

24 ♦ Siphonophores, Bud Colonies, and Superorganisms

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The problem of what constitutes an individual is an old one and was at one time much discussed by philosophers and naturalists. Attempts were made to classify animals and plants according to the level of individuality to which they had attained. Goethe, in suggesting that a plant could be viewed as an association of primary individuals (represented by leaves, stamens, petals, etc.), seems to have been largely responsible for a school of thought that, whatever truths it may have enshrined, produced some bizarre arguments. Perrier (1898) here serves us as a source of reference for the early writings on colonialism and individuality.

Individuality: Theories and Generalizations

From supposing that plants were colonies of organisms (phytons) the logical development was to treat animals similarly. It is true that authentic animal colonies exist: bryozoa, tunicates, corals, etc.; but zealous theorists extended the colony concept to the segmented worms and arthropods, viewing the annelid, say, as a sort of colony of segments (primary individuals, zoönites) united into a superorganism having its own, or secondary, individuality. This point of view necessitated granting to annelid worms an individuality of a different order from that of molluscs, a conclusion that would today find little favor. The vertebrates, a metamerically derived group, were also brought into line as "animaux zoonités," and there were outright statements by serious zoölogists that "the vertebrates are colonies" (e.g., Perrier, 1898). It is possible, of course, to regard the metazoön as a colony of cells, so individuality can be made to ascend in steps from the cellular level up through tissues (which according to Virchow possessed their own order of individuality) to organs (where Bernard maintained the same), to the segment (in the case of zoönited forms), and to the individual organism itself. This by no means represents the ultimate degree of individuality, for the animal colonies *sensu stricto*, particularly

the higher, polymorphic ones, require consideration as individuals on a super-organismic level. Above the individual level, too, we may find a social "organism" to which the primary individualities are subordinated. The insect society comes to be regarded as a superorganism. One can go further still, for colonial forms exist, such as certain calycophoran Siphonophora, in which the colony produces by strobilation groups of members ("colonies within the colony"—Beklemishev, 1958) that are eventually set free as eudoxids. For a time, while the eudoxid groups are attached and functional parts of the parent colony, the strobilating colony lays claim to status as a super-superorganism. If one is prepared to transfer the argument to the interspecific level the way is open, as Emerson (1939) points out, for classifying ecological associations by "ascending levels of super-superorganismic integration." The point arrives, however, when one comes to feel that the terms "organism" and "individual" are rapidly losing whatever meaning they originally had, and that it is time to stop classifying and return to an examination of basic principles. It immediately becomes clear that individuality is too elusive a thing to serve as a basis for classifications and schemes of a similar tendency.¹ Individuality is not simply a morphological concept nor an ecological one, but is equally genetical and physiological. Thus, separately born identical twins, though genetically one individual, are, in other respects, two; Siamese twins, on the other hand, though psychologically two individuals, are, in other respects and depending on the particular case, more or less one. We may exercise our minds with teasing questions all we wish. Is *Volvox* an individual metaphyte or a colonial protophyte? Is a tapeworm a "temporary bud-colony"? What is the status of the plasmodium? Is a multinucleate syncytial organism more or less colonial than a multicellular aggregate? Is the fusion aggregate (*Dictyostelium*) classifiable in the same terms as the fission aggregate (*Volvox*)? Are human societies "superorganisms" and, if so, how many humans and of what sorts are required to make one superorganismic unit? Questions such as these titillate the fancy and offer the same escape from actuality as "how many angels can dance on the point of a needle" offered participants in medieval disputations. But they in no way improve our understanding of organic relationships and may, indeed, if carried to excess, lead us out of touch with reality. Biology, as Stern (1962) has remarked, is like the giant Antaeus, becoming increasingly debilitated when lifted off the ground. Instead of attempting to classify end products of evolution, let us turn our attention to the processes by which they have arisen.

A conspicuous feature of organic evolution has been the achievement of increased complexity by means of replication of parts followed by their differentiation

¹ L. von Bertalanffy (*Problems of Life*, Watts & Co., London, 1952) provides a chapter on "Levels of Organization," which was overlooked when this paper was written. Bertalanffy suggests that the term "individual" is inapplicable to organisms produced by asexual fission or budding since, by definition, it applies to "something which cannot be divided." Even in higher animals the notion is difficult to apply when one considers cases such as the dizygotic individual newt produced by Spemann from fused half-blastulae, and the human monozygotic twin. Bertalanffy contrasts the "centralizing tendency" of the systems of integration (particularly the nervous system) with the "dis-integrative tendency" of the reproductive system and points out that a perfect individual would be one that did not reproduce, for reproduction "presupposes the construction of a new organism from parts of the old." Bertalanffy concludes that the concept of individuality "originates in a sphere quite different from that of science and objective observation. Only in the consciousness of ourselves as beings different from others are we immediately aware of individuality that we cannot define rigidly in the living organisms around us."

and specialization. Thus it appears that the Metazoa and Metaphyta arose from protistan ancestors (probably on several separate occasions—Nursall, 1962) by way of multicellular assemblages within which division of physiological labor and structural differentiation simultaneously and progressively became established. Among the Metazoa the same principle lies behind the process of metamerism, the serial repetition of parts within the body. In the earliest metameric forms the serialized units are presumed to have been similar, but in the evolution of higher groups the original series has often become diversified and altered almost out of recognition. Evidently, whatever the initial advantages of metamerism (and they may have been quite different in the chordate and annelid-arthropod stem groups), it predisposed its possessors to adaptive evolution on the grand scale. In the invertebrate bud colonies we have a third case where replication-differentiation has been at work. The simple bud colony consists of asexually budded units attached by direct tissue connections. The result is an interconnected assemblage of similar units, genetically all parts of one individual. One could think of the process as "external metamerism" or, alternately, one could think of metamerism as "internal budding," for the two phenomena are similar in principle. Originally bud colonies were monomorphic (and some still are), but in several existing groups, and most of all in the Siphonophora, evolution has led to considerable polymorphic specialization within the primitive series. A final example is that of the social insects. From the simpler communities, which are little more than persistent family groups, we pass to the higher societies with many sorts of individuals, so specialized and so interdependent, both metabolically and behaviorally, that they might as well be in direct physical connection. As Lüscher (1955) argues, the differentiation of castes in the termite society shows features analogous to cellular differentiation in a metazoan embryo.

It seems then that evolution, having produced an aggregate of similar units, next proceeds to develop them in different ways. In all four examples given, we start from simple aggregates. Differentiation ensues. The individual units lose certain functions and gain others. Corporately they become more interdependent as their individual potentialities become restricted. Carried to sufficient lengths, this process may lead to the submergence of the original individualities in the supervening and transcendent corporate individuality. The insect individual loses its individuality in the society, the cell in the body, the somite in the tagma, the zoöid in the colony. In each case a new individuality emerges on a higher plane.

It is doubtful if we can go much further than this in the way of meaningful generalization. The task now becomes one of examining in detail certain phases of the process as it applies in particular groups; we are here concerned with bud colonies in general and with siphonophores in particular.

Evolution of Simple Colonies

Asexually produced colonies are so common in the Invertebrata that one is bound to wonder what advantages the colonial arrangement offers and why it has so often been evolved. The bud colony is not far removed from the asexually reproducing organism in which the buds detach and in some groups both types of organism are found. Thus the majority of hydroids form bud colonies, but in *Hydra* itself the buds detach.

Asexual reproduction has clear advantages. It enables an organism to increase its tissue mass without increasing the size of the individuals. The proliferating tissues go to form numerous replicas of each genetic individual instead of toward making the individual larger. This avoids problems connected with large size and may be beneficial from the point of view of dispersion. The question then is—why were the first colonies, in which the budded individuals failed to separate, successful? One advantage of the colony would seem to be that the retention of the buds naturally leads to a branching, arborizing structure, “a very profitable mode of growth” (Thomson and Geddes, 1931), ensuring a high density of individual zooids in a given space without overcrowding. As Knight-Jones and Moyse (1961) comment, “the colonial habit regulates competition between zooids.” Where a strong exoskeleton is produced, the colony may form a towering structure, permitting utilization of water layers some distance above the bottom.

A number of advantages of the colonial habit are really advantages associated with close aggregation of individuals and would apply whether or not the individuals were physically connected. It is probable, however, that the first colonies were developed among organisms in which the individuals tended to aggregate, and that the tendency to aggregation later became formalized in the retention of primary connections. We can therefore consider the benefits of aggregation as relevant to our topic. In the case of filter-feeders, close proximity, in addition to increasing turbulence in moving water, would permit the combination of the individual feeding currents and hence shifting of water masses from considerable distances into the vicinity of the colony. In the colonial ectoproct *Plumatella fungosa* the lophophores over wide regions become orientated by muscular action so that they point in the same direction (Mackie, unpublished). In tunicate colonies effluent currents often combine to carry wastes far away from the colony, and, in *Pyrosoma*, to serve for colonial locomotion. Although waste disposal would seem at first sight to be a wholly desirable function in an aggregated population, it is possible that a tendency to accumulate certain metabolites in the vicinity of the population might be important. Loomis (1961) has shown that densely aggregated hydras become sexual through feed-back effects of accumulated metabolites in the micro-environment surrounding them, and there are other possibilities for coördination of functions by what Lucas (1961) calls “ectocrine” mediation. In an established bud colony, however, chemical coördination could be achieved much more directly by means of the connecting tissues, and it is doubtful that ectocrine influences continue to be important once the colonial stage has been reached. Knight-Jones and Moyse (1961) draw attention to a distinct advantage of the colonial organism over the non-colonial aggregate: if part of the colony is in an unfavorable location, the zooids and connecting tissues in that region can be absorbed and the material derived from them used elsewhere. In crowded, non-colonial populations (*e.g.*, barnacles) many individuals die wastefully. Finally, the bud colony has a clear advantage over the non-colonial aggregate in those cases where coördinating nervous mechanisms are developed. Coördinated withdrawal responses occur in corals (Horridge, 1957) and hydroids (Josephson, 1961) and in the ectoproct *Cristatella* (Mackie, unpublished). Stimulation of one zooid leads to a wave of contraction that spreads rapidly over part or all of the colony. Presumably the response makes the colony less vulnerable to predation. In a non-colonial aggregate a predator could work systemati-

cally through the group, without its presence being communicated to more than one individual at a time.

One need not suppose that all of these factors were equally important in the evolution of bud colonies, or that the different groups arose in response to the same needs, but it is clear that there are advantages in the colonial habit that enable one to explain the success of the first and simplest colonies without invoking the more dramatic benefits associated with polymorphism.

Integration in a Polymorphic Bud-Colony

In the first colonies evolved, polymorphism was presumably absent or developed only to a slight degree. Polymorphism has occurred to varying extents in the different major taxa, and it is possible to arrange colonies into categories according to the degree of polymorphism and the extent to which integration of functions has occurred. Thomson and Geddes (1931) offer such a series of categories (seven in number) culminating in the siphonophores. More recently Beklemishev (1958) has provided a valuable comparative account of animal colonies and has attempted to define the formative principles involved in colonialism. Theoretical treatment of this subject is, however, hampered by lack of exact knowledge concerning the functional organization of colonies. It is obvious, when one considers how the members of a siphonophore colony are morphologically specialized into six or more polymorphic types, that an equivalent degree of functional specialization must also exist and that, where the functions are spatially segregated in this way, integrative mechanisms are to be expected. Recent studies aimed at determining the extent and character of integration in the siphonophore colony can appropriately be reviewed, at this point, with *Nanomia cara* (suborder Physonectae) serving as an example.

While certain activities in this form are organized on a colonial level, others are carried on more or less locally. At the lowest level, that of cellular effectors, we find activities such as ciliary beating, discharge of nematocysts, and movement of pigment in chromatophores, which seem to be carried on without the direct involvement of the nervous system and are thus attributable, in Parker's sense (1919), to "independent effectors." (In other respects these cells are presumably no more independent than any other cells.) The chromatophore response is of recent discovery (Mackie, 1962) and requires further investigation, but the evidence now available indicates that the pigment movements are not endogenously controlled. The response is to light, the pigment dispersing in daylight, concentrating in the dark. The chromatophores in isolated members of the colony respond as do those in the intact colony. If part of the colony is placed in the dark and another part is illuminated, dispersion of the pigment occurs only in the region illuminated. Normal responses are exhibited by specimens subjected to prolonged deep magnesium anesthesia. From preliminary studies, acetylcholine and epinephrine seem to have no effect on the condition of dispersion or concentration. Here, then, we may have something approaching the ideal independent effector.

Moving from the cellular level up to that of the individual zoöid in the colony, we find certain activities that originate in and do not spread beyond individual zoöids. The latter behave, indeed, as if they were nervously isolated, though it is

always necessary to bear in mind that, while the effector response is exhibited locally, the nervous excitation causing it may be more widespread; Fulton's (1961) observations on the hydroid *Cordylophora* show that peristaltic movements in the hydranths, which at first sight seem to originate locally, prove to be coördinated over the whole colony. Local effector action in *Namonia* (fig. 24-1,A) is shown by posterior nectophores, which pulsate when lightly touched; by nectophores and bracts in autotomy; by gastrozooids ingesting and egesting food; by palpons eliminating wastes; and by tentacles performing spasmodic changes in length during fishing behavior (Mackie, in press; Mackie and Boag, unpublished). In some cases, however, instead of being expressed in pure isolation, activities spread to neighboring zooids. The contraction of a tentacle following stimulation leads to elongation and writhing not only of the associated gastrozooid, but of gastrozooids further up or down the stem. The stem itself shows no muscular response in this behavior, and it is assumed that the excitation passes to the gastrozooid by means of the nervous system. Such histological studies as exist indicate that nerves are present throughout most regions of the siphonophore colony—for instance, in *Physalia* (Mackie, 1960); but *Nanomia* itself has not yet been studied sufficiently from this point of view. The spreading of writhing behavior among the gastrozooids occurs naturally when food is captured, and the movements doubtless increase the rapidity with which the gastrozooids make contact with the food. After contact is made, the gastrozooid proceeds to spread itself over the food, ingesting it in whole or in part. Food taken in is submitted to extracellular digestion in the basal region of the gastrozooid, and the partially digested product passes into the stem canal through the basal valve. Both gastrozooids and palpons are equipped with basal valves, and the material contained within them may be isolated from the contents of the stem canal at certain times and be continuous with it at other times.

In the subsequent course of digestion an unusual sort of coöperation occurs between gastrozooids and palpons. Rhythmical contractions ensue in each of these members, by which fluid is alternately taken in and squeezed out through the basal valve. Cells in the walls of both types of zooid take up food particles and digest them intracellularly. Although each zooid seems to have inherent rhythmicity, it is a common observation that a gastrozooid, being larger than the palpons, comes to dominate several of the latter in its vicinity, filling them when it empties and emptying them when it fills. Thus local, rhythmically coördinated groups are set up. From time to time a palpon may withdraw temporarily from the group by shutting its basal valve and proceeding to expel wastes from the tip. The "integration" of these to-and-fro pumping movements is probably achieved by hydraulic means, and there is no reason to suppose that the neuromuscular mechanisms responsible for the individual rhythms are coördinated by the nervous system.

Turning finally to integration at the highest level, we find that certain activities are organized on a general basis throughout the colony by the integrative action of through-conduction systems. The response to strong stimulation of the siphosomal appendages and posterior nectophores is one of general contraction of the stem accompanied by a burst of forward-swimming movements by the nectophores (medusoid locomotory members). Stimulation of the float and anterior nectophores causes reverse swimming. Each nectophore has two muscle systems: the system of circular fibers lining the subumbrellar cavity, whose contraction causes the swimming jet; and a set of radial fibers at the upper corners of the velum (fig. 24-1, "fibers of

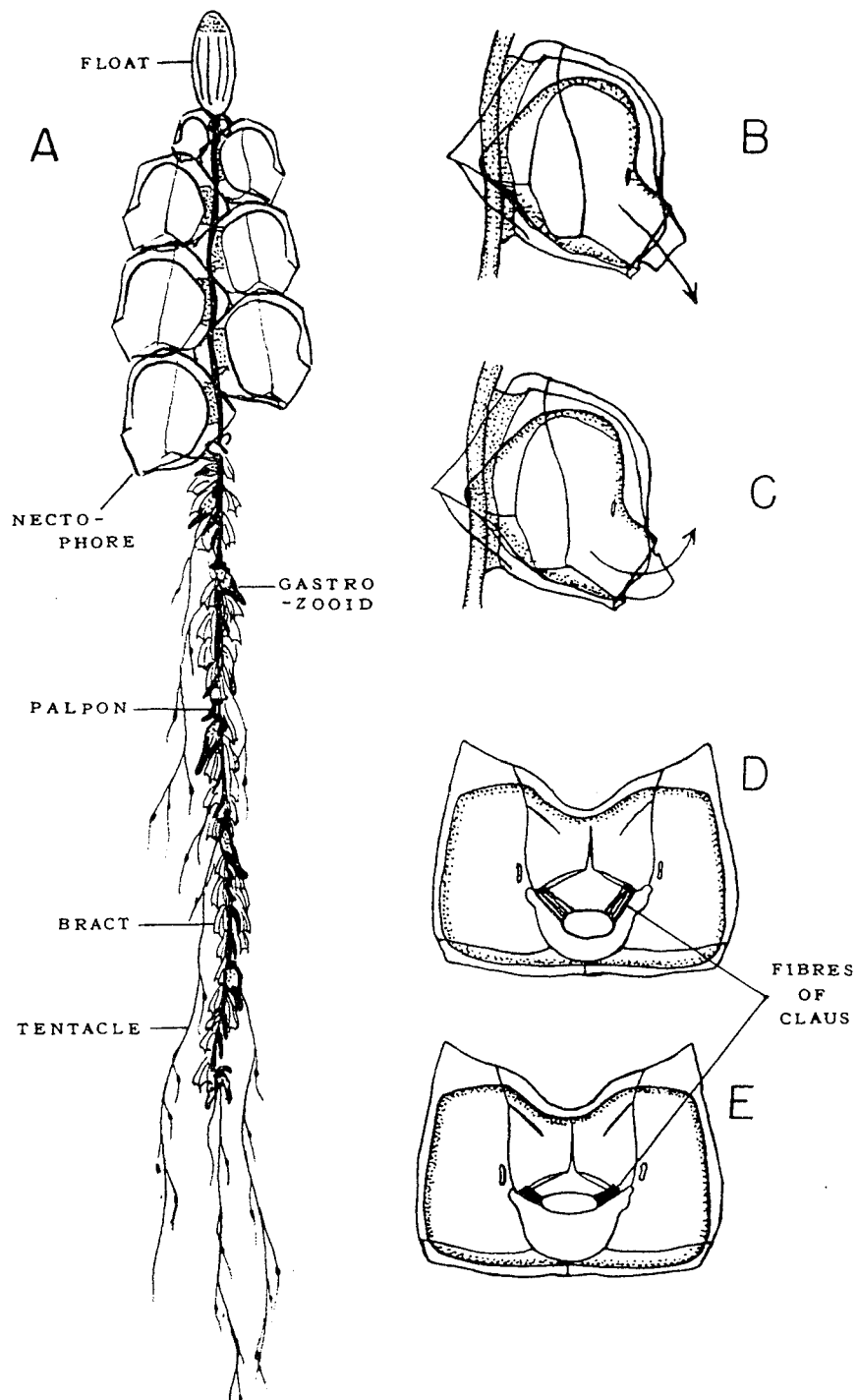


FIGURE 24-1. *Nanomia cara*: A, whole colony—a young specimen; B, lateral view of a nectophore in forward-swimming response; C, the same, reverse swimming; D, frontal (abaxial) view of nectophore, velar fibers of Claus relaxed, as in forward swimming; E, the same, fibers of Claus contracted, as in reverse swimming.

Claus")), which alter the shape of the velum, diverting the water jet forward. In forward locomotion, only the circular system contracts; in reverse, both systems contract simultaneously. Numerous observations and experiments (Mackie, in press) go to show that: (1) the nectophores act together as a group both in forward and in reverse swimming, showing either general activity or general quiescence at any given time; (2) the nectophores active at any time are either all swimming forward or all backward; (3) forward and reverse swimming responses are through-conducted by separate systems and can, to some extent, be selectively eliminated by surgical operations on the nervous system or by controlled levels of anesthesia.

We are not here concerned with the details of these responses and the three characteristics listed are simply given to show that, in locomotion, the activities of the individual members of the colony are completely controlled by, and subordinated to, the "colonial will" (*volonté commune*—Vogt, 1853). Not only is the morphology of the nectophore meaningless unless seen in the context of the colony, but its activity is useful only in the sense that it is useful to the colony.

The Colonial Individual

In locomotion and in some other activities, the siphonophore behaves as a well-integrated unit. It darts around in a rapid and agile manner, going into reverse on striking a resistant object, showing perfect coördination and "unity of purpose" throughout. The fact that certain other activities are carried on more or less locally does not mean that the organism is poorly integrated. There is no need for all activities to be integrated at the highest possible level; much can be left to local action systems. Even in man himself an important set of activities—the gut movements—is organized on a largely autonomous basis. No one would suggest that the siphonophores are "higher animals," but they are the most complex celenterates and the only ones to have explored fully the possibilities of colonialism. They have developed colonialism to the point where it has provided them with a means of escaping from the limitations of the diploblastic body-plan. The higher animals escaped these limitations by becoming triploblastic and using the new layer, the mesoderm, to form organs. The siphonophores have reached the organ grade of construction by a different method—that of converting whole individuals into organs. It is interesting to speculate that, had it not been for the invention of the mesoderm in some remote, diploblastic era, the highest animals on earth might now be, if not the Siphonophora, something similar to them in principle.

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