1

Porifera: The Sponges

Steven Sadro

Found at all depths and latitudes, sponges are among the most ubiquitous of marine organisms. With the advent of modern laboratory and field techniques (e.g., electron microscopy, histochemistry, the development of molecular biology and biochemistry, and the use of SCUBA for collection purposes) our knowledge of sponge biology has mushroomed (see reviews by Fell, 1974; Bergquist et al., 1979). The phylum Porifera is divided into four classes, three of which occur off the coast of the Pacific Northwest. Of the three classes present locally, this chapter deals only with the classes Calcarea (Table 1) and Demospongiae (Table 2). It does not present the Hexactinellida, which are found only in deep water. Of the two classes of sponges presented here, the class Demospongiae is the larger; indeed, containing 80% of the known sponges, it is the largest of all the classes (Fell, 1974).

Reproduction and Development

Sponges differ from other invertebrates in the maintenance of an almost protozoan like independence of their constituent cells (Bergquist et al., 1979). For this reason they are considered the most primitive of the multicellular animals. They lack organs but have well-developed connective tissue in which differentiated cells perform a variety of functions.

Sponges reproduce both asexually and sexually. Asexual reproduction takes a variety of forms (e.g. fragmentation, budding, formation of direct developing gemmules, formation of pseudolarvae) (Wilson, 1902; Fell, 1974) and serves both as a dispersal mechanism and a method of survival during periods of extremely unfavorable conditions. Many features of sexual reproduction in sponges have been described in detail (Fry, 1970; Brien, 1973; Fell, 1974; Bergquist et al., 1979). Consistent with their lack of differentiated organs, sponges do not posses true gonads. Rather, a major portion of the sponge body is involved in reproduction. Generally sponges are hermaphrodites. Sexual dimorphism does not exist in sponges. Most sponges are viviparous and, consequently, the eggs are retained and fertilized internally. Some sponges are, however,

oviparous; either fertilization takes place internally with the zygote eventually being released into the sea or oocytes are released and fertilization occurs externally. Within the sponge connective tissue, eggs develop from ameobocytes and sperm develops from either ameobocytes or transformed collar cells. Spermatozoa are shed into the excurrent canals and released into the sea.

Sponge larvae are relatively uniform in their morphology. They are always ciliated, but there can be regions of longer cilia or areas that lack cilia completely. There are two general types of sponge larvae, solid parenchymella larvae and hollow amphiblastula larvae. Sizes range from 50 µm to 5 mm in length. Differential pigmentation of the posterior or anterior pole is not unusual and commonly coincides with areas lacking cilia.

The solid parenchymella larvae (also known as stereogastrula larvae) (Fig. 1A) lack an internal cavity and bear flagellated cells over their entire surface, except (often) at the posterior pole. These larvae are similar in appearance to the cnidarian planulae (see Chapter 2). Many parenchymella larvae contain spicules that are frequently arranged in a bundle near the posterior pole (calcareous spicules would be apparent under crossed polarized light; see Chapter 10, Bivalves, for technique). Larvae may lack spicules at release, but these may develop later during the free-swimming phase. The amphiblastula larvae (Fig. 1B) are hollow blastulae with one hemisphere composed of small flagellated cells and the other composed of large, nonflagellated macromeres (i.e. cruciform, macrogranular, and agranular cells) (Minchin, 1896; Lévi, 1963; Fell, 1974; Franzen, 1988). In terms of cell differentiation, parenchymella larvae can be very simple or quite complex, whereas amphiblastula larvae are typically simple. Neither has any organization, however, beyond the cellular level of differentiation. Both amphiblastula and parenchymella larvae exhibit pronounced phototaxis and geotaxis and often reverse their response to light and gravity as metamorphosis approaches (Bergquist et al., 1979).

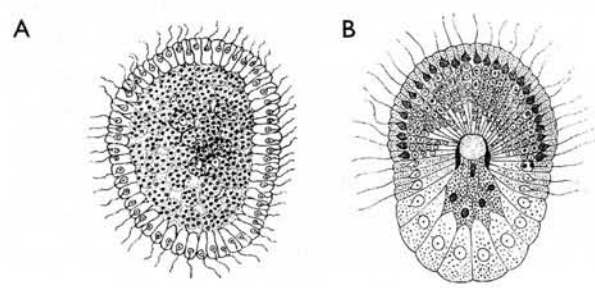

Fig. 1. Transverse sections through generalized sponge larvae. (A) Solid parenchymella larva. (B) Hollow amphiblastula larva. (A from Ruppert and Barnes, 1994; B from Minchin, 1896, Fig 3.)

Most sponge larvae spend only a brief time in the plankton, usually less than three days, before exhibiting settlement behavior. As settlement approaches, the larvae enter a short creeping stage (2–3 hours) that may be interrupted by additional periods of swimming before settlement and metamorphosis finally occur. The larvae of some Demospongiae species have no swimming period at all; they sink to the substrate after expulsion, where they creep until settlement. Some species do not release any larvae; instead, propagules are incubated within the endosome of the parent (Bergquist et al., 1979).

Identification of Local Taxa

Lacking morphological information on sponge larvae, this chapter does not attempt to serve as a taxonomic key. Rather, it compiles useful diagnostic characteristics based on information gathered from a limited number of sponge species within a limited number of orders. It is important to note that inferences are made regarding similar orders where no information is available. Identification to species is not possible from the information provided here, although identification to class and, in some cases, to order is sometimes possible. As is the case with many poorly studied larval groups, the only way to make an identification to species is to collect ripe adults and raise the larvae to the adult stage.

Relatively few characteristics are available to differentiate sponge larvae. Amphiblastula larvae are easily distinguished from parenchymella larvae based on their size (amphiblastula larvae are typically much smaller than parenchymella larvae) and their general morphology. Differentiating among amphiblastula larvae is difficult. The parenchymella larvae are morphologically more diverse and are consequently easier to distinguish. Important morphological characters include body length, distribution of cilia, cilia length, presence or absence of discrete bands of cilia (usually near the anterior or posterior pole), absence of cilia at the posterior or anterior pole, and pigmentation. Additional useful characteristics include larval phototactic and geotactic behavior and direction of rotation during swimming.

Class Calcarea

All species of the class Calcarea produce relatively small (usually <100 µm long) amphiblastula larvae. Most are simple flagellated blastulae with some nonflagellated cells at the posterior pole, but a few examples of more complex forms exist (e.g., *Granita compressa*). It is not possible to differentiate further

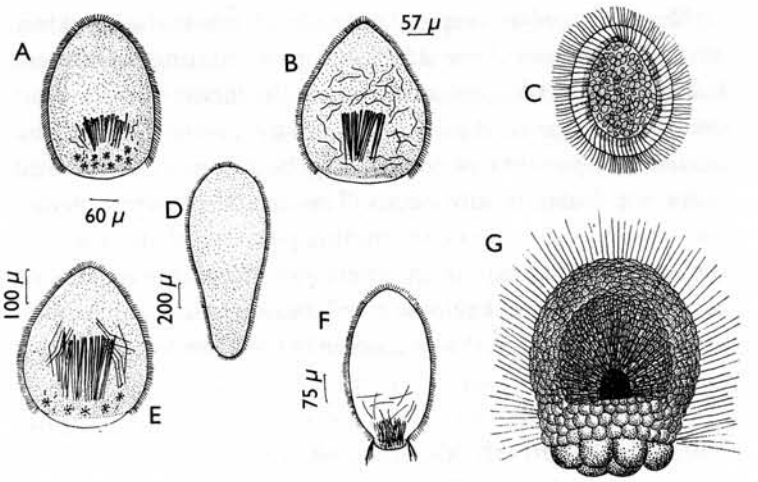

Fig. 2. Larvae from the classes Demospongiae and Calcarea. 1, 2, and 4–6 illustrate Demospongiae sponge larvae with internal spicules present. (A) ***Microciona*** *coccinea.* (B) ***Ophlitaspongia*** *seriata.* (C) Parenchymella larva of ***Clathrina***, a genera in the class Calcarea. (D) ***Halichondria*** *moorei.* (E) ***Mycale*** *macilenta.* (F) ***Haliclona*** sp. (G) Amphiblastula larva of ***Leucosolenia*** *variabilis*, a species in the class Calcarea. Genera in bold have local representatives. (A, B, D–F from Bergquist and Sinclair , 1968; C from Barnes, 1968, Fig. 4-12E; G from Minchin, 1896, Fig. 1)

among the amphiblastula larvae without specialized histological and biochemical techniques. Illustrations of typical calcareous sponge larvae are presented in Fig. 2. Table 1 lists local taxa.

Class Demospongiae

The majority of the species in the class Demospongiae produce parenchymella larvae, although some species in Clionidae and Plakinidae produce amphiblastula (Fell, 1974; Bergquist et al., 1979). Typical Demospongiae larvae are depicted in Figs. 2 and 3. Table 2 lists local taxa.

Information compiled by Bergquist et al. (1979) and others on the morphological and behavioral characteristics of the Demospongiae has been used to generate the following generalized larval descriptions, by order. Genera on which the descriptions are based are given in parentheses. Asterisks (*) indicate taxa represented locally.

Order Homoscleromorpha. *(Oscarella, Plakina*)* Larvae from two families have been described. Both possess small, uniformly ciliated and pigmented amphiblastula larvae.

Order Hadromerida. *(Polymastia*, Cliona*, Tethya*)* Larvae from three families have been described. All *Polymastia* and some *Cliona* species produce small amphiblastula larvae; all *Tethya* and most *Cliona* species produce small parenchymella larvae.

Order Dendoroceratida. *(Aplysilla*, Halisarca*)* Larvae from two families have been described, within which there is considerable variability in morphology and larval behavior. Both produce parenchymella larvae. *Aplysilla* species are uniformly ciliated, but the anterior pole can be bare of cilia and the posterior pole typically has a ring of longer cilia.

Table 1. Species in the class Calcarea from the Pacific Northwest (from Kozloff, 1996)

Subclass Calcinea
Family Clathrinidae
Clathrina blanca
Clathrina coriacea
Clathrina **sp.**

Subclass Calcaronea
Order Leucosoleniida
Family Leucosoleniidae
Leucosolenia eleanor
Leucosolenia nautilia
Leucosolenia **spp.**

Order Sycettida
Family Sycettidae
Scypha compacta
Scypha mundula
Scypha protecta
Scypha **spp.**
?Tenthrenodes **sp.**

Family Grantiidae
Grantia comoxensis
Grantia ?compressa
Leucandra heathi
Leucandra ?levis
Leucandra pyriformis
Leucandra taylori
Leucopsila stylifera
Sycandra ?utriculus

Family Amphoriscidae
Leucilla nuttingi

Halisarca species are colorless, whereas *Aplysilla* species are pigmented. Both rotate clockwise when swimming.

Order Poecilosclerida. *(Paracornulum, Coelosphaera, Ophlitaspongia*, Microciona*, Holoplocamia, Phorbas, Lissodendoryx*, Mycale*, Anchinoe, Tedania*)* Larvae from seven families have been described, all of which produce parenchymella larvae. Larvae are all of small to medium size (300–800 µm length) and ovoid in shape. They are uniformly ciliated, but in all cases there is a bare unpigmented region at the posterior pole. Only the ciliated areas are pigmented. *Lissodendoryx* species have a ring of cilia around the posterior pole. Spicules are present in larvae from all genera. All larvae have counterclockwise rotation while swimming. Only *Lissodendoryx* and *Mycale* species respond to light.

Order Haplosclerida. *(Adocia*, Haliclona*. Chalinula, Callyspongia, Reniera*, Sigmadocia*)* Larvae from three families have been described. Their larvae present a complicated assortment of morphologies and behaviors. All genera produce parenchymella larvae, but larval size ranges over an order of magnitude (length, 100–1,000 µm). In all cases, ciliated cells are unpigmented while unciliated cells are pigmented and the pigmentation is more pronounced posteriorly. There are three distinct larval types. *Reniera* species have uniform ciliation over the entire larval body. Larvae from species in the genera *Haliclona*, *Sigmadocia*, and *Adocia* possess an unciliated, pigmented posterior cap fringed by longer cilia. Larvae of *Adocia* species have a bare unpigmented anterior pole. All larvae rotate clockwise while swimming. Larvae of *Haliclona*

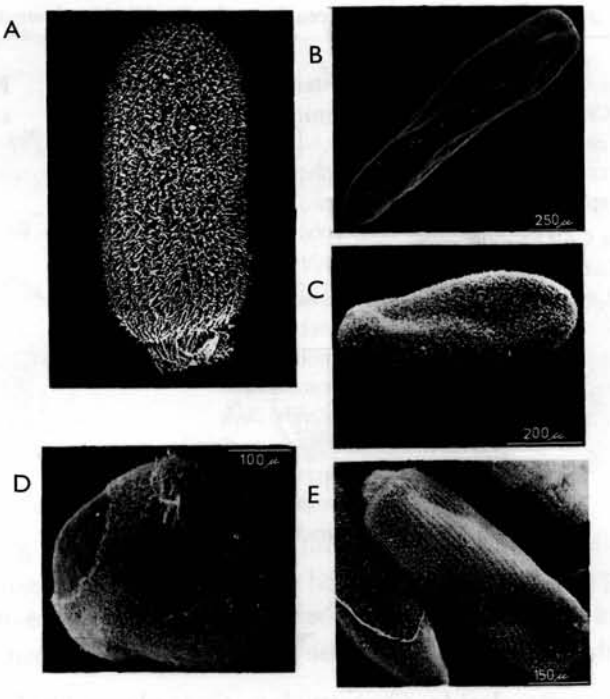

Fig. 3. Larvae from the class Demospongiae. (A) ***Halichondria*** *melanadocia*. (B) Large, uniformly ciliated crawling larvae of ***Halichondria*** sp. (C) Completely ciliated oval larvae typical of Haplosclerida with spicules. (D) Poecilosclerid larvae (*Phorbas* sp.) with uniform cilia, oval to spherical shape, and bare posterior region. (E) Larva of *Spongia* sp. (Dictyoceratida), illustrating posterior ciliary tuft, posterior bare ring, and left wound metacronal spiral. Genus in bold has local representatives. (A from Woollacott, 1990, Fig. 2; B–E from Bergquist et al., 1979)

and *Adocia* species are photopositive, larvae of *Sigmadocia* species are photonegative, and larvae of *Reniera* species show no light response.

Order Halichondriida. *(Halichondria*, Ulosa, Hymeniacidon*)* Larvae from two families have been described, and all have parenchymella larvae. Larval size ranges from 200 to 1,500 µm. There are two distinct morphologies within the order. Some *Halichondria* species are non-swimming, crawling forms. These large, elongate, posteriorly tapering larvae are usually uniformly ciliated and generally rotate counterclockwise during their crawling motion. *Halichondria* and *Hymeniacidon* species produce small, oval swimming larvae. Ciliated areas are pigments. These swimming larvae either have uniform ciliation with or without a bare posterior region or (some *Halichondria* species) complete ciliary coverage with a ring of longer cilia at the posterior pole. Swimming larvae rotate clockwise. Positive phototaxis is seen in species of *Halichondria*.

Table 2. Species in the class Demospongiae from the Pacific Northwest (from Kozloff, 1996)

Order Homoscleromorphida
Family Plakinidae
Plakina ?brachylopha
Plakina ?trilopha
Plakina **sp.**

Order Choristida
Family Stellettidae
Penares cortius
Stelletta clarella

Family Geodiidae
Geodia mesotriaena
Geodinella robusta

Family Pachastrellidae
Poecillastra rickettsi

Order Spirophorida
Family Tetillidae
Craniella spinosa
Craniella villosa

Order Hadromerida
Family Suberitidae
Laxosuberites **sp.**
Prosuberites **sp.**
Pseudosuberites **spp.**
Suberites montiniger
Suberites simplex
Suberites ?suberea
Suberites **sp.**

Family Polymastiidae
Polymastia pacifica
Polymastia pachymastia
Weberella ?verrucosa

Family Clionidae
Cliona ?argus
Cliona ?celata
Cliona lobatta
Cliona ?warreni
Cliona **sp.**

Family Tethidae
Tethya californiana

Family Latrunculiidae
Latrunculia **sp.**

Order Axinellida
Family Axinellidae
Axinella **sp.**
Phakettia ?beringensis
Pseudaxinella ?rosacea
Stylissa stipitata
Syringella amphispicula

Family Desmoxyidae
?Higginsia **sp.**

Family Raspailiidae
Hemectyon hyle

Order Halichondriida
Family Halichondriidae
Ciocalyptus penicillus
Eumastia sitiens
Halichondria bowerbanki
Halichondria panicea
Halochondria **spp.**
Topsentia disparilis
Hymeniacidon ?perleve
Hymeniacidon sinapium
Hymeniacidon ungodon
?Hymeniacidon **sp.**
Prianos problematicus
Stylinos **sp.**

Order Poecilosclerida
Family Mycalidae
Mycale adhaerens
Mycale bamfieldense
Mycale bellabellensis
Mycale hispida
Mycale macginitiei
Mycale richardsoni
Mycale ?toporoki
Mycalecarmia lobata
Paresperella psila

Family Hamacanthidae
Zygherpe hyaloderma

Family Cladorhizidae
Asbestopluma occidentalis

Family Biemnidae
Biemna rhadia

Family Esperiopsidae
Neoesperiopsis digitata
Neoesperiopsis infundibula
Neoesperiopsis rigida
Neoesperiopsis vancouverensis

Family Myxillidae
Acarnus erithacus
Ectyomyxilla parasitica
Forcepia ?japonica
Hymendecyon lyoni
Iophon chelifer
Iophon piceus
Jones amaknakensis
Lissodendoryx firma
Lissodendoryx **sp.**
Merriamum oxeota
Myxilla behringensis
Myxilla lacunosa
Stelodoryx alaskensis

Family Tedaniidae
Tedania fragilis
Tedania gurjanovae
?Tedanione obscurata

Family Hymedesmiidae
Anaata brepha
Anaata spongigartina
Arndtanchora **sp.**
Hymedesanisochela rayae
Hymenamphiastra cyanocrypta
Hymedesmio **spp.**
?Hymenanchora **sp.**
?Stylopus arndti

Family Anchinoidae
Podotuberculum hoffmanni
Hamigera ?lundbecki

Family Clathriidae
Axocielita originalis
?Dictyociona asodes
Microciona microjoanna
Microciona prolifera
Microciona primitiva
Ophlitaspongia pennata
Thalysias laevigata

Family Plocamiidae
Anthoarcuata graceae
Plocamia karykina
Plocamilla illgi
Plocamilla lambei
Stelotrochota hartmani

Order Haplosclerida
Family Haliclonidae
?Adocia **spp.**
Adocia gellindra
Haliclona ?ecbasis
Haliclona ?permollis
Orina **sp.**
Pachychalina **spp.**
Reniera mollis
Sigmadocia edaphus
Sigmadocia **spp.**
Toxidocia **spp.**

Order Petrosiida
Family Petrosiidae
Xestospongia trindanea
Xestospongia vanilla

Family Dysideidae
Dysidea fragilis
Spongionella **sp.**

table continues

Table 2. Species in the class Demospongiae from the Pacific Northwest (continued)

Order Dendroceratida
Family Aplysillidae
Aplysilla ?glacialis
Chelonaplysilla polygraphis
Pleraplysilla **sp.**

Family Halisarcidae
Halisarca sacra

Order Verongiida
Family Verongiidae
Hexadella **sp.**

Undetermined Family
Psammopemma **sp.**

References

Barnes, R. D. (1968). Invertebrate Zoology, 2nd Edition. W. B. Saunders Co., Philadelphia.

Bergquist, P. R. and M. E. Sinclair (1968). The morphology and behaviour of larvae of some intertidal sponges. N. Z. J. Mar. Freshwater Res. 2:426–37.

Bergquist, P. R., M. E. Sinclair, C. R. Green, et al. (1979). Comparative morphology and behavior of larvae of Demospongiae. In: Colloques Internationaux du C.N.R.S. N° 291—Biologie des spongiaires, C. Levi and N. Boury-Esnault (eds.), pp. 103–11.

Brien, P. (1973). Les demosponges. Morphologie et reproduction. In: Traite de Zoologie 3:P.-P. Grassé (ed.), pp 133–461. Masson et Cie, Paris.

Fell, P. E. (1974). Porifera. In: Reproduction of Marine Invertebrates, A. C. Giese and J. S. Pearse (eds.). Academic Press, New York.

Franzen, W. (1988). Oogenesis and larval development of *Scypha ciliata*. Zoomorph. 349–57.

Fry, W. G. (1970). The biology of the Porifera. In: The Biology of the Porifera, W. G. Fry (ed.). Symp. Zool. Soc. Lond. Academic Press, London, New York.

Kozloff, E. N. (1996). Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle.

Lévi, C. (1963). Gastrulation and larval phylogeny in sponges. In: The Lower Metazoa, Comparative Biology and Phylogeny, E. C. Dougherty (ed.), pp. 375–82. University of California Press, Berkeley and Los Angeles.

Minchin, E. A. (1896). Note on the larva and the post larval development *Leucosolenia variabilis* n. sp. with remarks on the development of other Asconidae. Proc. Roy. Soc. London 60:42–52.

Ruppert, E. E. and R. D. Barnes (1994). Invertebrate Zoology. Saunders College Publishing, New York.

Wilson, H. V. (1902). On the asexual origin of the sponge larvae. Amer. Natur. 36:451–59.

Woollacott, R. M. (1990). Structure and swimming behavior of the larvae of *Halichondria melanadocia* (Porifera : Demospongiae). J. Morph. 205:135–45.