

On Siphonophores
by
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The bracketed [..] and emboldened comments are Totton's marginalia.

Polyperson theory

For many years there have been some scientists who made comparisons between siphonophores and Hydrozoa in contradiction to the "polyperson theory". Among them, Lesueur is considered to be the pioneer who cited the analogous characteristics of various structural parts of siphonophores and the individual organisms of Hydrozoa by citing various structural characteristics. The reason that no scientist had accepted this theory can be readily understood by the reports made by the later taxonomists such as Lamarck (1816), Cuvier (1817), and Eschscholtz (1829) that the siphonophore is a single animal. Following Lesueur, Milne Edwards presented a similar interpretation. He compared, in his study of *Forskalia* (then *Stephanomia*) with the animals belonging to the family Pennatulidae that the former is composed of many individuals which are all in communication with one another. However, this theory, too, appeared to have escaped the attention of many scientists as Siebold (1848) repeated the biological analysis and the taxonomy used by Eschscholtz in his textbook. Vogt and Leuckart later insisted that siphonophores are a planktonic animal colony, and are extremely close to the Hydrozoa.

On the other hand, Vogt (1851) offered the same interpretation of eudoxids as the advocates of the "Polyperson theory" while Leuckart (1851) continued to adhere to the "Polyperson theory" by clearly defining that all the accessory parts of the animal body are individual organisms. Thus, this theory is commonly called Leuckart's "Polyperson theory".

Even with sessile *Hydra*, the individual organisms take varied forms because of their functional differences, such as a siphon with the mouth and spiral zooid (?) without it on the other hand. Further, the occurrence of pneumatophore, Skeletopolyp (?) Blastostyle and the sexual medusae that separate after budding out was then unknown. Already Lesueur and Milne Edwards, too, had noticed the similarity between siphonophores and Hydrozoa. Therefore, it was not at all an outlandish assumption that Leuckart had concluded that siphonophores are colonies whose various divisions of labour are highly developed, particularly such structural parts as nectophore, bracts and siphons, which were recognised as organs by those of the opposed school of thought as individual organisms of equal importance.

However, according to this theory, with all polymorphic animal colonies, there exists a morphological rule among the individuals by which the co-operate with each other and have a mutual relation among those of the same generation. This is not so much a morphological and functional coincidence but rather it is an adaptation to their biological function. Consequently the individuals of various generations along the entire colonial body cannot be distinguished but by correlating them all the complete life history can be observed. In other word, each and every individual and generation simply represents a sentence or a paragraph of the life history of this animal - it is merely a chapter linking the story together. But because of these diversified, specific functions, one individual organism loses the organs used by the other individual for their own characteristic functions. The tentacles are lacking on the siphons even in siphonophore catching their prey and protection of the colony is

entrusted to the tentacles themselves. In short, this theory is the result of application of the well known Leuckart's "Polymorphism" to siphonophores. It contradicts the "Polyorgan theory" and every anatomical part represents an individual organism though some individual loses some of its organs.

However, the alternation of generations too, parallels the polymorphic phenomenon and the relation of the sexually produced individuals to the maternal body is no different from the mutual relation between the individual organisms and it is interpreted that the alternation of generations is no more than the occurrence of "Polymorphic" phenomenon in the development of the animal.

Leuckart staunchly advocated this theory and in order to refute the theory that the eudoxid is a single medusa he cited the separate buddings of its anatomical parts such as bracts, siphons and gonophores. Further, to insist also on the independent character of the nectophore, bract, and siphon he challenged a different interpretation contemplated by those of the opposite school. In regard to the structure of pneumatophore he stated, contrary to the definition by Eysenhardt, etc., that the pneumatophore is an inverted umbrella, that the endodermal layer of its air-bladder is similar to the subumbrella layer of a medusa and that its exterior wall is comparable, at the same, to the exumbrella layer of a medusa.

Leuckart's "Polyperson theory" which had been derived from "Polymorphism" was widely adopted by German scientists of that time. Kölliker (1853), Gegenbaur (1854) and Claus (1863), etc. exerted much effort to amplify this theory from the structural and the embryological standpoint and to find an intermediate form between Hydrozoa and siphonophores. Consequently, the adaptation to this theory is quite obvious in German textbooks. For example Korschelt and Heider in their "Comparative Embryology" (1890) have stated, in attempting to establish the relation of siphonophores to Hydrozoa as its root, that if one hydrozoan is able to remain floating on the surface with a wide basal disc without attaching itself to other objects like Scyphostomae, it should not be difficult for it to transform into such a planktonic form as *Velella* or *Physalia*.

Thus, from the standpoint of the structure, the function and the alternation of generations, siphonophores have been defined on the one hand as an individual having complex organs and on the other hand as a colony showing a polymorphic phenomenon. But in the meantime, a general tendency to analyse the animal from the embryological standpoint was quite apparent. Without doubt, to investigate or to discuss the analogy between siphonophores and medusae or Hydrozoa means to debate, simultaneously, the question of the animal's lineal development. Consequently when "Biogenetisches Grundgesetz" appeared as the importance of embryological aspect was keenly felt by the investigators as the only rudiment in analysis of the systematic growth many scientists busily turned their eyes toward the developmental phase of the study, realising to investigate the characteristics of its larval form is of the utmost importance to conclude the before mentioned discussion. The theory by Metschnikoff, too, seeks its proof on this aspect. Haeckel in 1869 conducted the artificial breeding of 3 genera of Physonectae in order to study their growth, bearing in mind the fundamental importance of such an investigation from which he has reached the conclusion that their larval forms correspond to a medusa, the former's hat-like bract, the siphon and the tentacles compared with the umbrella, the stalk and the marginal tentacles of the latter, respectively. Further he stated that the subsequently developed group of appendages are similar to the *Hydra* individuals and the adult form of siphonophore is a colony like Hydractinia.

Revival of "Polyorgan theory"

(1) Haeckel when he was about to present his study on siphonophores in the Challenger Report (1888), made known his “Medusome Theory” in which he attempted to give the true meaning of “Polyorgan” and “Polyperson” theories by changing the already discussed interpretations of adult siphonophores. Medusome collectively signifies each part of a siphonophore system which has recognised to represent a medusa. By further summarising this point it is obvious that siphonophores directly descended from the velum medusae because of the “Palingenetic import” although the initial larval form of siphonophores is generally a simple medusa which changes “coenogenetically” to a degree during its evolution. However, this medusoid appears in two fundamentally different forms - the first is the eight radial “Disconula” traces its roots to Trachymedusae while the second is the [bi]laterally symmetrical “Siphonula” which descended from Anthomedusae.

(2) While the various parts of the larval forms are developing into the adult siphonophore, some become medusoid individuals while others appear with only their organs overlapping. Inasmuch as the overlapping of the nectophores and bracts do not infer an individual organisms but rather organs, and further the cormidia are the result of a continuous inversion of the medusome group (segmentally) yet the latter grows, sometimes, at intervals on the stem. Therefore, Haeckel stated that these two cases should be differentiated as “Ordinal Cormidia” and “Dissolved Cormidia” respectively.

Now the question of systematic growth of the organisms is indispensable in study of morphology and embryology, etc. However, especially according to Haeckel’s theory, it is clearly evident that the discussion on a concrete [objective] developmental aspect accompanies the questions of the structural analysis [theory] - henceforth, these questions were always closely associated. However, to minimise the complexity of the subject it would be better, we feel, to proceed with the anatomical discussion by setting aside the embryological aspect for the time being.

According to Haeckel’s analysis a pneumatophore is a furrowed gas gland on top of the exumbrella of the larval medusa. With this medusa, the stalk transforms to the exumbrella layer, having lost its subumbrella layer, therefore, the ectodermal wall of the pneumatophore is not the subumbrella layer, coinciding with Eysenhardt’s statement.

However, the former’s interpretation that a medusal stalk becomes the stem of a siphonophore is similar to that of Eysenhardt. Of the several parts budding from the stem, the gonophore and the special nectophores (observed in *Elysia*) are single medusiform individuals, and the primitive nectophore present in Calycophorae is an organ of the pneumatophore. The nectophore is an organ resulting from changes in position and overlapping; siphons and palpons are medusae lacking all parts but the stalk and the tentacle is an organ belonging to the siphon. In general summarisation of various parts of a siphonophore some are medusae while others are organs. [NO]

However, because it is the same as the previous statement that such a part of the gonophore already recognised as a medusoid individual even in the “Polyorgan Theory” the difference between the theories of Haeckel and Metschnikoff lies in their interpretation of the pneumatophore and the special nectophore. In general not the slightest difference can be detected between the hitherto known “Polyorgan theory” and Haeckel’s “Medusome theory” as far as their recognition of the anatomical parts of siphonophores consisting of medusae and the organs concerned. Consequently, the latter may be said to be a slightly varied definition of the former. Therefore, conclusively there is hardly a ground for a doubt that such strong opposition to the theory by Chun (1888) and Claus (1889) the advocates of “Polyperson theory” during

that time was no more than a repetition of the criticism brought about by Leuckart (1872, 1875) and Claus (1878, 1883) on the interpretation of the subject by Metschnikoff and Müller.

Present definition of “Polyorgan theory”.

This theory is a composite form of the criticisms advanced by several investigators against the “Medusome theory” of Haeckel and later discovered 32 or 3 facts on the subjects. Yet, despite the change in the interpretation of the “Polyorgan theory” with time there has never been any different definition of the “Polyperson theory” except the discussion of the systematic growth of siphonophores. From the beginning it has been accepted that each anatomical part is functioning independently. Therefore, it is sufficient to say that Chun’s definition represents the recent conception of the theory.

Chun opposing Haeckel’s analysis and the previous interpretations of the “Polyorgan theory” had strongly refuted first of all, the change in the positions of the organs and gave the following biological data. One, there is no conclusive proof of Leuckart’s statement that the bracts, siphons and tentacles all bud out individually like the gonophores, thus they must all be of equal value. Further, he stated that although the followers of the “Polyorgan theory” insist that the so-called tentacles are formed through shifting of position by marginal tentacles of a medusa from its stalk to its basal siphon, the regeneration of siphonophore tentacles, the sense organs (found at the base of the medusan tentacles) and stalks takes place at the original position. Continuing still further he reported that according to Haeckel despite the nectophore being an organ developed through a change in position and overlapping, the special nectophore which undergoes an identical structural growth must be considered as an individual medusa. Finally, Chun interpreted a small umbrella present on the bract of *Athorybia* and *Rhodophysa* as reported by Haeckel, as indicating that the bract itself is an individual medusa unconnected to any other part.

In 1897 Chun again brought up this subject for discussion, pointing out that the stem of the siphonophore compares with the stalk of a medusa which grows at the aboral side of the primitive medusa in the Calycophorae and which occurs connected to the external stem in case of Physophorae. It is analogous to the budding of a medusa in an identical shape on the aboral side of the larval form of the Aeginidae observed by Metschnikoff. But he continues that with Anthomedusae, which are often compared with siphonophores, the stalk does not develop such a subordinate part and grows an isomorphic medusa at all times.

Chun, further, concluded that Hautlaub’s (1896) observation of the regeneration of the stem of *Sarsia* by overlapping cannot be seen under ordinary conditions. By refuting the comparison made by Hautlaub as well as by Metschnikoff that if a medusoid and a polyp simultaneously developed on the stem (*Sarsia*) it is quite difficult to compare the stem of siphonophores with the stalk of medusae. This difficulty, according to Chun, resulted in defining a pneumatophore (air bladder) as a depression of the exumbrella wall following Haeckel’s precedent, but this definition does not apply in the case of the primitive nectophore in the Calycophorae. The budding out of the exumbrella layer cannot be found in any other metamorphosis such as the change in the position of the tentacles to the base of the stalk or the connection of the stalk to the end of the exumbrella layer. Therefore, he concluded that one thus encounters many difficulties in analysing the structures of siphonophores with “Polyorgan theory” while no obstacle would occur should the subject be analysed with Leuckart’s “Polymorphism”.

When these various theories are summarised, it is obvious that the hitherto known definitions of siphonophores have progressed by way of two parallel roads. The first is the "Polyorgan theory" and its variations have been advocated by Metschnikoff, Eysenhardt and Eschscholtz. These older students of the subject have compared a mature siphonophore to a medusa carrying many buds on its stalk. While Huxley defined it as an individual and Metschnikoff and Haeckel insisted that an immature animal is a medusa and an adult form is also a medusa but with medusoids and organs budding out together on its stalk. Although this theory has not received much support in recent years it is not altogether discarded. Balfour and Sedgewick adopted this interpretation. The second is the "Polyperson theory" which starting with the comparison of Hydrozoa, was roughly formed by Leuckart's "Polymorphism" - later it was constructed into a finer state. There is one point, however, he should have taken into account - that is these theories do not coincide. However, the difference at present is slightly varied in its interpretation from the argument resulting from a discussion of the individual merits of the theories by Huxley and by Leuckart. From these considerations, this author feels that it is perhaps quite appropriate to call these theories the "Polyorgan theory" and the "Polyperson theory".

Theory on Lineal Development (p.37)

This author has previously recalled Haeckel's attempt to find the siphonophore ancestor in two medusae. However, the discussion relative to the lineal growth of the organism did not arise at the same time as it has already been clarified in the previous chapter. the "Polyorgan theory" defines the primitive form of siphonophore as a medusa based on its embryological development, while with the "Polyperson theory" it is interpreted as a planktonic colonial hydromedusa. At any rate, the existence of a close relation between the individual and its lineal development has then been recognised by everyone, but the two theories came to name different ancestral origins. The former theory advocated that the primitive siphonophore is a medusoid stage with an umbrella. From this planktonic organism grow the locomotory organs, such as the nectophores and the pneumatophore by a change in position and big overlappings. Scientists admit that the polyp stage is more rudimentary than the medusoid form and that the latter secondarily assumes a planktonic stage in which a radial jelly-like disc grows and the stalk develops from the gastric tube of the polyp. On the other hand, adherents of "Polyperson theory" insist that the primitive siphonophore is a polyp lacking an umbrella. Therefore, all the locomotory organs are new structures which did not develop from similar organs on the rudimentary form. Thus, the question arises how do we interpret the larval siphonophores which actually have developed from the eggs? According to the first theory, this larval organism is truly a single medusa individual having a morphological value and the result of hereditary repetition of the original primitive form. Therefore, it has a tremendous value from the standpoint of genetics. On the contrary, the "Polyperson theory" acknowledged that the larval form is a polyp which has undergone special metamorphosis having an appropriate value as such.

Then, how did Haeckel cast his ballot in selection of these theories? Of course, without doubt, he has supported the "Polyorgan theory" from which it is apparent that the "Medusome theory" is clearly a transformation of this definition. Precisely, as explained in the first half of the "Medusome theory" he cited the proof that the larval siphonophore, having a medusa form ancestor, possesses a value from the standpoint of genetics, but the existence of two larval forms signifies that siphonophore are derived from two ancestors - that is two medusae.

The followers of the “Polyperson theory” all sought the ancestral siphonophores in the polyp form but they did not agree on transitional stage from the polyp to siphonophore. Leuckart concluded after studying the larval form of *Agalmopsis*, that the larvae of the Physophorae are the most primitive siphonophores and that the (mature) siphonophore is a hydrozoan colony entering a planktonic life. However, Claus (1884) presented an analysis differing slightly from the former. He believed that the Calyphorae are the most rudimentary siphonophores and furthermore he rejects the theory of the sessile hydromedusa adopting a planktonic habit. He states that perhaps a primitive larva similar to *Podocoryne* or *Hydractinia* becomes a colonial hydromedusa by entering a sessile stage similar to *Podocoryne* or *Hydractinia*. Those that do not complete the sessile stage become Calyphorae, budding polyp and medusoid forms at the aboral end. Then, finally, other siphonophores were differentiated. These two scientist differ only in the manner of approach in discussing the ancestor. Leuckart maintained that first a colonial hydromedusa appeared and then a siphonophore, while Claus claimed these two stages simply branched out from the same origin.

Schneider (1898) following Leuckart’s interpretation cited the lineal differences between Calyphorae even in the most rudimentary form and other siphonophores and opposed Claus’s analysis of the latter. He denied the primitive character of the Calyphorae which he claimed to have been derived from an altogether different larval form. Finally he concluded that as far as the lineal growth of siphonophores is concerned, the development of a conglomeration of individuals from planulae can be readily understood from the continuous growth of the individual organisms from colonial hydromedusa, polyps from planulae, followed by further budding of new polyps. Thus, the developmental difference lies at this point as pointed out by Korschelt and Heider.

Consequently, Schneider claimed that a siphonophore is neither a medusa as interpreted by the “Polyorgan theory” nor a polyp with a budding zone at the aboral end as claimed by Claus but rather a group of orderly developed polyps already showing their complexity when first grown out from the planulae. However, during this period, he continued, they are quite in uniformity. Each organism appears to be more like an organ than an individual. Yet, every one is equipped with the parts found in the mature animal and situated at the proper positions, Therefore, these larval parts are just as important morphologically as those of the mature animal.

Chun, too, has sought the ancestral siphonophore in polyp stages. But first he denied the descent of *Verella* larvae from octoradial medusae and the fundamental differences between the larvae of Chondrophorae and of other siphonophores. Then, on the question of the developmental change from a polyp to a siphonophore he definitely rejected the theory of Leuckart and Schneider but adopted Claus’s interpretation. Then he called attention to *Nemiopsis gibbesi*, observed by McGrady (1859), and its planktonic adaptation with its tentacle although it is not sessile. He also cited *Diplograptus* as having a floating existence so that it was thought to be closely related to siphonophores by many scientists. He stated that even though such a relation may not be true, some *Diplograptus* actually maintain a planktonic life. Therefore, there might be a missing link to clarify the origin of siphonophores among these yet unknown forms. However, the comparison is commonly made with the medusae and this idea has been chiefly adopted by English and American scientists.



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○多數個蟲説 (Poly-person theory)

多數機官説に反對して、早くから管水母とヒドロ群體とを比較した學者がある。ルーソー氏(一八一三)は實に其嚆矢で、氏はアボレミア(當時はステファノミア)と云ふ管水母の體の性質を述べて、體の諸部分とヒドロ群體の種々の個蟲との類似を擧げた。併し此考へは何人も同意する人がなかつたことは、此時以後に現はれたる分類學者ラマーク(一八一六)、キュビエー(一八一七)、エシユ

シオルツ(一八二九)等の人々の著述には、皆管水母を單

一の動物と記載したのに徴して知らるゝのである。ルー

ソー氏に次で全様な考を懷いた人はミルン、エドワード氏である。氏はフォルスカリア(當時はステファノミア)の

研究に於て、體は多數の個蟲が集まつて成り、全體が相交通するものであるとして、ペンナチユリ科の動物に比較した。併し此説も尙學者の注意に洩れたと見え、シーボルト氏(一八四八)の教科書に全くエシユシオルツ氏の解釋と分類を襲用してあつたが、フオグト、ロイカルト兩氏出づるに及んで、管水母は浮游性の動物群體であることを主張し、管水母はヒドロ群體に甚だ近いものであると云つた。

但しフオグト氏(一八五一)はユードキシ體の説明に於て多數器管説者と全じ考を述べたが反之ロイカルト氏(一八五一)は、明らかに凡ての附屬物を個蟲なりと述べ、後益此多數個蟲説を主張した。之れに依つて此學説をロイカルト氏の多數個蟲説と呼ぶのを常とする。

抑も固着性のヒドラ類に在つても、個々の動物が分業の結果として種々の形を取ることがあつて、口を備ふる營養體もあれば、口のない Spiralzoid もある。其他にも Nematophore, Skeletopolyp, Blastyle 及び之れより芽出して後に分離する生殖水母のあることは、何人も認めた

時代で既にルーソー、ミルン、エトワード兩氏も管水母とヒドロ群體との類似を注意したから、今ロイカルト氏は管水母を分業の進んだ群體とし、各部分特に泳鐘保護葉營養體の如き反對論者が機官と見做した部分をも、全價値の個蟲であるとしたのは決して突飛な考ではなかつたのである。

さてロイカルト氏の説に依ると、總て多形の動物群體には、澤山の個蟲が相協同し世代が相關聯して、其各個の間には形態學上の規律が成立するが、各は形と作用に於て一致するのではなく、全體としての生理的機能に對して相應して居る。従つて世代の個々は自分だけでは全群體を示すものでなく、それ等を綜合して始めて完全な輪換的發生を見得るのである。換言すれば個々の部分世代は單に此動物の生活史に於ての章句斷篇であつて、全章中の一階梯一連鎖に過ぎない。而して個蟲が分業の結果各自獨特な作用を營むが爲めに、他の個蟲の營む作用に使はるゝ機官は消失し去る。管水母に於ても營養體が觸手を缺いて居るのは、食物を捕へること群體の防護す

ることは、之れを觸手に譲つたからであると云ふのである。要するに此説は有名なロイカルト氏の多形 (Polymorphism) 説を管水母に適用したもので、多數機官説に反對して、凡ての部分は(或機官を失へるものもあるが)孰れも一箇の個蟲を代表するものである。而して世代の交番も亦多形の現象に伴ふ所の一現象で、有性的に發達する個蟲が其母體に對する關係は、群體中の個蟲相互の間に於ける間に於けるものと變ることなく、世代の交番は多形現象が發生の方面に現はれたものであると解釋するのである。ロイカルト氏は飽くまで此説を主張して、ユードキシ體を一個の水母と見做すことを否定する爲めに、其各の部分即ち保護葉營養體觸手並びに生殖體は皆別々の芽より生ずることを挙げ、又泳鐘保護葉營養體が獨立せることを主張する爲めに、反對論者が當時尙未が明には主張しなかつたけれども、隱約の間に認めつゝあつた變位なることを毫も證據のないことと言つた。又氣胞の構造に就ては、アイゼンハルト氏以下の人々が氣胞は傘の裏返つたものであるとしたことに反對して、内胚葉層

の凹入することが他の水母の生ずる際に現はれる芽核と全じものであるから、氣胞の内部氣囊の内面を被へる層は水母の傘下層に相當するもので、氣胞の外側壁は矢張水母の傘外層に相當するものであると言つた。

多形説より成り立つた此ロイカルト氏の多數個蟲説は、當時の獨逸學者の採用する所となつて、ケリケル（一八五三）デーゲンバウル（一八五四）クラウス（一八六三）等の諸氏、或は構造の上より或は發生の上より、之れを敷衍せんとし、且つヒドロ群體と管水母との中間の形を探るに腐心したのである。従て獨逸で出來た教科書には多く此多數個蟲説を採用して居る。一例を舉ぐればコルシエルト、ハイダー兩氏の比較發生學（一八九〇）には管水母をヒドロ群體から導かんとして、今ヒドロ群體が一個の廣い底板を有するとし、之れが他物に固着することを廢めて、往々吾人が *Schypostomae* に見る如くに、水面に浮游し、此有様で永く生存することが出来る様な好都合の狀況にあつたとしたならば、カツノカムムリ、カツノエボシの様な浮游性の形に移ることは了解するに

管水母に就て（川村）

難からぬ事であると言つて居る。

斯くの如く管水母は構造作用世代交番等の點より、一方に於ては重複した機官を有する個蟲と解釋せられ、他方に於ては多形現象を明示する群體と説明せられつゝあつたが、此間に更に發生の方面より管水母を解釋しやうと云ふ一般の傾向が顯はれた。言ふ迄もなく管水母と水母又はヒドラ群體との相同を詮議することは、同時に管水母の系統發生を論ずることとなるので、有名な Biogenetisches Grundgesetz が表はれて、發生學的の發明が系統發生を論ずる唯一の根據と思はれた頃から、多くの學者は幼蟲の性質を研究するのが前記の議論を解決する捷徑であるとして、大に發生の方面に注目する様になつた。先きに述べたメチユニコフ氏の説も其證據を此局面に求めて居る。ヘツケル氏も此方面に注意を向けて、一千八百六十九年 *Physonecta* の三屬に就て人工受精によりて發生を研究した結果、幼蟲は單一の水母に相當するもので、帽子狀の保護葉は水母の傘に、營養體は柄部に、觸手は水母の縁にある觸手に比較すべきもので、其他の後

管水母に就て(川村)

四

より生ずる附屬部分は凡てヒドラの個蟲に相當するものであるから、管水母の成體はヒドラクチニアの様な群體であるとの結論に達した。

○多數機官説の再現

然るにヘッケル氏は一千八百八十八年チャレンジャー報告の管水母を公にするに當つて、右に述べた成體の解釋を變じて、氏の所謂「多數機官説及び多數個蟲説の眞理の元素を包含し誤謬を避けんとする」メヅソーム説(Mesosome theory)を發表した。メヅソームとは相集まつて一個の水母を代表すると氏が見做した管水母體中の各部分を呼んだ名稱である。此説の主要を述べれば、(一)管水母の最初の幼蟲は常に簡單な水母で多少進化の途中に(Coenogenetically)に變異することはあるが、系統上の意味(Palingenetic import)を保有するものであるから、管水母は縁膜水母から直接に降り來つたものである。而して此水母形幼蟲は根本的に違つた二つの形に表はれる、其一は八放射對稱を有するデスコムラ(Discomula)幼蟲で、之れは Tracomedusae より降り來つたものなること

を示し、其二は左右對稱を保つサイホムラ(Siphonula)幼蟲で、之れは Anthomedusae より降り來つたものなることを示すのである、(二)此幼蟲から成體の管水母を作る際に、種々の部分が或ものは水母形個蟲で、他のものは水母の機官のみが重複して表はれる。而して泳鐘保護葉等が重複するのは、個蟲が重複するのではなく、機官が重複するのであるが、分群はメヅソームの群が環節的に反覆連續したものであるが、時にメヅソームは幹の上に散布して表はれるから、前者の場合と後者の場合は整正分群(Ordinal Cornidia)と分散分群(Dissolved cornidia)と、して區別すべきものであるといふのである。

抑系統發生の問題は、形態學發生學其他と寸時も離る可からざる關係あること勿論であるが、ヘッケル氏の此説に至つて特に明瞭に具體的な系統發生の議論が構造解釋の議論と提携して現はれ、此時以後は此兩問題は常に癒合して表はれるに至つた。併し茲には混雜を避ける爲めに、系統發生の問題を暫く措いて構造解釋に關する徑路を進むのが便であらう。

ヘッケル氏の解釋に従ふと、氣胞は幼蟲の水母の傘外層の頂點に於て凹入した瓦斯腺で、此水母は傘下層が無くなつて柄部が直接に傘外層に移り行く様になつたものであるから、氣胞の外側壁はアイゼンハルト氏等の云ふ如くに傘下層ではなくて、傘外層に相當するものである。

併し水母の柄部が管水母の幹となることはアイゼンハルト氏等の考へと全様である。此幹より芽出する諸部分の中、生殖體と特別泳鐘(エルサエアに見る)は各一個の水母形個蟲で、Calyophore に現はれる原始的泳鐘は氣胞の一機官、泳鐘は變位重復したる機官、營養體感觸體も水母の柄部のみ残つたもの、觸手は營養體に屬する一機官である云ふものである。概言すれば、管水母の諸部分は水母なるものあり機官なるものあると言ふのである。

然るに既に多數機官說にても生殖體の如きは水母形個蟲と見做されて居たことは前に述べた通りであるから、ヘッケル氏の考がメチュニコフ氏等の考へと異なる點は、氣胞とか特別泳鐘とかの部分の解釋如何に在つて、大體

管水母に就て(川村)

に於て管水母體中の諸部分を水母個蟲と機官との混合せるものと見做すことは、從來の多數機官說とヘッケル氏のメヅソーム說との間に聊かの差異もない。此故にメヅソーム說は多數機官說が少許の變形を成して再現したものと謂ふことが出来る。従つて當時の多數個蟲說論者クーン氏(一八八八)クラウス氏(一八八九)等が直ちに反對して出した駁論が、恰も先きにメチュニコフ氏及びミューラー氏等に對してロイカルト氏(一八七二、一八七五)クラウス氏(一八七八、一八八三)氏が爲した駁論を今一度繰返した様なものであつたのは少しも怪むに足らないのである。

○近時の多數個蟲說

右に述べたヘッケル氏のメヅソーム說に對する諸氏の駁論と、其後に發見せられた二三の事實の引證とが所謂近時の多數個蟲說を組立て居る。而して多數機官說が時代と共に變形したのに反して、多數個蟲說は管水母の系統發生に關する議論を除いては、ロイカルト氏以後聊かの變化をも見ないで、徹頭徹尾體中の凡ての部分が個々

獨立の個蟲であると説明して居る。今近時の多數個蟲説として唯クーン氏の所説を述べれば充分であらう。

クーン氏はヘッケル氏並びに其以前の多數機官説に反對して先づ機官が變位して現はれるといふ事を否定して、ロイカルト氏の如く其證據を見ないことで、却つて保護葉營養體觸手は其初め生殖體と全く同様な個々の芽より生ずるものであるから、此等の凡ては皆同價値のもので、個蟲でなければならぬ。又多數機官論者は觸手は水母の縁端にある觸手が該水母の柄部なる營養體の基部迄變位したものと云ふが、管水母に於て觸手感覺器(水母の觸手の根本にある)並びに柄部が現れる時には、必ず元來存すべき位置に於て現はれる。又ヘッケル氏の言ふ處に従へば、泳鐘は變位重複した機官であるのに、之れと全く同様な構造發生を有する特別泳鐘は一個の水母と見る様な矛盾に陥らなければならぬ。ヘッケル氏の報告中にあるアトリビヤ(*Atoribia*)ロドフィサ(*Rhodophysa*)の二屬に於て、保護葉に小さな傘の存在する事實は保護葉が一個の水母で、決して他の部分と連合して一つの水母に

値するのではない事を示すと言つた。

千八百九十七年に至つてクーン氏は再び此問題を論じて管水母の幹部は *Calycephore* では最初の水母體の反口極に生ずる點に於て、又 *Physophora* の氣胞の外側の幹に續く處にある點に於て、水母の柄部に比較すべきものであつて、メツチュニコフ氏が見た *Aeginide* の幼蟲に於て、其反口極に同形な水母を芽出することゝ相同ではあるが、常に管水母と對比せらるゝ *Anthomeduse* には、柄部は決してかゝる從屬的な部分を發生することなく、常に同形の水母を作ると言つて居る。クーン氏は更にハルトラウプ氏(*Hirtland* 一八九六)がザーシアの柄部が再生する力があつて屢重複して生ずることを見てメチュニコフ氏の爲したる管水母とザーシアとの比較に賛同したことに對して駁論を試み、ハルトラウプ氏の見た様なことは普通の狀態に於ては未だ見られた事がない。若し假りにザーシアの柄部に水母體と水蛭體とが混交して生ずることとしても、管水母の幹を水母の柄部に比較することは困難である。此困難は即ちヘッケル氏を驅りて、氣胞を

傘外層の凹入だと説明するに至らしたが、此説明は *Calyceophore* の原始的泳鐘には適用することが出来ぬ。

傘外層が重複して泳鐘保護葉を突き出すことは、恰かも觸手が柄部の基部に變位すること、又は柄部が傘外層の端に續く様になること等と同様に、他に類似を見ない事で證據のないことである。かく多數機官説を以て管水母の構造を解説しやうとせば、排し難い困難に遭遇するが反之ロイカルト氏の多形現象の説を以てすれば、少しも此麼困難に邂逅することがないと結論した。

以上述べ來つた諸氏の説を概括すると、管水母に關する古來の解釋は互ひに平行した二つの徑路を踏み來つたのである。甲は多數機官説並びにその變形であるメヅーンム説で、アイゼンハルトエシユシヨルツ等の古い學者は管水母の成體を、柄部に多數の芽を擔ふ單一の水母に比較し、ハツクスレー氏は氏の個蟲の定義から單一の個蟲とし、メチユニコフ、ヘツケル等の諸氏は、幼蟲は單一の水母で、成體は其水母の柄部に水母體と機官とが交つて芽出したものであると言つた。此説は近年有力な賛成

管水母に就て(川村)

者を得ないが、全く放棄されたものでもなく、バルフォア、セジウイク兩氏は之れを採用した。乙は多數個蟲説で、ルーソー、ミルンエドワード兩氏のヒドロ群體との比較に始まつて、ロイカルト氏の多形説により大成せられ、後ケリケル、ゲーゲンバウル、クラウス、クリーン、シユナイダー氏等によりて敷衍せられたものである。注意すべき事は、今日に於て甲乙二説の相一致せざる點はハツクスレー氏の説とロイカルト氏の説とが相反目した時代に於けるものとは、稍趣を異にして居ることである。此事實からして云へば、今日兩説を多數機官説多數個蟲説と呼ぶのは或は穩當でないかも知れぬ。

六 系統發生に關する學說

曩きにヘツケル氏が管水母の祖先を二種の水母に求めたことを述べたが、系統發生に關する議論は決して此時に持ち上つたものではない。既に前章に於て明なる如く、多數機官説は管水母の發生學上の原始的の形を水母なりとし、多數個蟲説は浮游性のヒドロ群體なりとした。而して當時個體發生が系統發生と密接なる關係のあると認め

られて居たから、兩方の説は管水母の祖先を各水母とヒドロ群體とに指定した譯である。同時に又一般學者に水螅形は水母體よりも一層原始的な形で、後者は遅い時期

に二次的に作られ浮游生活に適應したもので、水螅に見ない放射形盤狀の寒天質より成る水母の傘は此際に作られたもので、柄部は水螅の營養管(Gastrotube)から移つたものと認められたから、多數機官説に於ては管水母の原始的の形は、既に傘を有した水母體であつて、此浮游性の動物から等々の運動機官例へば泳鐘氣胞等が變位又は重複に依つて生じたと主張し、反之多數個蟲説では管水母の原始的の形は傘のなき水螅體で、從て運動機官は全く新しい構造で、決して以前原始形に存して居た運動機官より導かれたものではないと主張するのである。然らば實際に卵より發生して生ずる管水母の幼蟲は此兩説によりて如何に見做されたかと云ふと、多數機官説によれば此幼蟲は眞に單一な水母形個蟲の形態學的價值のあるもので元來の原始形が遺傳的に繰返されたものであるから、系統學上に重大なる價值のあるものとし、反之多

數個蟲説によれば、此幼蟲は單に適應の結果と見る價值のあるもので、水螅が特に變形したものに過ぎないと云ふのである。

然らばヘッケル氏は此孰れに左袒したかと云ふと、勿論多數機官説の解釋である。メヅンム説が多數機官説の變身であることは之れでも明瞭である。即ち氏はメヅンム説の前半にある通り、管水母の祖先を水母形でありとし、幼蟲が系統學的に價值を有するから、幼蟲に二種の形のあることは管水母か二種類の祖先即ち水母より降り來つた證據であると述べた。

多數個蟲説を信じた人々は一様に管水母の祖先を水螅に求めたが、併し此水螅より管水母に移る所の推移形に關しては意見が同一でない。ロイカルト氏はアガルモブシス(Agalnopsis)屬の幼蟲を研究して、Physophoreの幼蟲を最も原始的な管水母の形として、管水母は多形のヒドロ群體が、浮游生活に移つたものだ云たが、クラウス(一八八四)氏は此考より少しく離れて、Calycephoraを最も簡單な管水母とし、固着して居るヒドロ群體が浮游

生活に適應したと云ふ考を排斥して、多分ヒドラクチニア、ボドコリネの幼蟲の様な一つの原始的な動物が有つて、之れが他物に附着したものがヒドラクチニア、ボドコリネの様なヒドロ群體となり、附着を遂げなかつたものが反口極に水蛸水母を芽出して *Calyceophore* となり、次で他の管水母ともなかつたのであると云つた。即ちロイカルト、クラウス兩氏は管水母の祖先を論ずるに至つて揆を別にし、ロイカルト氏はヒドロ群體あつて後に管水母ありとし、クラウス氏は兩者が同じ祖先より兩方に分岐したのであると云つたのである。

シュナイダー氏(一八九六)はロイカルト氏の説を採つてクラウス氏が *Calyceophore* を簡單なる管水母としたのに反對し、*Calyceophore* を最も簡單なるものと見ても、此れと管水母との間には系統上の差異がある。*Calyceophore* は全く別の幼蟲の形から導く可きもので、決して原始的の形ではない。管水母の系統發生に於て、ブラヌラから個蟲の集團が生ずることは、ヒドロ群體の個蟲が漸次發達増加し、ブラヌラから水蛸となり、更に新らしい水蛸

を芽出することを考ふれば、毫も説明するに困難を感ぜない。コルシエルト、ハイダー氏が考へた如く、推移點は玆に在ると云つて居る。從てシュナイダー氏は管水母は決して多數機官説の云ふ如くに水母でもなければ、又クラウス氏の云ふ如くに反口極に出芽部を備へた水蛸でもない。甚だ規則正しく造られた水蛸の群集で、ブラヌラから生じた初めの時期に、既に水蛸蟲の複雑を示すものである。但し此時期には尙一つの下に歸着して居るから、其各個蟲は個蟲よりも寧ろ機官の様に見えるが、成體に備はる諸部分既に幼蟲に於て具備せられ、正しい配置は分布して居るから、幼蟲の諸部分も亦成體と同様に形態學上の價值あるものであると云つた。

クーン氏も管水母の祖先を水形蛸に求めて居るが、氏は第一にヘッケル氏が二種の水母に祖先を求めたことを駁して、カツノカムムリの幼蟲は決して八放射形の水母より降り來つたものでなく、*Chonothopne* の幼蟲も他の管水母の幼蟲も根本的に異なる所はないと云ひ次に水蛸形より管水母を生じた徑路に關しては、ロイカルト、

シュナイダー兩氏の説を排して、クラウス氏の云ふ如くに、一つのブラヌラより分れて、ヒドロ群體と管水母との二つに成つたものであると云つて、マツク、クレデー (Mc Crady 一八五九) 氏が見たるノイコブシス、ギツベシイ (*Neuropsis gibbesi*) というヒドラ類は固着せずして、觸手を動かして浮游し、且つ其水蛭には水母が芽出することを注意し、更に又デプログラフィタス (*Diplograptus*) と云ふ筆石類の化石が、物に附着せずして浮游生活を營んだもので、多くの學者によりて管水母に甚近い關係があると思像されたことを述べて、よし此化石が管水母に關係ないにしても、筆石類の或ものは明に浮游生活を營んだもので、此邊に吾人が未だ知らないもので、管水母の起因を示すものが有るのであらうと云つて居る。

●有用動物

(明治四十一年四月三十日受領)

理學士

田中茂穂編

(第二回)

狗 *Canis familiaris*.

人類に隨伴する動物にして、毫も私慾を知らず、忠實に己れの主と頼む人の爲に働く者、夫れ狗を措いて何處に求むべき、狗は人類の最も好む動物にして、人類の有る處、狗伴はざる事無く、主として寒帶及温帶の者なれども、熱帶にも伴はれ、毫も生命を損傷する事無し、然れども熱帶の地は温度過激なる爲め、多くは其特性たる怜悯を鈍ならしむ。

斯の如く人と狗とは終始離るゝ能はざる者にして、將來も亦長く人類と相親む者なるべく、其起源に至つては數多の學者頗る苦心して研究したれども、終に全く知る事を得ざる處の者なり或は「ドーレー」より出つとし、或は「ブアンヌアー」より出づと云ひ、或は狼より出づと云ひ