms of fission. Hand & Jones (1957) reported this behavior for an unnamed small mud-dwelling hydroid from San Francisco Bay. That hydroid had a single basal whorl of filiform tentacles. Recently, Wehling (1979) reported on an unnamed species of interstitial hydroid that undergoes paratomous transverse fission to result in three daughter polyps; e.g., two fission planes are formed, the proximal plane resulting in mirror-imaged oral ends, and the distal resulting in pedal discs. The latter species is found in the same localities as *E. ruthae* (personal observation) and is of interest here because it, too, appears to be a corymorphid, although it has only oral capitate tentacles (Wehling, personal communication). Hand & Jones (1957) mentioned the presence of a *Euphysa* sp., also having reversed hydranth buds, in San Francisco Bay.

The budding process of *E. ruthae* incorporates morphogenetic aspects of heteromedusoid gonophore formation but forms a polyp in which much of the tissue is derived directly from corresponding parental tissue. Perhaps the bi-layered structure that is formed is indeed homologous to a heteromedusoid entocodon, or it may only be analogous. Rees (1957) notes that *E. aurata* hydroids have "... polyp or hydranth buds of a distinctly actinuloid appearance . . .," as recorded here for *E. ruthae*. Although this appearance may be superficial and coincidental, in terms of the relationship between the genus *Euphysa* and the Tubularoidea, it should not be ignored, even though gametes or embryological stages have not been recognized. The inner (exumbrellar?) "heteromedusoid" layer buds cells into the "bell cavity," producing a structure rather similar, and possibly analogous to the free resting cyst of *E. aurata* described by Werner (1959). Werner (1980) also notes that the families Tubulariidae, Corymorphidae, and Margellopsidae "... exhibit direct development of the embryo into the polypoid larval actinula . . ." The similarity between *E. ruthae* buds and actinulae is made more interesting by an observation of Berrill (1952). He found that the actinula of *Paryppha crocea* (= *Tubularia crocea*) forms its mouth toward the spadix, regardless of the original polarity of the egg. Further, Van de Vyver (1980) suggests that in actinulae "... cells differentiate mainly in the peripheral layer and more precisely at the place where they will perform their specific function in the polyp . . ." (in contrast to planulae). If indeed we are observing the equivalent of an actinuloid stage, we may be witnessing a more general application of Van de Vyver's assertion; e.g., much of the incipient bud already has been provided in the form of parental tissue, and the differentiating, "heteromedusoid" primarily provides specialized cells for the basal region of the hydroid.

Alternatively, the termination of "heteromedusoid" construction, with concomitant formation of an asexual bud, may be a response to environmental conditions; e.g., medusa vs. secondary polyp formation in *Coryne tubulosa* and *Syncoryne desipiens* can be regulated by temperature (Werner, 1963). However, it appears that *E. ruthae* produces its peculiar buds independent of physical variables; the morphogenetic sequence being identical in spring and summer, and for freshly-collected or laboratory-reared specimens. The copious mucoid material, accumulated about the anlage of the basal region, is suggestive of adaptive preparation for attachment to the substratum.

Westblad (1947) faced a similar *cul-de-sac* in interpreting the gonophore of the minute, solitary hydroid *Boreohydra simplex*, which he considered to be closely related to *E. aurata*. He describes a highly modified gonophore, forming a cryptomedusoid in much the same fashion as the "heteromedusoid" of *E. ruthae*. The gonophore appears to separate from the parent before producing germ cells. Possibly, it also forms a new polyp, even though *B. simplex* also undergoes transverse fission.

Euphysa ruthae reinforces certain characters that appear to be useful in formulating hypotheses of relationship within the genus *Euphysa* and related taxa. Certainly, an affinity with the genus *Corymorpha* has been greatly strengthened on the basis of the synapomorphic nature of the papillae (rhzoids). We could not interpret the cnidom of *E. peregrina* clearly, but it does include stenoteles and possibly desmonemes, as well as bacilliform nematocysts in the hydrocaular gastrodermis (unpublished observations) to support a reasonably close relationship with the euphysines. The several marked points of similarity between the euphysine and moerisiid hydroids and medusae (Rees, 1966), including moniliform tentacles, polarity reversal, and desmonemes, are suggestive of a close (although, possibly old) relationship between the two groups. That premise calls into question the primitiveness of the moniliform condition and, concurrently, the primitiveness of separate single whorls of tentacles as envisioned by Rees (1957). The statocysts of the corymorphids clearly appear to be adaptive innovations by a particular phyletic line and they have no phylogenetic relationship to other cnidarian statocysts. Thus, one hesitates to postulate homology of statocysts found in other interstitial hydroids (an environment well known for that structure), especially when two types are in inverse positional relationship to one another with respect to tentacles (e.g., *Halammohydra* and *Otohydra*). Polarity reversal, as observed in several small solitary hydroids, and the peculiar mode of bud formation observed in *E. ruthae* (and possibly *Boreohydra simplex*) also may be indicative of particular adaptive trends, or they may in fact be divergences from the primitive conditions surrounding sex and/or actinula formation in hydrozoans.

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