Reproduction, Development and Phylogeny of Siphonophora

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INTRODUCTION

From a review of literature it is seen that the nineteenth century had been an era of active systematic studies on the various groups of animals and speculations (theories) on their organization, relationships and phylogeny. The morphological and physiological peculiarities which distinguish the Siphonophora from other Cnidaria (Coelenterata) have led to various theories as to the real nature and import of their organization. Of these the older "Poly-Organ" theory considered the adult organization of all siphonophora to be a simple "medusa - like animal" which is distinguished from the typical medusae only in the multiplication and differentiation of its polymorphic "organs", the individuals remaining basically a Hydromedusa (Eschscholtz, 1829; Huxley, 1859; Muller, 1871, Metschnikoff, 1874).

In contrast, the "poly-person" theory considered the adult Siphonophora organization to be a colony of animals, composed of many polyp-like individuals ("Persons") which according to the laws of the division of labour have undergone various modifications both in the way of specialisation and reduction, the colony remaining basically a Hydropolyp (Vogt, 1854; Leuckart, 1851, 1854; Kolliker, 1853; Gengenbaur, 1854; Claus, 1863, 1878; Chun, 1882, 1897; Schneider, 1898).

A new theory - "Medusome theory" - based on the comparative anatomy and ontogeny was postulated by Haeckel (1888), which according to him, incorporated the truths in the two views given above and eliminated their errors. According to this theory the primitive larva which arises directly from the gastrula of the Siphonophora is a simple medusa with two distinct forms - the *Disconula* larva giving rise to the radially symmetrical Chondrophora and the *Siphonula* larva giving rise to the bilaterally symmetrical Siphonophora. The *Siphonula* larva by unilateral budding from the stomach wall of manubrium give rise to either medusiform persons or special organs of the same *i. e.*, all the zooids of the Siphonophore colony were interpreted as dislocated parts of so many dismembered medusoid buds of a proliferating Anthomedusa (Haeckel, 1869, 1888; Metschnikoff, 1874; Balfour, 1885; Moser, 1925).

Even though these theories were based on the comparative morphological and some developmental studies of various species of Siphonophora, more detailed studies of the early embryological and larval development were needed. After more than three decades of intensive study of this group Totton (1965) had put forward the "Paedophore" theory as to the organization of Siphonophora. According to this theory, a fully grown Siphonophore is essentially an overgrown oozooid polyp that remains juvenile and asexual (larva 1) nurse - carrier (-paedophore-) of large number of other

unseparated asexual juvenile polyps the gastrozooids, palpons and bracts as well as sexual adults the medusoid gonophores and asexual adults - the medusoid nectophores - all budded from the original and often much elongated oozooid or from other juveniles. The sexual adult medusoid gonophores usually separate from this permanent larval stage and lead a short independent life until their germ cells ova and sperms are shed.

These controversial theories on the organization, origin of various polymorphic structures, phylogeny and the arrangement of the different taxa within the group can be proved or disproved and understood clearly only by means of detailed study of the embryology and early larval development of many species of Siphonophora.

Reproduction and Development

Gonads in Siphonophora are just aggregates of sex-cells produced on the manubrium of special medusoid structures - the gonophores. A single gonophore is of one sex only, even though both sexes may occur in any cormidium. Usually the Siphonophores are hermaphroditic except *Physalia physalis* which is unisexual. In Cystonectae the highly branched gonodendra occur at the bases of reduced gastrozooids - the palpons. The gonophores are sessile, highly reduced into sporosacs (styloid type). In the physonectae the gonophores are borne on highly reduced blastostyles and occur at the bases of palpons. The gonophore are small but with well developed medusae (codonid type). In Calycophorae the older cormidia are freed as eudoxids which consists of a protective bract covering the gastrozooid, its tentacle, gonophores and at times special nectophores. The first budded gonophore of an eudoxid may be of one sex and the second one may be of the other sex. The gonophores are usually freed from the eudoxids as

Fig 1. Gonophores of some Siphonophora. Figs. 1-3 *Physalia physalis* 1. male gonophores, 2. female gonophores, 3. Enlarged figure of female gonophore showing ova. Figs. 4-6. *Rhizophysa filiformis*. 4-male gonophores; 5-female gonophores; 6-enlargement of figure 5. showing ribbons of ova; *Halistemma* rubrum. Fig. 7. male gonophore and sperm Fig. 8. female gonodendron. Fig. 9. *Agalma elegans* stem showing male (on the left) and female (on right) gonophores. Fig. 10. *Diphyes dispar* female gonophores. Fig. 11. *Hippopodius hippopus* female and male gonophores, occurring together near gastrozooid. Fig. 12. *Eudoxia macra* female eudoxid phase Fig. 13. *Abyla* sp. male gonophore. Fig. 14. *Enneagonum hyalinum* female gonophore.

Fig 2. Development of Siphonophora: Figs. 1-10 development of *Nanomia cara* Figs. 11-12, 16 & 17. planula with bud of larval / definitive nectophores of *Sulculeolaria quadrivalvis* Figs. 13-15. formation of pneumatophore by invagination of *Agalma elegans* Fig. 18. larval bract of *Sphaeronectes* sp. Figs. 19-24. Development of *Abylopsis tetragona*, Fig. 25. Development of larval bract of *A. elegans*.

Legends:

an   —   anterior nectophore
dn   —   definitive nectophore
end   —   endoderm
l br   —   larval bract
l n   —   larval nectophore
n   —   nectophore
pgz   —   primary gastrozooid
t   —   tentacle

1

2

3

4

·5mm

5

6

·2mm

7

8

9

·2mm

10

11

4mm

12

13

1mm

14

2mm
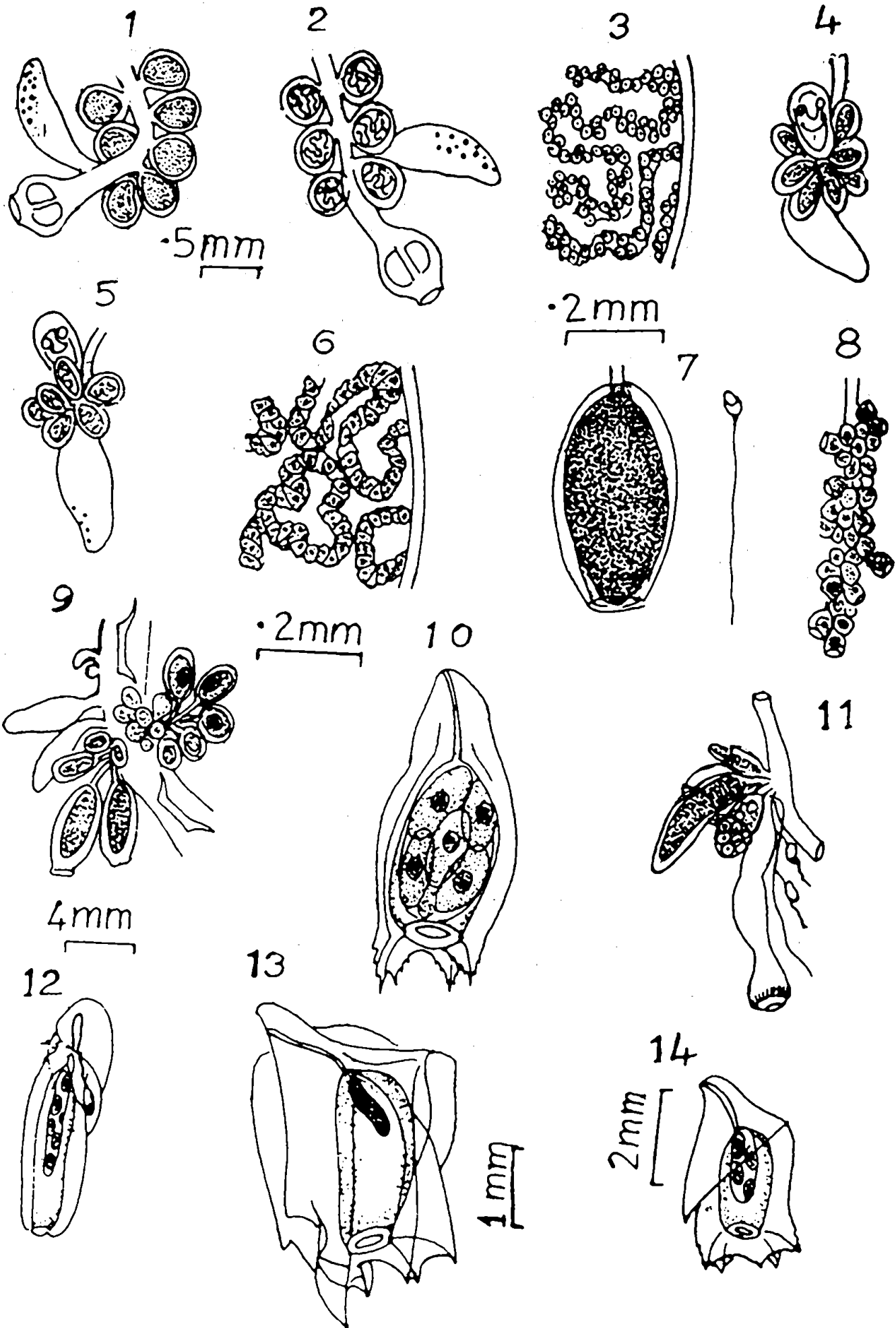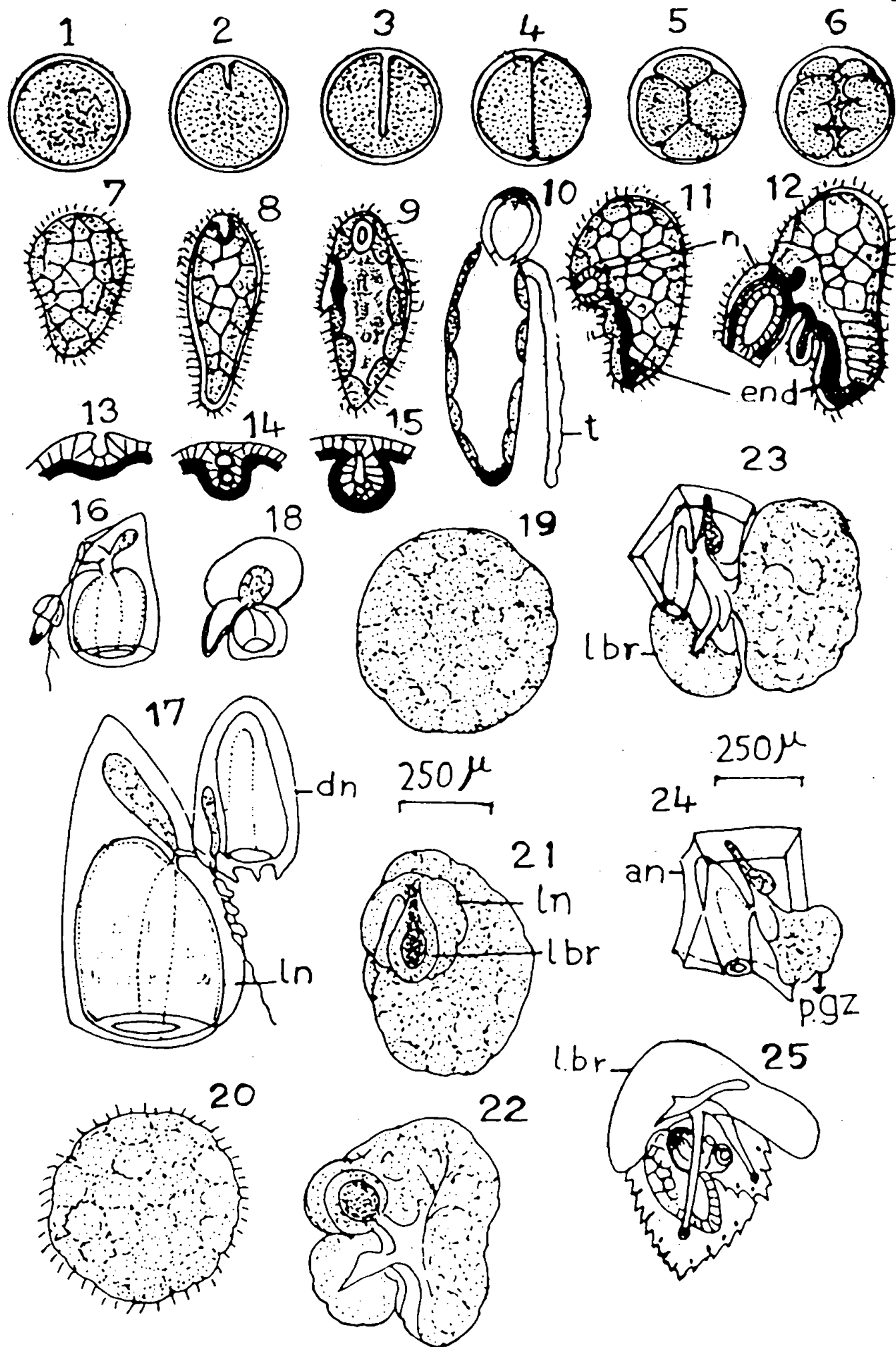
sexually mature adults which after shedding the ova and sperm die off because the manubria bearing them are without mouth-opening and are therefore incapable of feeding. In Cystonectae the individual reduced gonophores do not become free but the whole or terminal part of the complexly branched gonodendra break away and keep floating due to the pulsating movement of the asexual nectophores.

Totton (1965) was able to observe a mature male gonophore of a diphyid emitting a continuous jet-stream of sperm into the water until the manubrium shrank to a vestige. There are no detailed description or figure of the spermatozoa or their maturation in any species of Siphonophora. Vogt (1854) was able to figure only the head of the sperm of *Halistemma.rubrum* and Totton was able to observe a complete sperm of the same species with a tail fifteen times as long as the head.

The Siphonophore eggs vary from 0.4 mm - 0.6 mm in diameter, usually spherical (or oval or tetragonal in shape while immature) transparent to translucent and contain a large quantity of buoyant sap or yolk. The eggs of *Nanomia vara* are so transparent that they are almost invisible in water. The mass of protoplasm within form a net-work (Fewkes, 1886/88). In Cystonects - *Physalia* and *Rhizophysa* the small numerous eggs are borne on a winding ribbon - like structure on the surface of the female gonophore (gynophore). In physonectae each gynophore produces a single large ovum on the manubrium. In Calycophorae the sexually matured eudoxid phases produce as many as four to sixteen ova in the manubrium of usually well - developed gonophores. Fertilization (probably) and development take place in the water after the germ cells are shed.

Development

The embryology of a very few species and the post-embryo larval development of many species of Siphonophora are known and they are dealt under each sub-order (See Figures in Plates 1 & 2).

I. Sub-Order Cystonectae : Nothing is known about the development of the species of Bathyphysa and Rhizophysa and the early embryology of *Physalia*. Early development of *Physalia physalis* probably takes place in the depths. The earliest known larva - the 'cystonula' which comes to the surface-after the development of the float, primary gastrozooid, its tentacle and a few small buds of secondary gastrozooids on the ventral line and its further development have been studied in detail (Delage & Herouard, 1901; Okada 1932; Totton, 1954, 1960, 1965).

II. Sub order physonectae : The early embryological and/or the larval development of quite a number of physonects are known so far : *Agalma elegans* (Fewkes, 1880, 1885; Metschnikoff, 1874; Woltereck, 1905; Totton, 1932, 1954, 1956, 1965); *Nanomia cara* (Fewkes, 1886/88); *Nanomia bijuga* (Metschnikoff, 1874; Chun, 1897 a; Totton, 1954; 1965); *Halistemma rubrum* (Metschnikoff, 1874; Woltereck, 1905); *Physophora hydrostatica* (Totton, 1954, 1965) *Agalma okeni* (Totton 1965) and *Athorybia rosacea* (Haeckel, 1869.)

Fewkes observed the eggs of *Nanomia cara* to be highly transparent, colourless and almost invisible in water and their interior filled with a spongy net-work of pro-

toplasm and a thin covering of protoplasm around it. The first primary cleavage furrow is formed by the bending in of the outer wall of the egg at one pole. In one hour's time this furrow deepens and the two-cell stage is reached. In about another hour the second cleavage plane is formed and a well marked four cell stage is developed. In *Agalma*, Fewkes has noted a peculiar warping of the first cleavage plane by the formation of the second. It was seen that by the growth of the second cleavage furrow at right angles to the first, it was brought about in such a way that the plane of the first cleavage was broken near the equator of the egg. In the same manner, in the division of the *Nanomia* egg, the second cleavage plane is so formed that the continuity of the first plane is like-wise broken. The eight - cell stage is produced by the formation of two new furrows bending in on one side of those cells already formed as in *Agalma*. The eggs of *Halistemma rubrum* are so large that the segmentation stages can be followed without the aid of a lens (Metschnikoff, 1874). Finally the primary morula is formed.

Gastrulation . In many species no distinction can be drawn between the embryo and the larva in the shape and size. For examples the larger and yolkier larvae of *Agalma* spp. and *Athorybia* retain their spherical form of the egg long after the first larval buds are formed. In all cases these buds make their appearance long before the endoderm has completed its de-lamination from the yolky cells of the primary morula. The germ-layers are formed along a particular meridian - 'ventral' - and then extend to right and left, first the ectoderm, then the endoderm more slowly until gradually the whole surface of the yolk is covered. In minor details these changes vary in different species. There is a tendency towards the acceleration of the process aborally, but the region opposite the meridian is the last to be differentiated. The region of the meridian is the side of precocious budding - *i.e.*, the precocity of budding takes place in the patch of the embryo where the two germ layers (diploblastic) are formed first, while the rest of the body is solid with yolk. Further, this precocious budding takes place long before the larva exhibits the typical features of an actinula larva. Therefore, it appears that the slow bilateral course of gastrulation, combined with the precocity of budding, is the main reason for the unilateral 'budding line' and the bilateral symmetry of the Siphonophora.

Planula larva May be spherical or slightly oval in shape. It is solid, its interior being filled with yolk filled cells usually referred to as the primary endoderm. The end of the larva where the future float develops is the aboral pole and the opposite end where the future primary mouth opening of the protozooid is formed is the oral end. The larva is covered with cilia and is capable of locomotion. After the development of various buds on the ventral line, the larva is termed as 'Siphonula' or more correctly as 'physonula' (c.f., Totton 1965, p. 17 - foot note).

I. FLOAT OR PNEUMATOPHORE : For years until recent times the float was regarded as the homologue of a nectophore (nectocalyx - Medusa) (Schneider, 1896; Chun, 1897 a; Moser, 1925). This was disproved when the development of the float and the nectophores in physonects and calycophore was studied. In the physonects the float is apical and is formed at first as a shallow open invagination of ectoderm which later closes as in *Nanomia* and *Halistemma* (Chun, 1897 a; Woltereck, 1905). Therefore, there is nothing in the early rudiment of the float to point specifically to a medusoid origin (Garstang, 1946).

2. BRACT OR HYDROPHYLLUM The origin and nature of the characteristic appendages - the bracts in Siphonophora has been under much dispute as to its polypoid or medusoid nature (Haeckel, 1888. Moser, 1925, Hyman, 1940, Garstang, 1946). According to Haeckel they were considered as the split and isolated umbrella of ancestral medusae in some cases (*e.g.* larval bract of *Physophora hydrostatica* and in others as the simply elongated and degraded (reduced) nectophores ('athorybia' larva of *Agalma elegans* with supposedly reduced nectophores, at the tips of the coronal bracts). However, recent workers disproved the existence of supposedly reduced nectosacs, in larval bracts and proved their polypoid nature after developmental studies.

The larval bract in *Physophora hydrostatica, Agalma elegans* and *Athorybia rosacea* arises very early even before the pneumatophore develops. It is smooth, dome shaped, gelatinous, sub-apical in position and covers the float. It grows larger due to the accumulation of mesoglea and serves to float the larva. This larval bract falls off after the nectophore becomes larger and functional. In *Halistemma rubrum* the nectophore develops earlier and the larval bract fails to appear (Metschnikoff, 1874) or has a precarious existence (Woltereck, 1905).

Gastrozooid and its tentacle The basal half of the planula after gastrulation by de-lamination, absorption of the yolk-filled cells and the formation of the endoderm along the 'ventral line', develops the primary gastral cavity. On the ventral side, the bud of the developing filament - tentacle is formed very early and elongates as it grows. The nematoblast or cnidoblasts develop at the basal region of this protozooid (Primary gastro-zooid).

III. Sub order Calycophorae : Embryological and the larval stages in the development of few Calycophorae are known : a species of Paryid (Delage & Herouard, 1901 - cf. Leloup, 1954); *Hippopodius hippoups* (Chun, 1897 a, Totton, 1954); *Muggiaea kochi* (Chun, 1882); *Muggiaca atlantica* (Russel, 1938); *Sulculeolaria quadrivalvis* (Metschnikoff, 1874; Lockmann, 1914); *Sphaeronectes gracilis* (Metschnikoff, 1874); *Abylopsis tetragona* (Carre, 1967) and *Chelophyes appendiculata* (Totton, 1965). The larva of a Calycophore is known as *Calyconula*.

A detailed and clear description of the development of *Abylopsis tetragona* from the egg stage onwards has been given by Carre (1967). Development of most of of the species of Calycophorae are known only from the planula stage onwards.

Development of Abylopsis tetragona

The egg of *Abylopsis tetragona* is relatively large being 500 μ in diameter, transparent, and orange in colour. The cortical region of the cytoplasm is granular, while the cytoplasm in the interior is vacuolar, reticulate and rich in yolk. The large nucleus is eccentric in position.

Segmentation and gastrulation Egg cleavage starts shortly after fertilization. The cleavage is complete, almost equal and of the radial type. After some hours the morula stage is reached. It is spherical, measures 500 μ in diameter and is formed by a mass of compact identical cells. The gastrulation is accomplished by secondary de-lamination and form the secondary endoderm.

Planula.   By the rearrangement of cells the spherical gastrula is transformed into an ovoid young planula. The peripheral cells bear cilia and are rich in phloxinophilic cytoplasmic granules and constitute the ectoderm. The ectoderm surround other cells which are vacuolated and rich with yolk. These cells are referred to as the primary endoderm which disappear later.

The larva assumes a pyriform shape and the two poles anterior and the posterior are distinguished on the face of the planula. Large opaque orange coloured material occur in cells. The ventral face differentiates into two raised patches ('Couches' -Carre, 1976, p. 187).

Calyconula   The two days old planula starts budding primary structures on the ventral zone and develops into the typical larva of the calycophorae called *Calyconula*. On the median ventral line the germ layers ectoderm and endoderm are formed. The bud of the larval bract is formed at first and as it is developing the larval nectophore is formed right in front of it. A cavity lined by endoderm is formed within the bud of the nectophore (somatocyst) and a similar cavity or canal lined by endoderm extend into the rounded larval bract (Phyllocyst). These two structures grow large due to the formation of mesoglea. The mesoglea in the bract helps the larva to float. The yolk filled primary endoderm acts as the yolk-sac until all the yolk is used up by the developing larva. The primary endoderm encloses the cavity of the primary gastozooid. This endoderm in the larval nectophore forms the somatocyst and the radial canals arising from its base run along the sub umbrella of the nectophore and join the ring-canal around the ostium. To begin with, the larval nectophore has a rounded appearance and as it grows larger the adult prismatic facets are formed. As the nectophore becomes functional with the development of the velum, the larval bract drops off. The shrunken part of the yolk-filled endoderm covered with ectoderm comes to lie within the hydroecium of the nectophore and becomes the primary gastrozooid. This larval nectophore persists in the adult as the anterior nectophore and therefore it is not caducous as in those species of the families Prayidae and Diphyidae.

In the formation of the larval bract in *Abylopsis tetragona* resembles the species of physonects and *Sphaeronectes* spp. During the differentiation of the larval nectophore there appears a medusal nodule which is typical during medusal budding of hydroid polyps (Carre, 1976, p. 192).

The development of other species of Calycophorae is known from the planula stage onwards and agrees with the main features the development of the planula of *A. tetragona*. In all these Calycophores the aboral extremity of the planula larva atrophies so that the pneumatophore of the cystonects and physonects has no homologue in this group, medusoid or otherwise. The primary nectophore is developed as a ventral bud which secondarily assumes a sub-apical position. The aboral region of the larval body remains stuffed with yolk during the critical stages of development, and is finally absorbed as the larva grows large (as in *Muggiaea kochi* & *M. atlantica, Sulculeolaria quadrivalvis Chelophyes appendiculata*).

As observed in the species of *Muggiaea, Chelophyes, Sulculeolaria* and probably in species of *Rosacea* and *Sphaeronectes* sp. (Metschnikoff, 1874; Schneider, 1896; Chun, 1882; Russell, 1938 and Totton, 1965 and in the review of literature by Garstang, 1946) the primary nectophore (i.e., the larval nectophore) in the possession of a soma-

tocyst (which is equivalent to the phyaocyst)*and in its great gelations nature prove that it is really a compound structure formed by the fusion of bract and nectophore. It is further seen that the somatocyst develops from a small gastral-cavity of the young planula close to the base of the larval nectophore, between the latter and the apical pole, exactly where the cap-shaped bract of a larval physonect takes its origin. The endodermal origin and the identity of the two structures were subsequently recognized by Woltereck (1905), Moser (1925), Garstang (1946), Totton (1965) and Carre (1967). In almost all the species of the families of Calycophorae except in Abylidae and Sphaeronectidae this primary nectophore is shed and a new definitive nectophore is developed from the stalk of the somatocyst. In the Abylidae the larval bract is caducous and does not fuse with the larval nectophore which persists as the anterior nectophore in the adult. While in *Sphaeronectes* the larval bract, fuses with the larval nectophore and persists throughout life.

CONCLUSION

The importance of developmental studies is seen in the changes that have been brought in the classification of Siphonophora, origin of the various zooids and theories on organization.

The suborder Chondrophore (*porpita, Velella* and *Porpema*) was removed from the Order Siphonophora since their origin and development differed entirely from the latter.

The previous arrangement of the various families within the order followed by Eschscholtz (1829), Chun (1888), Haeckel (1888), Lens & Van Riemsdijk (1908) and Bigelow (1911) was considered not valid (Tooton 1954, 1965; Daniel 1974). Therefore, the sub orders were rearranged placing the passively floating Siphonophores - the Cystonectae with large pneumatophore (float) but without nectophores as the most primitive and then the physonectae with small pneumatophore and nectophores and lastly the actively swimming Calycophorae which have undergone the most radical changes. It is considered that the atrophy of the aboral extremity of the Calycophore larval body may imply the previous possession of an aboral float, which has been discarded in favour of a precocious nectophore. Further, arrangement of species within a family was also changed as in the case of species with one nectophore - Sphaeronectes (Family Sphaeronectidae) considered as the most primitive among the Calycophorae is transferred and put between families Clausophyidae and Abylidae after the significance of its development was understood more clearly.

Medusoid origin of pneumatophore and bract is disproved, the former forming as a simple invagination lacking the characteristic presence of entocodon ("Glockenkern") found in the developing nectophore (medusa) and the latter forming as an evagination like those of polyps.

Older theories on organization of Siphonophora have become obsolete. According to the latest theory (paedophore hypothesis by Totton, 1960, 1965) the Siphonophora arose during a comparatively recent radiation, after the new type of neotenic organism-the actinula. The fully grown asexual polyp never becomes an adult (the sexual medusa) but gives rise to it by budding. The reverse phenomenon is usually not seen in the Hydroids *i.e.*, a medusa rarely or never truly gives rise by budding to a polyp, which always develops from an egg or from another polyp showing the polyp's larval character.

Nothing is known, in spite of all the morphological and developmental studies, t tne gametogenesis, chromosomes, physiology, neurosecretion, and genetics in Sipphora which is often considered to be a large ·interbreeding population (Totton,

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