

2 Siphonophores

A metaphysical case study

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2.1 Introduction

The problem of biological individuality, as it is called, is as important as it is unfortunately named. Its importance lies in its role as a point around which we can organise a good deal of metaphysical thinking about biology. The poor name lies in the use of the term “individuality”. If we do not allow ourselves to be misled by terminology, we can get a clearer view of what the problem is and why it matters. Once we have that, we can *test* our preferred solution against the biological data. For metaphysics must be answerable to science even as, from my neo-Aristotelian vantage point, it reigns over science as an a priori discipline supplying the conceptual framework without which science itself makes no sense.

The unwise reliance on the term “individuality” or “individual” is that it is too general; therefore, it is capable of interpretations that put biologists and philosophers at cross purposes among themselves and with each other. An individual is, if nothing else, a *countable unit* of some kind. (This is all there is to individuality for Lowe 1998, p. 160, 2009, p. 55.) Oak trees and salamanders are individuals but water and gold are not (though pools of water and lumps of gold *are*). Bees are countable; so are their colonies. The legs of kangaroos are countable units: all normal kangaroos have two of them. The species of kangaroo are also countable units, of which there are four. Kangaroo DNA, by contrast, is not countable, though we can count kangaroo chromosomes (16 for both species of grey kangaroo).

We might insist on more than mere countability for individuality, but we will still have a very generous and not highly discriminatory bag of biological particulars.¹ Adding a spatial criterion, for example – a particular location, a set of boundaries (however fuzzy), contiguous matter – will still let in entities that, for important metaphysical reasons, we should keep separate. Colonies of organisms and parts of organisms have locations and boundaries (however rough and ready for the former), and the skeletons of calcium carbonate connecting the polyps of many coral species turn a colony of organisms into a contiguous unit.

Metaphysically, we should want to distinguish *parts* of organisms from *organisms* themselves, and both from *groups* of organisms (of which colonies are the ones of special biological interest). As Ellen Clarke puts it:

The problem of biological individuality can be distinguished from the problem of defining living systems by focusing on what properties separate living individuals from living *parts* and from living *groups*, while taking the property of life itself for granted.

(Clarke 2010, p. 316; emphases in original)

Here, by “individual” she clearly means “individual organism”. It is the status of organism rather than the status of individual that should be our preoccupation. Stephen Boulter frames the question as being whether “the working biologist can readily identify the individuals of a given species, and distinguish these individuals from their biological parts and from the groups they may join” (Boulter 2013, p. 608). Again, the tripartite distinction is arguably correct, but the question should *not* be thought of as solely – perhaps even primarily – one for the working biologist. Nor, evidently, does Boulter himself think so. Rather, the metaphysician should *inform* biological practice by giving biologists the conceptual tools for placing biological entities into one of these three ontological categories.

Is the tripartite distinction – between (i) parts, (ii) organisms, and (iii) collectives, colonies, or groups of organisms – correct? By this I mean: is the distinction exhaustive and mutually exclusive? For a neo-Aristotelian, the answer must be yes, given Aristotle’s own strict distinction between substances, parts of substances, and pluralities of substances. As a neo-Aristotelian, I subscribe to thesis **T**: all concrete biological particulars are either organisms or parts of organisms or collectives of organisms, and do not belong to more than one of these categories.

We all accept the existence of members of each category, but the interesting question is whether any biological particular can belong to more than one of the categories or to none. If the answer is affirmative, it is likely to be because of the truth of the second disjunct – that it can belong to none of the categories – rather than the first. For, at least on the traditional understanding of these things, to be a part of an organism is precisely *not* to be an organism, to be an organism is *not* to be a collective, and so on. My gut bacteria and I live in a symbiotic relationship, but it would be plain bad science to say that the bacteria were literally *part* of me – organs like my kidneys or liver, or parts like my skin or blood cells. A lion might belong to a pride but is not *itself* a pride, nor a member of a school of fish itself a school, nor is any organism literally *composed* of other organisms, and so on.

It would be more plausible to wonder whether there were a biological particular that fit into *none* of the three categories – perhaps because it had enough features of more than one of the categories for there to be no

sufficient reason to place it in any particular category rather than another. In any case, whether one allowed that such a particular might demonstrate the categories not to be mutually exclusive or whether one thought that it showed them merely to be non-exhaustive, it would refute the tripartite distinction as usually understood by Aristotelians. In other words, *thesis T* is *falsifiable*. Does this make it an empirical hypothesis? Or does it mean that metaphysical theses can sometimes be falsified by empirical data? Probably the best way to understand *T* is as a hybrid – an empirical hypothesis essentially informed by metaphysical considerations. If a falsifier exists, this will be an empirical matter, but its existence will show the underlying metaphysics behind *T* to be wrong. Whatever the correct interpretation of the methodology, thesis *T* opens up an excellent opportunity to test a broadly Aristotelian understanding of life.

2.2 Parts, organisms, colonies

The specific test case on which I focus as a possible falsifier of thesis *T* is that of the siphonophores, in many ways the most curious of the marine animals. Before examining them, however, we need to understand the content of *T*. (For more detail, see Oderberg 2018.) What is it that differentiates parts, organisms, and colonies? (Rather than looking at groups in general I limit the analysis to colonies since this is where the controversy over siphonophores is most acute.) I do not propose to give a formal definition of these three kinds of biological particular, as this would require an article of its own. In general, I adhere to an “ontological independence” view of substance as understood in the Aristotelian tradition. (The view broadly agrees with that of Lowe 1998, chapter 6.) An organism is an individual substance of the biological kind. Its independence consists in its not being *essentially* dependent on any other particular except for its own parts. The concept of essential dependence here is quite strict. Loosely, organisms essentially depend on food, water, oxygen, an ecosystem, and so on, but this loose dependence is *causal* in kind. Food, water, and the like are necessary for keeping an organism in existence, enabling it to develop, or flourish, or adapt to its environment. Organisms are the *kinds* of things that need food, water, and so on. Moreover, taking in some kinds of nutrition and not others (carnivore versus herbivore, for instance) can be part of *what it is to be* a certain kind of organism, but only in the sense that organisms have certain *properties* – Aristotelian *propria* in the strict sense – that are necessary for belonging to the essential kinds to which they belong. (See Oderberg 2011.)

Strictly, however, by which I mean the strictness of *essential constitution*, an organism – as a living substance – is not *defined* in terms of things other than itself, by which I mean other than its own body plan, structure, arrangement of parts, suite of functions, and so on. All organisms will have at least one part, and one function, that relates essentially to things distinct from the organism and its parts – other organisms, organic entities such as

types of food, inorganic entities such as air and water, and so on. But that does not mean the *organism* is defined in a way that depends necessarily on the *existence* of any of these other things. A colonial organism might not live long without a colony to inhabit, but its *definition* – its classification in the ontological scheme of organisms – does not require that any colony actually *exist*.

Contrast organisms with parts and colonies. A part of an organism *cannot* be defined except in terms of things other than itself – that is, things other than its own structure, functions, arrangement of its own parts, and the like. The part must be defined in terms of the whole organism it subserves – an entity beyond the boundaries of the part itself. For the part to exist – for it to *be* a part of an organism – there must also exist an organism of the right kind for the part to subserve. Aristotle was right to hold that a part without a whole to subserve is a part in name only – his famous “homonymy” principle (*Metaphysics* Z:10, 1035b23 and elsewhere, Ross 1928). We can speak of organs grown in labs, organs kept on ice after the organism has died, and other “edge” cases, but strictly such entities are better thought of as *proto*-organs, or *former* organs that may (if transplanted) become literal organs once again. (For more on edge cases, see Oderberg 2018.)

A colony looks as though it can, like an organism, be defined wholly in terms of its own structure, functions, arrangements of parts, and so on. This, however, masks the asymmetry between colonies and organisms. Colonies do not, strictly speaking, have parts: they have *members*. Or perhaps more precisely, they cannot *only* have parts but must have members as well, whereas organisms do not have *members* except in the archaic biblical sense synonymous with *organs*. If, for example, we take a beehive (the artificial housing structure) to be part of a bee colony – though I find this a more dubious way of talking than speaking of the hive as a structure used by the colony though not strictly part of it – then we can see that bee colonies cannot be defined solely in terms of parts such as these. They must be defined – not merely additionally but *primarily* – in terms of *members*. And these members – the individual bees – are themselves organisms that are *not* defined in terms of the colonies to which they belong, even if the colonies are obligate. As I suggested earlier, a colonial organism might need a colony to survive, just as it needs food, but neither its food nor its colony has to *exist*, definitionally speaking, in order for the organism to exist.

Still, it might be objected, the asymmetry between organisms and colonies is not yet clear. If the organism is a substance because it is defined wholly in terms of its own structure, body plan, functions, and arrangement of parts, without the existence of anything else being metaphysically *entailed* by this definition, why isn't the colony also a substance? When defining colonies we still do not “stray outside” the colony itself: we can define it solely in terms of its functions, the identity and function of its parts (if it has any parts), the identity and function of its members, the structural and organisational relations between them, and so on. The existence of nothing else is entailed

by defining the colony in this way. In reply, the objection does not show that the cases are symmetrical. When defining the colony in terms of its members we *do* stray outside the colony proper, so to speak. This is because the members, as organisms, do not have a *complete definition* in terms of their functions in respect of the colony; unlike a part of an organism – an *organ*² – which *is* completely defined by its subservience to the whole of which it is a part. So while it is true that an organism's existence entails, metaphysically, the existence of its parts,³ and a colony's existence entails, metaphysically, the existence of members,⁴ the former entailment does not take us, metaphysically, beyond the organism, but the latter entailment does take us beyond the colony.

It is crucial to appreciate that by “metaphysically” in this context the neo-Aristotelian means “definitionally, as constitutive of the kind of thing an entity is”. When we “zoom in” on the organ, ontologically speaking, our purview never goes beyond the organism – since the organ can only be completely understood in terms of its function in respect of the whole. When we “zoom in” on a colonial member, by contrast, our purview can and does go beyond the colony. This is because a complete definition of, say, the individual bee, or ant, or coral polyp, or bacterium includes non-colonial elements – individual structure, internal function, parts, and so on. In other words, the colonial members must be understood as organisms in their own right before their colonial functions are taken into account. Even if the colonial behaviour is obligate, and even if this behaviour enters into the essential definition of the kind (about which we need not have any settled view), it cannot be completely defined by such behaviour. Hence the earlier metaphor of “straying outside” the entity in question cannot be cashed out in purely spatial terms. We have to grasp what it is we must look at when we seek to define the entity. When we see things in this way, the asymmetry between colonies and organisms is as manifest as that between organisms and organs.

2.3 Siphonophores

With this stage setting in place, let us now examine perhaps the hardest case for Aristotelians and their adherence to thesis **T** – the siphonophores. These are an order of marine animal⁵ belonging to the phylum *Cnidaria*, the latter defined by the possession of cnidocytes or explosive cells containing nematocysts or organelles that fire toxic structures into the cnidarians' prey. The phylum includes sea anemones, corals, jellyfish, and multifarious hydrozoa or “sea serpent animals” that have either or both of a polypoid form (vase-shaped structure with a base at one end and a circular mouth surrounded by small tentacles at the other) or a medusoid form (floating, bell-shaped structure with trailing tentacles).

The siphonophores themselves come in three sub-orders – physonects, cystonects, and calycophorans (Totton 1965). These are distinguished by the combination of primary structures present, and there are three of these

as well. The first, moving from top to bottom, is the pneumatophore, which is a gas-filled float enabling flotation and vertical motion through the water column. The second is the nectosome: a stem-like region containing nectophores, individual bell-like structures or medusae enabling the siphonophore to swim through the water forward, backwards, and in turns. The third is the siphosome: a stem-like region containing a large number of diverse structures performing specialised functions of the type we would expect from any organism – feeding, predation, reproduction, protection, and excretion being the main functions. The physonects have all three primary structures; the cystonects have a pneumatophore and siphosome only; the calycophorans have only a nectosome and siphosome. *Physalia physalis*, known popularly as the Portuguese man-of-war, is a cystonect and is the best known of the siphonophores. Although I will speak generally of the siphonophores and refer to other species, I will refer more frequently to *Physalia physalis* as an exemplar of the order: certainly it exemplifies the metaphysical problems that make all of the siphonophores such a threat to thesis T. It is impossible even to scratch the surface of the entire order of siphonophores in a single, relatively short discussion. Many species are poorly understood, some barely at all. If, though, the Aristotelian can defend thesis T against the claims of *P. physalis* and a few other specific examples, it is highly probable, albeit not certain, that it can be defended against siphonophores as a whole.

2.4 “Colonial organism” and “poly-person”

Ever since Thomas Huxley, Ernst Haeckel, and Louis Agassiz did their heroic work in the 19th century expanding our knowledge of the siphonophores, including their taxonomy, biologists have wrestled with how they are to be understood at the basic level: are they individual organisms or colonies of organisms? The standard contemporary answer is given by Stephen Jay Gould: “Are siphonophores organisms or colonies? Both and neither; they lie in the middle of a continuum where one grades into the other” (1984, p. 29). This idea is embedded in the view expressed by Jack Wilson. He first states: “the same intuitions that allow us to count puppies and tomato plants with confidence leave us perplexed when we try to count colonial siphonophores like the Portuguese man-of-war” (1999, p. 1). He goes on to propose a kind of ontological pluralism, whereby a siphonophore counts as a “sufficiently functionally integrated living entity” to be what Wilson calls a “functional individual”, lying on a spectrum of greater and lesser integration (1999, p. 63f.). This indifference to the strictures of thesis T is found also in E. O. Wilson, who first writes that although siphonophores “resemble organisms”, each one “is a colony”. This looks like adherence to T, but Wilson immediately goes on to say: “The resolution of the paradox is that siphonophores are both organisms and colonies” (Wilson 1975, pp. 383, 385).

Indifference to thesis **T** is seen in the common nomenclature, whereby siphonophores are routinely described as “colonial organisms” or “colonial animals” (Wilson 1975, p. 386, Dunn 2009, p. 233, Siebert et al. 2015).⁶ If **T** is true, nothing can be *both* a colony *and* an organism or animal. It might be a colony with some organism-like properties, or an organism with some colony-like properties, but this does not seem to be the way the description is applied. The implicit rejection of **T** goes back to Ernst Haeckel, who coined or at least brought to prominence the terms “poly-organ” and “poly-person” to describe the theories that siphonophores were, respectively, single organisms with organs or else colonies of organisms. He considered both the poly-person and the poly-organ theories to be right in some ways, but that each exaggerated the phenomena supporting its side. Rather, he claimed, “the truth lies midway between the two interpretations” (Haeckel 1888, p. 2f.).

Biologists typically do appeal to the sorts of phenomena that metaphysicians are also concerned with when it comes to overarching metaphysical classifications of biological particulars. To attribute to them any self-conscious, let alone systematic, *metaphysical* thinking about what they are investigating is usually, however, hasty. For instance, George Mackie, probably the leading contemporary expert on siphonophores, in one place describes them as “complex, highly polymorphic creatures, whose ‘colonies’ are composed of many polypoid and medusoid ‘individuals’, and yet they function physiologically as single individuals” (Mackie, Pugh, and Purcell 1987, p. 98). Yet in another, published in the previous year, he characterises them unambiguously as colonies (Mackie 1986). In neither place, though, does he recognise the apparent inconsistency of his claims. What is required is a biologically informed, metaphysical analysis of siphonophores, rather than relatively breezy or relaxed assertions whether from biologists or philosophers.

2.5 Structure and function: the zooid

It is useful to follow Gould by dividing into three the kinds of phenomena that give rise to so much classificatory difficulty: structure and function; phylogeny; and reproduction and growth. (Gould speaks of “growth and form” for the third, but form belongs to structure and function, and the points he raises for the third category touch reproduction and growth more than form, despite some overlap (Gould 1984, p. 28).) The first concerns the very structure and function of the siphonophore. Everything ever written about siphonophores, at least since the end of the 19th century, will tell you that they are constituted by *zooids* – literally, “animal-like” beings. The term “zooid” itself is as slippery as the metaphysical classification of siphonophores is thought to be. It is used to denote locomotive biological particulars produced by and living within an organism, in particular spermatozoa. Is a spermatozoon an organism? If thesis **T** is correct, then given

that it is neither a colony nor in any obvious sense a *part* of the organism that produces it, it must itself be an organism. That said, it has to be admitted that spermatozoa are rather strange organisms, given that they do not themselves fall within the usual biological taxonomy – they do not belong to species although they belong to the producing organisms that *themselves* belong to species. They are highly specialised; indeed, they have a single function: find an ovum and fertilise it. They do not themselves reproduce; on the other hand, they possess locomotion, which is at least necessary for animality (Oderberg 2007, pp. 183–193). Whether, however, they are sentient – necessary and sufficient for animality (ibid.) – is barely explored, though they may well have a form of memory (Brugger, Macas, and Ihlemann 2002). The difficulty of assessing the metaphysical status of spermatozoa is, so many believe, found equally if not more so in the zooids of the siphonophores.

Taking *Physalia* as our exemplar, its zooids divide into medusoid and polypoid: the medusoid zooids are bell-like structures usually with tentacles or tentacle-like attachments near the mouth and hanging down, and the polypoid zooids are polyp-like, that is, roughly tubular in shape with mouth and tentacles pointing up. Its main zooids are: gastrozooids for feeding; gonozooids for reproduction, containing further zooids called gonophores – sacs containing gametes; various protective and defensive zooids such as palpons and dactylozooids attached to long tentacles descending from the pneumatophore, which is the large, gas-filled float that keeps *Physalia* floating and drifting on the ocean surface. The pneumatophore is part of the protozooid – a polyp that develops from the embryo and gives rise, through budding, to all the other zooids. The tentacles contain the nematocysts, or stinging cells that deliver the well-known, painful venom to many a hapless swimmer. An important zooid lacking in the Portuguese man-of-war is the nectophore, a medusoid structure used for swimming. This places *Physalia* in the sub-order of cystonects, siphonophores having only a pneumatophore and a siphosome – the part of the stem with the feeding, reproductive, and protective zooids. *Physalia* might, according to some observation, have nectophores and vestigial nectophores in the siphosome, but it is doubtful that they are for locomotion and they are poorly understood (Bardi and Marques 2007, p. 432; see Totton and Mackie 1960 for the most detailed study of *Physalia physalis*).

There is an immense amount of polymorphism among the siphonophores and their constituent zooids, but virtually all the zooids are for the purpose of feeding, locomotion, reproduction, or defence – as one would expect from any animal. Why, then, should they not be categorised as *parts* of the organism – as *organs*? Critics of thesis T, including those whose criticism is implicit in the relaxed use of the term “colonial animal”, claim that siphonophores “have a life cycle wherein multiple asexually produced zooids, each of which is homologous to a free-living solitary animal, remain attached and physiologically integrated throughout their lives” (Dunn and Wagner

2006, p. 743). Homology is the sharing of traits derived from a common ancestor, the implication being that the zooids are so similar to their free-living homologues, both derived from ancestral animals, that they are “persons” as much as “organs” – impoverished organisms whose function is to serve their colonial master.

The response to this point is twofold. First, whether the zooids are homologous to free-living animals is irrelevant, as I will argue when discussing the phylogenetic criterion of metaphysical status in Section 2.6. Second, the bare assertion that they are homologous begs the question whether the implication of the assertion is that the zooids are *as good as* organisms. Consider Julian Huxley’s view (1912, p. 120):

In the majority of Siphonophora, the persons of the colony have mostly only a historical individuality: some of them are sometimes so much modified and reduced that it has baffled all the zoologists to decide whether they are homologous with individuals or with mere appendages of individuals: and in function each is devoted so little to itself, so wholly to serving some particular need of the whole, that if one were separated from the rest, it would appear a perfectly useless and meaningless body to an investigator who did not know the whole to which it belonged.

Huxley’s use of the term “person” notwithstanding, the thrust of his remarks is that the zooids are *parts* of the whole rather than *members* in the colonial sense. On this, at least as far as structure and function go, I submit that he is correct. The zooids do not function like organisms, do not look like organisms, and have no free-living phase (Gould 1984, p. 24). Each zooid is highly specialised, performing a single task – whether feeding, protection, locomotion, reproduction, among others.

Note that the free-living eudoxid stages of calyco-phorans are *not* independent zooids that have detached from the polygastric siphonophore. The siphosome on all siphonophores is a repeating column of sections called cormidia, consisting of zooids in similar arrangements. In *P. physalis*, each cormidium contains a gastrozoid, gonodendron, and dactylozoid with tentacle (Totton and Mackie 1960, Bardi and Marques 2007). Most calyco-phorans release a *cormidium* that develops into a free-living sexual unit – the eudoxid stage – that releases gametes via its gonophores, with the gametes fertilising to form the larval stage of a new polygastric calyco-phoran. This gives us no reason to think the cormidium that is shed was an individual organism while belonging to the polygastric siphonophore. In its free-living state, it is plausible to consider it an organism whose sole purpose, like that of a locomotive gamete such as a spermatozoon, is reproductive. (The same can be said of the released sexual medusoids of other siphonophores such as the physonect agalmids.) It has a gastrozoid and tentacle for feeding, a bract for protection, and the gonophore also serves for locomotion due to

the lack of nectophores (Carré and Carré 1991, p. 30). As part of the polygastric calyphoran, however, it is no different to any of the undetached cormidia, and as such should be regarded as a part.

As for the transition from part to free-living organism, we can simply invoke the Aristotelian homonymy principle broadly understood. Just as a dead, severed part of an organism is a part in name only, and a corpse of an organism is an organism in name only, so a *living* part produced through autotomy, as in the case of calyphorans, is no longer truly a part but an organism in its own right, having undergone a substantial change on detachment. This is a form of asexual reproduction, accompanied by the sexual reproduction resulting from gametes released by the eudoxid. It is obviously not alternation of generations, which is both haploid and diploid, but the alternating of sexual and asexual reproduction in the calyphoran parallels alternation of generations and so is hardly a source of mystery on this score.

The status of the zooids as organs is clear from their extreme specialisation. The nectophores are purely for locomotion (Mackie 1964): they rely on other zooids for capture and distribution of food and for protection. In *Physalia*, the gastrozooids and gonozooids rely on the tentacles and dactylozooids for protection, the gastrozooids rely on the tentacles for food capture, the gastrozooids supply nutrition to the other zooids, they all rely on the pneumatophore for flotation and motion, and so on. Contrast this with, say, a bee or ant colony. We should generally, I submit, treat their colonial behaviour as a property of the individual organisms – in the strict Aristotelian sense of a characteristic metaphysically “downstream” from their constitutive essence and so not part of their *definition*. But even if, in some cases, the colonial behaviour is part of the very definition of the kind, it will not exhaust our understanding of the function and behaviour of the colonial organism, which must always be an organism *first* and colonial in nature *second*. With siphonophore zooids, however, their constitutive essence – what they are in their very nature – is to be specialised parts of a whole.

Again, although siphonophore zooids have “nerve nets”, loose distributions of neurons considered primitive precursors of central nervous systems in animals with bilateral symmetry; this does not mean that they are independent organisms working together as members of a colony. In physonects, for example, there is a “giant axon” running along the stem and a connected ectodermal nerve net linking the giant axon to all the zooids, making possible a quick contractile reaction to stimuli (Grimmelikhuijzen, Spencer and Carré 1986, p. 474). Indeed, according to Mackie, the interactions between the stem and the other zooids give siphonophores “behavioural capabilities equalling or surpassing those of other cnidarians”, including by implication true jellyfish – which are agreed on all sides to be individual organisms and yet with nervous systems of similar primitiveness (or sophistication!) to siphonophores (Satterlie 2011). In physonects and calyphorans, moreover, although there are nerve nets and nerve rings in each nectophore, they are all connected by nerve tracts to the stem, enabling their typically graceful

and totally co-ordinated swimming movement (Gould 1984, p. 24, echoing Mackie 1973). Contrast this with corals, which form a true colony: each has a nerve net, but these are not connected (though corals do sit on a shared exoskeleton).

In short, there is nothing in the structure and function of siphonophore zooids themselves that points to their being individual organisms within a colony. Their extreme specialisation, co-ordination, nervous connections, and inability to survive as free-living units indicate clearly, albeit not infallibly, their metaphysical status as true *parts* of a whole organism, defined entirely in terms of their function in respect of the whole. This is not to say, given our relatively thin understanding of siphonophores, that we might not discover something about the zooids that overturns this judgement. But if we are after absolute certainty, biology is not always the best place to look.

2.6 Phylogeny: the evolution of coloniality

According to Gould (1984, p. 24), by the criterion of evolutionary history the siphonophore zooids are “individual polyp or medusa organisms” since siphonophores are colonies that “evolved from simpler aggregations of discrete organisms, each reasonably complete and able to perform a nearly full set of functions (as in modern coral colonies)”. He goes on to assert: “But the colony has become so integrated, and the different persons so specialized in form and subordinate to the whole, that the entire aggregation now functions as a single individual, or superorganism”. Note first that the term “superorganism” is not merely useless but positively invites confusion. Strictly, it is applied to colonies of conspecific organisms such as ants and termites (Hölldobler and Wilson 2009); loosely, it is abused to the point where even human beings have been described as superorganisms (Kramer and Bressan 2015), with the implication that very few metazoa end up as individual organisms at all. In neither the loose nor strict sense does the “super” prefix yield ontological illumination. Gould’s usage here is perhaps a *ne plus ultra* of obfuscation, since “single individual” is disjoined with “superorganism” – the former is qualified by “functions as”, and the disjunction is qualified by “entire aggregation”. Not that we should have expected a philosophical treatise from a biologist writing a popular article, but rather the cloudiness of expression is symbolic of the overall confusion and (perhaps understandable) lack of philosophical care taken by biologists in general.

That said, the thrust of Gould’s claims is clear enough: since siphonophores evolved from single organisms coming together into increasingly integrated colonies, the zooids of siphonophores are persons and the whole is a colony. Mackie (1986, p. 176) quotes Dendy (1924) as stating an “important biological truth”, namely that “evolution consists, to a very large extent, if not mainly, in the progressive merging of individualities of a lower order in others of a higher order”. Lest one think Mackie concludes that the

“individualities of a higher order” include siphonophores as individual organisms, note his insistence that “while the general concept (individuality) is useful, we run into problems when it comes to calling specific objects individuals” (1986, p. 176). This does not mean he regards them as true colonies either; rather, the question of metaphysical status is, as it is for Gould, not deep enough to be important or precise enough to be answerable.

Yet why should we even think that the conclusion of Gould’s argument follows from its premises? As background, we know very little about how the cnidarians evolved, let alone the siphonophores in particular. As Mackie, Pugh, and Purcell (1987, p. 121) put it, citing Scrutton (1979): “The numerous gaps in the palaeontological record hamper any attempt to establish a phylogeny and in the case of siphonophores it is debatable whether any fossil record has been found”. Moreover, they add, citing Werner (1973), recourse to inferring ancestral structure from investigation of current morphology and life history is perilous, since “such information can be interpreted in different ways and any evidence can be taken to support totally different theories”.

There does seem to be general agreement that so-called “colonial organisms” such as the siphonophores represent a stage in the evolutionary road to truly multicellular organisms, if not chronologically – since the zooids are already themselves multicellular – but conceptually, inasmuch as they are at the highest level of colonial integration short of full individuality as organisms. Whereas, some speculate, the triploblastic animals (most animals on earth) were able to develop true organs due to the presence of a mesoderm, the diploblastic siphonophores escaped their limitations by developing functional specialisation of the zooids that were once, presumably, free-living organisms that found an adaptive advantage in attaching to each other and acting in a highly co-ordinated manner (see further Wilson 1975, pp. 384–386, Mackie, Pugh, and Purcell 1987, p. 110, Niklas and Newman 2013).

Suppose all of this is true. How is it relevant to the metaphysical status of actual siphonophores? It does not follow, from the assumption that siphonophores evolved from free-living, unspecialised organisms, that their specialised zooids are themselves organisms. Compare the speculation about siphonophores to the endosymbiotic theory of Margulis (1970) concerning the origin of eukaryotic cells. According to the theory, these originated from the colonial integration, via symbiosis, of various prokaryotes – most notably the bacteria that became the mitochondria of the eukaryotic cell. If the theory is true, this does not imply that actual eukaryotic cells are colonies. If it did, then it would turn out that there were far fewer individual organisms in existence than anyone ever thought.⁷ only the bacteria and archaea would make the cut! The implication is absurd, as is the thought that if multicellular organisms evolved colonially from free-living single-celled organisms, the former must themselves *be* colonies. In other words, a colonial *origin* does not entail a colonial *status*. More generally, the thesis that

ontology recapitulates phylogeny is as untenable as the discredited biogenetic law, associated with Haeckel but going back euphonically to Meckel, that *ontogeny* recapitulates phylogeny. There is simply no good reason to think that we can read off, from the phylogenetic origin of a species (where I use “species” in the broad, metaphysical sense⁸) its metaphysical status as colony or organism. What it *is* and where it *comes from* are distinct questions. To be sure, homologies between zooids on the one hand, and free-living polyps and medusae on the other might give us good indicators of the evolutionary origin of siphonophores. From that, however, we cannot infer that zooids, metaphysically speaking, are just like their free-living homologues except for serving a colonial master. On the contrary, what we know of siphonophore zooids, in terms of their structure, function, and overall morphology, tells us that they are organs – parts of organisms – even if it is true that they arose from a radical transformation of prior, free-living polyps and medusae.

Indicative of the confusion between ontology and phylogeny is Beklemishev’s account of the evolution of colonial animals, as recounted by Wilson (1975, p. 387). Beklemishev, says Wilson, was influenced by “two venerable ideas: the concept of the superorganism and the view that biological complexity evolves by the dual processes of the differentiation and integration of individuals”. He identified

three complementary trends as the basis of increasing coloniality: (1) the weakening of the individuality of the zooids, by physical continuity, sharing of organs, and decrease in size and life span, as well as by specialization into simplified, highly dependent heterozooids; (2) the intensification of the individuality of the colony, by means of more elaborate, stereotyped body form and closer physiological and behavioral integration of the zooids; and (3) the development of cormidia, or “colonies within colonies”.

(Wilson 1975, p. 387)

It does not, however, take much reflection on (1) and (2) to see that these are not criteria of increasing *coloniality* but of increasing *individuality* – the individuality of the organism, of which each part is defined wholly in terms of its subservience of the whole. As to the third criterion, it cannot be used as a criterion of coloniality without begging the question. That aside, we have no more reason for thinking of cormidia as colonies within colonies than we do for thinking of them as organisms in their own right.

2.7 Growth and development

Gould believes that growth and development provide an “*embarras de richesses* by presenting evidence for and against both theories”, namely the poly-person and poly-organ theories (1984, p. 28). In support of the latter

Gould observes, correctly, that “a siphonophore begins life as an unambiguous person”, whose later development is but the “elaboration of this one individual”. Why? Because all siphonophores develop from a *single embryo* (leaving aside eudoxids, which, if they are organisms at all, are, I tentatively suggest, no more siphonophores than the gametes they produce). The embryo develops into a protozoid, the original polypoid zooid that then buds all the other zooids of the siphonophore. At its most general, metaphysically speaking, the budding of zooids from an embryonic siphonophore is no different to the budding of limbs and organs in a human embryo, each individually, or in groups, specialised for a given suite of tasks serving the organism.

Given this pattern of embryological development, a problem for the colonial view immediately arises: if the mature siphonophore is a genuine colony, is the larva also a colony? What about the planula, a free-swimming cylindrical entity with no zooids yet budded? Why would one call this anything other than a unitary organism, except because of retrospective bias in favour of the view that siphonophores *must* be colonies because of the zooids? Yet if one weakens the view to one of indifference as to whether the larva is a colony or an organism, how is this a more reasonable position? There is no reason for indifference about the status of the larva other than the magic – as opposed to the non-existent virtue – of 20/20 metaphysical hindsight.

For Gould, however, ontogeny is not as decisive as I claim it to be. He argues:

Admittedly, each colony begins life as a single ovum, but it then develops a series of entities – full persons in this view – by budding from a common stem. This is a familiar mode of growth for many aggregations conventionally regarded as colonies. A stand of bamboo or a field of dandelions may trace its origin to a single seed, yet we usually view each budded stem or flower as an individual.

(Gould 1984, p. 28)

We must immediately put an irrelevant consideration to one side, namely that the genetic identity of the zooids of a single siphonophore entails their belonging to a single organism. Clonal colonies, such as bamboo, are also genetically identical (copying errors and mutations aside). What differentiates the bamboo from the siphonophore for present purposes is the nature of the processes in each case. Gould is guilty of conflating the way in which siphonophores *grow and develop* with the way in which bamboo *reproduce*. When siphonophores bud zooids they are not reproducing themselves; reproduction is a wholly separate process involving the gonozooids and their gametes, resulting in a new protozoid from which bud new zooids, giving rise to a new siphonophore. By contrast, when a bamboo grows rhizomes that bud new culms, what results are precisely that – new culms, that is, new

mature bamboo stems *reproduced* (asexually) by the parent, which itself was reproduced via rhizomes from another culm, or from a seed produced by another culm, or from a cutting. What results each time are new bamboo trees, completely the same in morphology and function to their conspecific asexual parent. To analogise this *reproductive* process to the *developmental* process of zooid budding is either to miss the point or to beg the question in favour of prior indifference to thesis T.

The same point can be made against Gould's analogy between zooid budding and dandelion reproduction. The *Taraxacum* genus, containing the many species of dandelions, reproduces new plants by sexual or asexual methods, including sexual self-pollination. Each method results in a new plant morphologically and functionally identical to the parent and, like bamboo, sometimes physically separated and sometimes not. Again, the disanalogy with siphonophores should be apparent. Gould's phrase (1984, p. 28), "trace its origin to a single seed", is therefore highly ambiguous since there are many ways in which this can apply to an organism or a colony. Moreover, to regard the siphonophore as tracing its *origin* to a single embryo is, at least on the interpretation implying numerical distinctness between siphonophore and original entity, to make a metaphysical mistake – since the embryo *is* the siphonophore at a juvenile phase. If it is not, then what is it? No biologist suggests anything other than what I have just stated to be a metaphysical truth, albeit such a truth is low level enough to be a staple of biological literature. If the siphonophore is a true colony, then so is the embryo, the planula, and the later immature larval stages before zooid differentiation has taken place. Yet this seems absurd on its face – for what is colonial about a planula?

2.8 Conclusion

There is no question but that the siphonophores are a fascinating class of marine creatures, about which our ignorance is still great despite over a century of investigation. That there is a real debate to be had about their metaphysical status is evident from the historic disagreements among biologists over how to understand them, a disagreement that biology itself, without being philosophically informed, is unable to resolve. Moreover, the more recent indifference to thesis T – a thesis that implies a binary way of answering the question whether the siphonophore is an organism or a colony, in other words whether the zooids are themselves organs or organisms – itself belies the metaphysical position such indifference implies. For to take a pluralistic approach to status whereby several incompatible understandings apply, or an indifferentist approach whereby no particular status truly applies, is itself to take a metaphysical stand – to endorse the proposition that, as Gould (1984, p. 29) puts it: "since nature has built a continuum from colony to organism, we must encounter some ambiguity at the center. Some

cases will be impossible to call as a property of nature, not an imperfection of knowledge”.

If my analysis is correct, then siphonophores provide no evidence for the truth of this proposition. If my analysis is merely plausible but not determinative, then at the very least both biologists and philosophers should be less hasty than they often are when pronouncing in favour of the claim that Gould, and others such as Mackie, put forward. What should be most welcome on all sides is a proper debate about the metaphysical status of the siphonophores (and other magnificently troublesome creatures) so as to determine finally whether – as I have argued – thesis **T**, with the Aristotelian metaphysic behind it, withstands attack on this front and retains its place as being, so Aristotelians believe, in full conformity with natural science.

Notes

- 1 I speak of “biological particulars” here rather than “biological entities” so as to make clear that my concerns in this chapter are not about processes, events, properties, species, other taxa, and so on, all of which are biological entities in a broad sense. A biological particular, so understood, is not merely a unitary entity, a countable thing, but a *functioning* entity – a biological thing that operates, behaves, exercises powers, is a participant in events and processes, and possesses properties. It should therefore be evident that I do not subscribe to the “process ontology” account of biological particulars found most notably in Dupré (2012), though it would take a separate article to evaluate processual theories in the detail they deserve.
- 2 Note my somewhat loose use of the term “organ”. I do not mean merely something recognised as an organ in an anatomy textbook, but any part of an organism – such as a patch of skin, a lump of tissue, a fragment of bone – that has a function in respect of the whole, whether as part of an organ proper or of some other discrete structure or functional entity within the organism.
- 3 Again, not any particular parts, just parts of a certain kind; and not in *abnormal* cases, where an organism can exist without a part of some kind (such as a leg or tail).
- 4 Not any particular members, just members of a certain kind (queen, drones, workers, etc.).
- 5 They belong to the kingdom *Animalia*, but by calling them animals I do not mean to prejudice the very question of whether they are organisms or colonies!
- 6 The meaning here being quite distinct from the usual one of “organism/animal that *lives* in a colony”.
- 7 Unless one entertained the idea that an individual metazoan organism could literally be composed of billions of colonies; not an idea I recommend anyone take seriously.
- 8 Meaning, in other words, the sense of the term “species” – as in Aristotelian genus and species – from which the biological sense historically derives. In biology, the species is what an Aristotelian metaphysician regards as the *infima* or *lowest* species in the taxonomic hierarchy. Metaphysically, the infima species is one of many levels of species, which for the biologist are all taxa with their own technical names (such as *order*, *kingdom*, or *family*). Note that the metaphysical sense

of “species” carries across all of reality rather than being confined to biology. Even non-Aristotelian metaphysicians happily speak of “species of artefact” or “species of chemical compound”.

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