FORMS OF ANIMAL LIFE

G. ROLLESTON AND W. H. JACKSON

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A MANUAL OF COMPARATIVE ANATOMY

WITH DESCRIPTIONS OF SELECTED TYPES

BY THE LATE

GEORGE ROLLESTON, D.M., F.R.S.

LINACRE PROFESSOR OF ANATOMY AND PHYSIOLOGY

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REVISED AND ENLARGED BY

W. HATCHETT JACKSON, M.A.

NEW COLLEGE

F.L.S.; NATURAL SCIENCE LECTURER, ST. JOHN'S COLLEGE

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The *Siphonophora*, the third order of *Craspedota*, are pelagic and colonial. The various parts which may enter into the composition of a colony[1] are as follows. (1) The polypite or gastrozooid, universally present, usually attached to the coenosarc of the colony by a longer or shorter pedicle, and consisting of three regions, a basal with thickened ciliated ectoderm containing cnidoblasts, a central somewhat dilated, and a terminal oral ciliated portion, extremely changeable in shape. Cnidoblasts are to be found round the mouth. The endoderm cells are vacuolate, and those of the middle region are pigmented, produced into longitudinal ridges[2] or villiform processes. (2) *Hydrocysts* or *feelers* (=Taster of German writers), absent in *Calycophoridae* and *Discoideae*. These structures are polypites in which the distal or oral extremity is imperforate and usually armed with cnidoblasts[3]. The pedicle is absent or short, and the three regions (*supra*) are not differentiated, no trace of the basal ectodermic thickening being even discernible. The endoderm is vacuolate and rarely elevated into ridges (*Apolemia*). The hydrocysts are represented in the *Discoideae* by small zooids (blastostyles) with mouths. (3) *Tentacles*. These structures in the *Discoideae* are simple and tubular; in *Porpita* dilated terminally and provided with a number of short capitate processes. The large tentacles of *Physalia* attain sometimes the length of many feet. Each tentacle, whether large or small, consists of a conical hollow sac (? = hydrocyst) covered with cnidoblasts, a long hollow filament attached to the base of the sac but connected by a membranous expansion with its side. The first section of the filament is coiled from side to side, but the greater portion of it hangs freely. One of its aspects is covered with transverse hollow reniform elevations in which cnidoblasts are aggregated. The tentacles of other *Siphonophora* are, with the partial exception of *Athorybia* and *Abyla*, attached to the pedicles of the polypites, on a special elevation of ciliated ectoderm containing cnidoblasts, from which new 'nettle batteries' are derived in growth. They are branched except in *Apolemia*, and each branch terminates in a single nettle battery, the structure of which is often extremely complicated and characteristic of a genus, or even species. The tentacles of the hydrocysts are unbranched. (4) The sexual zooids or gonozooids are medusiform. In the *Discoideae* they are medusae, and are borne in numbers upon blastostyles (gonoblastidia) which are disposed in a

[1] See p. 775, *post*, on the character of the colony.

[2] They are due to the contraction of endodermal circular muscles.

[3] An opening is present at the apex of the hydrocyst of *Halistemma tergestinum* (*pictum*) and of *Physalia* (?). So too in a young *Agalmopsis* (*Agalma*) *Sarsii*, where it afterwards closes. The apex of the hydrocyst is pigmented, and it has been observed that irritation of the animal in *Forskalia* causes this pigment to be shed into the water, giving the latter an opaque and red tint. The contained fluid is highly albuminous and dense, and probably serves to keep the walls of the hydrocyst tense, and thus render it more sensitive (Korotneff). Hydrocysts occur among the nectocalyces in *Apolemia* but not in other *Siphonophora*.

zone round the large central gastrozooid. The medusa of *Velella* is known as *Chrysomitra striata*; it is a quarter of an inch in diameter, has a single tentacle, and its generative products are developed in four groups on the manubrium as in *Anthomedusae*[1]. The female zooid of *Physalia* is probably detached as a medusa. In all other instances the zooid is a medusoid: it has typically four radial canals, a circumferential canal, and an imperforate manubrium or spadix which bears the sexual products. The *Calycophoridae* have many ova, the *Physophoridae*[2] a single ovum. The spadix in the latter grows round the ovum, and its cavity becomes reduced to a system of branched canals, sometimes confounded with the radial canals. A velum is present in the sexual zooid of the Diphyozooid (p. 773) but not in other instances[3]. In the Calycophorids *Hippopodius* and *Epibulia* (= *Galeolaria*) and in *Physophoridae*, the bell itself consists only of three layers, an endodermal lamella bounded by two ectodermal, an outer and inner, and the bell cavity is small. The zooids are numerous in *Physalia*, *Physophoridae*, and the Calycophorid *Hippopodidae*, developed in grape-like bunches on the pedicle, or as in *Physalia* and *Physophora* extending up the sides, of the hydrocysts, male and female in connection with the same hydrocyst, or as in *Agalma rubrum* with different hydrocysts. In the *Diphyidae* they are developed successively one after another on the pedicles of the polypites. The zooids, male and female, are detached in *Hippopodius* and *Epibulia*, or the male only is so, e.g. in *Physophora*, *Halistemma*, *Forskalia*, swimming by means of the cilia covering the bell. The sexual zooid in a Diphyozooid discharges the sexual products, and is detached when its successor is ready to replace it. The colonies are usually hermaphrodite. *Abyla pentagona* and some species of *Diphyes*, however, are of separate sexes. (5) The *hydrophyllia* or *bracts* (=Deckstücke), absent in *Discoideae*, *Physalia* and *Hippopodidae*, are protective zooids of a leaf-like character but of various shapes, attached by a short pedicle either to the coenosarc (*Physophoridae*) or to the pedicles of the polypites (*Calycophoridae*). They consist of a lamina of mesoglaea covered by ectoderm, in which cnidoblasts are frequently to be found at the apex or projecting angles of the hydrophyllium. They contain a central endodermic canal from which, as in *Crystallodes* (*Agalma*) *rigidum*, a process may extend to the lateral angles. (6) *Nectocalyces* absent in *Discoideae*, *Physalia*, *Athorybia*, and *Rhizophysa*. They resemble a craspedote Medusa with four radial canals, *minus* a manubrium, mouth and tentacles[4]. (7) The *pneumatophore* or *float*, an air-

[1] But see Metschnikoff, 'Medusologische Mittheilungen,' Arb. Zool. Inst. Wien, vi. p. 238 (p. 2 of paper). The female, according to him, only brings one ovum to maturity.

[2] This term is used in the text to denote the sub-order, not the family.

[3] Chun's genus *Lilyopsis* is no exception to this statement, for the groups of zooids are not detached; see note, p. 773, and SB. Akad. Berlin, 1886, p. 688.

[4] The absence of a manubrium is a great peculiarity; it has been observed by Mereschkowsky as a constant occurrence in certain species of *Bougainvillea*. See A. N. H. (5), iii. 1879.

vesicle distinctive of *Physophoridae*, *Physalidae*, and *Discoideae*. The float is in the last-named circular and slightly concavo-convex in *Porpita*, rhomboidal with a diagonal solid vertical crest in *Velella*; in both genera composed of a series of concentric chambers which communicate in *Velella*, have chitinoid walls, and are covered by coenosarc. The chambers open externally on the upper surface by apertures, restricted in number in *Velella* and placed close to the base of the vertical crest, very numerous in *Porpita*, urn-like in shape, ranged upon the summits of radial ridges, and becoming closed in the central chambers by the deposition of fresh chitinoid layers. The lower surface of the float in *Porpita* has hollow radiating ridges from which, and from the central chamber, innumerable pneumatic filaments depend, passing into the walls of the polypite and blastostyles. The corresponding filaments in *Velella* are few and branched (?). The float of *Physalia* is large and fusiform, one end long and drawn out, with an aperture into the contained chitinoid saccule. In *Physophoridae* it is a small more or less globular body. It consists essentially of the expanded proximal portion of the coenosarc which has typically, e. g. in *Forskalia Ophiura*, a medusoid structure. The part corresponding to the manubrium forms an air-vesicle, and what should answer to the cavity of the bell is occupied by a brittle cuticular lamina formed on the surface of the manubrium, which is represented in the species named by two layers of cells. The cuticular structure in shape resembles a retort, mouth downwards. The mouth corresponds to the spot where the manubrium passes into the wall of the bell, which in this instance contains seven radial canals opening basally into the cavity of the coenosarc. The typical structure is more or less disguised in most cases. The cavity of the air-vesicle is said to open at its apex to the exterior in *Rhizophysa*[1].

The coenosarc in the *Discoideae* and *Physalia* simply invests the float. The zooids in the former are spread over one, the ventral aspect, a large polypite s. gastrozooid in the centre surrounded by a zone of blastostyles, and these in turn by a zone of tentacles or dactylozooids. The coenosarc of *Physalia* is produced into a prominent crest, vertical and exposed above the water in the natural position. The zooids are aggregated in one or more ventral masses, and the float may in some species attain a length of eight inches. Among *Physophoridae* the coenosarc of *Athorybia* is almost globular, of *Physophora* somewhat elongated, but the portion bearing the zooids is short and saccular. In all other *Siphonophora* it is elongated and tubular. The float of *Physophoridae*, or the nectocalyces of *Calycophoridae*, occupy its proximal end.

[1] The development of the air-vesicle, which was first observed by Metschnikoff, corresponds, as he stated, with the view that the float is a Medusoid structure. A solid ingrowth of epiblast = an entocodon, takes place as in the development of a Medusa where it forms the ectoderm of the sub-umbrella and manubrium. In the case of the float it gives origin to the air-vesicle and its walls.

The nectocalyces of the *Physophoridae*, when present, come next to the float. The rest of the coenosarc carries the other zooids which are arranged in distinct groups in the Physophorid *Apolemia*, and in all *Calycophoridae*. Segments bearing several groups of zooids are detached in *Apolemia*, and single groups (bract, polypite, tentacle) are set free in some species of *Diphyes*, in *Abyla*, *Monophyes*, and *Muggiaea*. These single groups are known as Diphyozooids, and have received special names, e.g. *Diplophysa* (*Monophyes*), *Eudoxia*, &c. (*Diphyes*). The Diphyozooid developes a succession of sexual zooids. The nectocalyces and zooids are developed along one and the same aspect of the coenosarcal tube; but, owing to the fact that it is spirally twisted in *Physophoridae*, they appear to be disposed in two or more rows, and the real arrangement is not evident. The twist of the nectocalycine region is in the opposite direction to that of the rest of the coenosarc. New nectocalyces in the *Physophoridae* appear distally to the float: the other zooids distally to the nectocalyces both in *Calycophoridae* and *Physophoridae*[1]. The coenosarcal tube is eminently contractile. Its ectoderm developes a circular and a longitudinal layer of muscle cells, its endoderm a circular.

The colonies of *Physophoridae* are mostly of moderate size, but *Agalma elegans* attains a length of four feet, *Apolemia uvaria* of twenty to thirty feet. The *Calycophoridae* are small, the largest, e.g. *Diphyes*, is a few inches long, *Galeolaria* two feet or less. The colony is retractile within a furrow or canal formed at the side of the distal nectocalyx in *Diphyes* and *Abyla*; by the two nectocalyces in *Praya*; or into a pit in the side of the single nectocalyx in *Monophyidae*. The *Siphonophora* are found in the Mediterranean and the open seas, sometimes at considerable depths (eight hundred to fifteen hundred fathoms or even more). *Physalia* is brilliantly coloured: *Velella* and *Porpita* are greenish blue. The majority are hyaline with spots of colour on the float, the polypites, hydrocysts, and tentacles.

The ovum appears to be impregnated and to develope while floating freely. It is devoid of a membrane save in *Hippopodius*. Segmentation is regular, and results in the formation of a solid ciliated planula with large vacuolated central cells. The

[1] It appears that in the *Diphyidae* the functional nectocalyces are constantly replaced by others. The new nectocalyx is produced distally to the old, not proximally as in *Physophoridae*. See Chun, SB. Akad. Berlin, 1885, pp. 521 et seqq.; and Korotneff, Mitth. Zool. Stat. Naples, v. 1884, pp. 279 et seqq.

The *Hippopodidae* differ from other *Siphonophora* in the fact that the nectocalycine section of the coenosarc is bent parallel to the section bearing the remaining zooids, and the point at which the flexure takes place is also the one at which the rudiments of both nectocalyces and other zooids are formed. Other notable peculiarities in the Order are the presence of hydrocysts among the nectocalyces of *Apolemia*, and the addition of a nectocalyx to each group of zooids in certain species of *Praya*, hence erected by Chun into a genus, *Lilyopsis* (SB. Akad. Berlin (1), 1885).

permanent hypoblast is differentiated from this central mass of cells as a superficial layer of cells beneath the epiblast, the central cells undergoing gradual absorption. In the Calycophorid *Galeolaria filiformis*=*Epibulia aurantiaca*, a nectocalyx, a polypite, tentacle, hydrophyllium are formed. The second nectocalyx appears on the pedicle of the first group of zooids, i.e. on the developing coenosarc. The buds of a second polypite, tentacle, hydrophyllium, grow out, and the colony is established by the development of successive groups of zooids in the order named. The cavity of the first nectocalyx in *Hippopodius* is remarkably small, but its mesoglaea extends as a cap over one extremity of the planula. A provisional hydrophyllium is developed in the first instance in most *Physophoridae*,—*Athorybia*, *Physophora*, *Agalmopsis*, and *Crystallodes*, but not in *Halistemma*. The float appears next in succession; see note, p. 772, *ante*. *Agalmopsis* and *Crystallodes* have a set of provisional hydrophyllia (the so-called *Athorybia*-stage), and the tentacle knobs of the young Physophorid are different in character to those of the adult. *Halistemma* has a single provisional nectocalyx. A portion of the planula persists for some time as the yolk-sac of *Crystallodes*.

A well-developed diffuse system of ganglion cells has been detected in the *Discoideae*. Ganglion cells occur also in the tubular coenosarc of some other *Siphonophora*. The nervous elements are especially differentiated in *Physophora*. Remarkable branched cells, 'neuro-muscular cells,' in connection with the longitudinal musculature of the coenosarc, have been described in some forms by Korotneff; cf. Mitth. Zool. Stat. Naples, v. p. 235, Pl. 14, Fig. 13.

The Diphyozooid (*supra*) swims by means of the medusiform sexual zooid. If it is derived from a hermaphrodite colony, it is said nevertheless to be itself unisexual. But one derived from the unisexual *Abyla pentagona* has been observed by Chun to develope first a male and then a female zooid.

The sexual products of the Discoidean medusa are developed *after* the medusa is detached, therefore probably from the ectoderm of the manubrium; in all other *Siphonophora* properly examined from the endoderm: in *Epibulia* (=*Galeolaria*) in the rudiment of the gonophore: in *Hippopodius* in the bud of the future peduncle of the bunch of gonophores: in *Forskalia* in the rudiment of the peduncle: and in *Agalma* in the rudiments subsequently differentiated into several gonophores. The young sexual cells are not sub-epithelial at first, as they are in those *Hydroidea* where they appear in the endoderm, but they project into the cavity of the bud: but whether or no they really originate in the first instance from endoderm cells is not known. The sexual cells in the male wander into the ectoderm of the manubrium: so too in the female of the Calycophores named, but the endoderm subsequently grows round each ovum, furnishing it with an incomplete follicle placed to the outer aspect. But in the Physophores *Forskalia* and *Agalma* the single ovum is arrested in the endoderm, and surrounded by the spadix as stated p. 771.

Chun has propounded a theory of *cyclical* development in *Monophyidae*; e. g. (1) a form called by him *Monophyes primordialis*, which has been shown by Claus to be a larva, gives origin to (2) a second form=*Muggiaea Kochii*, in which the swimming bell of the *Monophyes* is replaced by a second and differently shaped nectocalyx, and the coenosarc developes groups of zooids: and (3) one of these groups of zooids is detached as a Diphyozooid, the sexual *Eudoxia Eschscholtzii*. Cf. Chun, SB. Akad. Berlin (2), 1882, and A. N. H. (5), xi; Claus, Arb. Zool. Inst.

Wien, v. 1884. According to Chun, the nectocalyx of the genus *Monophyes* is a second nectocalyx; cf. op. cit. (1), 1885; and Claus, Z. A. viii. 1885.

A Siphonophoran has been variously regarded (1) as an assemblage of organs, or (2) as a colony of polymorphic zooids. The former view appears to have been based upon the idea that in any Hydrozoan colony the several factors represent organs of an individual, the individual being the colony itself. Such a view cannot be regarded as any longer tenable. There can be no reasonable doubt that a Hydroid colony is an assemblage of zooids which remain connected instead of separating after their formation by budding. It is no less certain that in a Siphonophoran, the nectocalyx, pneumatophore, sexual zooid, a polypite or hydrocyst, represent so many polymorphic individuals, and that structurally a Siphonophoran is as much a colonial organism as a *Sertularia*[1].

As to the special character of the colony two views have found acceptance. One is, that the coenosarc, as it is called, is the homologue of the manubrium of a Medusa, the primitive hydrophyllium, present, e. g. in the larval *Physophora*, representing the umbrella: the other that it is a floating colony, the individuals of which are connected by a coenosarcal stem or stolon the equivalent of a hydrorhiza. The former theory is supported by the analogy of such a medusa as *Sarsia* or *Willia*, in which the manubrium produces medusae by budding. The following objections, however, appear fatal to it. (1) A primitive hydrophyllium is not present in all *Physophoridae*, and is not present at all in *Calycophoridae*, and to suppose that it has been aborted in these instances is the purest assumption; (2) that the hydrophyllium itself is probably the homologue of a medusa in its entirety; (3) that it is a lateral appendage invariably of the coenosarc, and there is no reason to suppose it is anything else in the planula; (4) taking such a form as *Epibulia* (Calycophore) or *Halistemma* (Physophore), it is clear that the coenosarc is attached to the aboral apex of the exumbrella of the first nectocalyx developed, and cannot possibly represent a manubrium. For these reasons the second view mentioned above is certainly to be preferred. The coenosarc of a Siphonophoran is then comparable to the aboral stolon of the young Narcomedusan *Cunina rhododactyla*, or of *Cunocantha octonaria*, which produces buds for a stated period[2]. The fact that the planula

[1] The hydrophyllium is usually regarded as the homologue of a nectocalyx. Its central endoderm canal is furnished with accessory canals such as occur in the nectocalyces of *Diphyes* and *Praya*. The homology of the tentacle is more difficult. In the *Discoideae* it probably represents a zooid, i. e. is a dactylozooid, but in *Physalia* it is possible that the sac represents a hydrocyst. The tentacle itself is in that case attached to this hydrocyst in the same position, i. e. at its base, as is the tentacle of most other *Siphonophora*. The position is a most unusual one, but Metschnikoff states that he has observed a single tentacle attached similarly to the base of the manubrium of a Medusa (*Dipurena*). The Siphonophoran tentacle, however, is sometimes attached directly to the coenosarc as in *Athorybia rosacea*. And it may be noted that in the Physophirid *Stephanospira insignis* the hydrocyst bearing the female zooids is prolonged apically into a tentacular process with lateral branches bearing nettle-batteries; see Gegenbaur, Nova Acta, xxvii. p. 399. It is quite possible that such a structure as the tentacle of *Porpita*, beset with capitate processes, represents a zooid form from which the more complicated tentacles of other *Siphonophora* have been derived. In determining such a question, much stress cannot be laid on the origin of the tentacles from separate buds. The tentacles of a *Hydra* originate in the same manner. The place of origin of the buds is however another matter.

[2] See Metschnikoff, Z. W. Z. xxiv. 1874, pp. 28 et seqq., Pl. V. Figs. 4–8; and Brooks, Mem. Boston Soc. Nat. Hist. iii. (12), 1886, pp. 362 et seqq.

gives rise to more than one zooid is simply an instance of precocious gemmation, to be paralleled by the fission of the embryo of *Lumbricus trapezoides*, and possibly of the Acrasped *Chrysaora*. It may be noted also that the Hydroid planula does not always form the hydranth directly; e.g. in *Eutima* it attaches itself and produces a hydranth by gemmation, itself becoming a hydrorhiza [1].

The Craspedota are classified as follows—

I. Order *Trachymedusae = Trachylinae* (Haeckel). Tentacles solid, sometimes replaced in part in the adult by hollow; tentaculocysts or auditory organs with endodermal axis, containing one or more otoliths. Development by metamorphosis from free hydroid larvae.

(1) *Narcomedusae:* tentaculocysts always free; tentacles at some distance from margin of bell to which they are connected by peronia; margin of the bell lobed; radial pouches to the stomach sometimes present, sometimes absent; festoon canals generally present; genital organs on the subumbrellar aspect of stomach, extending beneath radial pouches or restricted to the latter. Four families, *Cunanthidae*, *Peganthidae*, *Aeginidae*, *Solmaridae*.

(2) *Trachomedusae*: tentaculocysts either free or inclosed in capsules, which may be sunk in the mesoglaea; radial canals (4, 6, 8) and a circumferential canal; caecal centripetal canals sometimes present; genital organs on the subumbrellar aspect of the radial canals. Four families, *Petasidae*, *Trachynemidae*, *Aglauridae*, *Geryonidae*.

II. Order *Hydroidea*. Hydranth small as a rule; sexual only in *Hydra*; sometimes non-colonial, but usually giving origin by gemmation to a plant-like colony; often polymorphic. An exo-skeletal perisarc usually investing the coenosarc, chitinoid, sometimes calcareous forming a coenosteum. Sexual zooid or Medusa craspedote with ocelli or entirely ectodermic otocysts, produced by gemmation from the coenosarc or a hydranth; frequently more or less degenerate, see p. 762, and p. 768.

(i) *Tubulariae* s. *Gymnoblastea*. Hydranth of very variable appearance, non-tentaculate in *Micro-* and *Proto-hydra*; its tentacles varying in character and arrangement; rarely specialised as a blastostyle; sometimes non-colonial (*ante*, p. 755), and in *Hydra* locomotive; usually colonial; coenosarc of colony invested by a perisarc which never forms hydro- or gono-thecae but generally extends on to the hydrocephalis, and in *Bimeria* even invests the bases of the tentacles; Medusa bell-like, ocellate, belonging to the *Anthomedusae*, see *ante*, p. 760. *Hydra*, *Clava*, *Cordylophora*, *Coryne*, *Syncoryne*, *Eudendrium*, *Tubularia*, *Corymorpha*, *Hydractinia*, *Podocoryne*, &c.

(ii) *Hydrocorallina*. Hydranth polymorphic, either a gastrozooid (pp. 758–9) or dactylozooid (p. 758); colonial; skeleton a calcareous coenosteum with gastro- and dactylo-pores (p. 756). (1) *Milleporidae*: coenosteum arborescent or encrusting composed of a superficial living and a number of deep dead layers; pores crossed by tabulae, either scattered or in systems with dactylopores grouped round a central gastropore; sexual products developed in capsules of the coenosarcal canals; *Millepora*. (2) *Stylasteridae*: coenosteum arborescent; either entirely living or with deeper dead layers; pores either scattered or grouped in systems

[1] Brooks, op. cit. *ante*, p. 403; and cf. pp. 764–5, *ante*.