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WHAT IS A PART?

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INTRODUCTION

Anyone familiar with bicycles would have little trouble listing the major parts: handlebars, frame, seat, front wheel, back wheel, pedals, drive chain, and so on. The hierarchical structure of parts in bicycles is also fairly obvious: for example, the links in the drive chain are parts of the chain and therefore what might be called "subparts" of the bicycle. In machines, the parts are usually quite distinct, and the hierarchical level at which a part occurs—part versus subpart—is fairly unambiguous. This is less true for organisms. For example, in a primate, a hand might seem to be a part of the whole animal, but it also seems to be a part of the arm, and therefore a subpart of the animal. In an individual in a bryozoan colony—a zoid—it is not clear whether the caecum (stomach) is merely a continuation of the pharynx (anteriorly) and of the pylorus (posteriorly) or whether it is a part distinct from both of them. (We will return to this example later.) What is a part, in principle? And how can we identify parts in practice and determine the hierarchical relationships among them in real organisms?

For many studies of organismal structure, parts can be taken as unproblematic. Phylogenetic systematics is mainly interested in the homology of parts (and of their attributes), functional anatomy is interested in how parts interact to perform tasks, and studies of morphological and functional complexity are concerned with numbers of different types of parts in organisms. In these areas, we typically identify parts using preexisting perceptual mechanisms, or gestalts. The success of our analyses ordinarily leaves little reason to doubt that these gestalts are highly reliable, that the parts we have identified are biologically significant features of organisms. Also, in these areas, we can often choose parts opportunistically, incorporating into our analyses only structures which would be recognized as parts by any observer, the uncontroversial parts. For example, in studies of complexity, limb-pair types have been used as parts of the limb series in arthropods (Cisne, 1974), and vertebrae as parts of vertebral columns (McShea, 1993). At the level of the whole metazoan, cells have been used as the parts (Bonner, 1988; Valentine *et al.*, 1993; Bell and Mooers, 1997).

For certain purposes, however, reliance on gestalts and uncontroversial parts is quite limiting. In studies of complexity, it would be helpful to be able to count numbers of part types in whole organisms, not just in serial structures like vertebral columns, and to make these counts at any chosen hierarchical level, not just the cell level. In particular, our motivation in examining the parts issue here is mainly to develop methods for testing a certain hypothesis about the evolutionary relationship between numbers of part types and the emergence of new hierarchical levels.

The hypothesis is the following. In the history of life, as organisms combined to form higher-level functional entities, functional demands on these organisms would have been reduced. For example, as metazoans formed from clones of free-living eukaryotic cells, or as integrated marine invertebrate colonies formed from the budding of free-living polyps or zooids, functional demands on each cell, polyp, or zooid would have been reduced. Then, assuming that number of functions is correlated with number of part types (McShea, *in review*), the reduction in functional demands on the organisms should have been accompanied by a reduction in the number of part types they contain. That is, selection should have favored a 'loss' of part types in the interest of economy. Thus, cells in metazoans and land plants should have fewer part types than free-living eukaryotic cells, and zooids or polyps in highly integrated colonies should have fewer part types than those in less integrated colonies. (For details and alternative formulations of the hypothesis, see McShea (*in press*)).

The hypothesis will not be tested here. For present purposes, the point is only that in order to test it, we need methods for identifying and counting part types, say, within bryozoan zooids, in a consistent fashion. Importantly, a proper test requires that we identify the parts at a specific hierarchical level. The hypothesis predicts that the loss of part types will be most manifest at the level closest to and just below the zooid (McShea, *in press*), roughly at what might be called the organ level (although see later). Thus, while it might be tempting to use cells as the parts

in zooids, or even genes, because counting types is convenient, both lie a number of hierarchical levels too low.

Methods for identifying parts could be useful in other areas as well: for example, in phylogenetic studies, giving equal weight to parts at different hierarchical levels can bias the analysis, but it may be difficult to establish the level at which a part occurs. Thus, methods for identifying parts at a single level in a consistent way would help to weight parts appropriately.

Here, we propose a technical definition for the term "part," one which corresponds fairly well with its colloquial meaning and with our gestalts, and then briefly discuss the relationship between parts and other concepts, including the subject of this volume, characters. Next, we propose a way to (partly) operationalize the definition, a series of protocols for identifying certain kinds of parts, what might be called object parts or structural parts, at the hierarchical level just below the organism. We argue that, for certain comparative purposes, counts of object parts can be used as a proxy for counts of true parts (i.e., all parts fitting the technical definition). Then, we formalize the protocols with a "parts key," which shows how to use the protocols to identify object parts in apparently simple organisms. Finally, we use the key to produce a tentative list of object-part types for certain bryozoan zooids.

The protocols, key, and parts list were the major goals. However, this paper was also an exercise, an experiment, to investigate the following: given an *a priori* definition of parts, can protocols consistent with that definition be devised and then consistently applied to produce an intuitively reasonable list of part types? By this standard, the exercise was fairly successful, although—as will be seen—practical difficulties remain. However, a more telling test of the usefulness of the exercise lies ahead: if the parts identified in this way are biologically significant, then robust associations should be found between these parts and other variables. One example would be the correlation discussed earlier, between number of part types and the emergence of higher levels of functionality. Others can be imagined.

The intent here is not to introduce a new concept. In much of biology, including anatomy, systematics, and the study of adaptation, we routinely assume that organisms have identifiable parts. Rather, the point is to try to formalize and to (partly) operationalize our understanding of a notion that is already commonplace, indeed, that is foundational.

Our discussion is based on analytical treatments of individuality by Campbell (1958), Hull (1980), Mishler and Brandon (1987), and Ghiselin (1997), of integration and isolation by Olson and Miller (1958) and Bonner (1988), of modularity by Mittenhall *et al.* (1992), Wagner and Altenberg (1996), and Raff (1996), and of hierarchy by Wimsatt (1974, 1994) and Saithe (1985, 1993).

PARTS: IN PRINCIPLE

A. A Technical Definition

In the present discussion, a part is a system that is both integrated internally and isolated from its surround. Concretely, a crystal, such as a diamond, is a part. A free diamond is integrated internally in that its component carbon atoms are tightly bonded to each other, and it is isolated from its surround in that they are only weakly bonded, or not bonded at all, to the atoms in the surrounding air. By the same standard, most bicycle frames and individual organisms are parts.

Integration refers not just to bonds between components but to any interactions that produce correlations in the behaviors of the components (Campbell, 1958). Systems are integrated to the degree that interactions among components are many or strong, or both. Thus, interactions can also take the form of signals among components, in which case a spatially distributed system can also be a part. In organisms, possible examples include a hormone-mediated control system, or at a higher hierarchical level, a local population of crickets chirping in synchrony.

It has been pointed out that correlations may occur as a common response by components to an external cause, without any interactions among them (J. Padgett, personal communication). For present purposes, interaction-based parts seem sufficient; however, a more inclusive definition may be necessary at some point, as the investigation is extended.

Isolation is a reduction in, or termination of, integration. In some parts, isolation is a consequence of an intervening boundary, as in a gas-filled balloon or a cell. In others, the isolation is a consequence simply of the termination of integration, such as occurs at the surface of a crystal. In spatially distributed parts, isolation may be a consequence of the specificity of the signaling with which integration is achieved. The chirping cricket population may be a part, even if individuals of other species occupy the same space, perhaps the same patch of lawn, provided the chirp signals responsible for the integration are species specific, and therefore effectively isolate the population.

Integration and isolation are both required for parts. A group of people sitting in a train car may be isolated from a similar group in the next car, but neither group constitutes a part if its members are not interacting among themselves. Conversely, an arbitrary subset of guests at a cocktail party may be interacting strongly with each other, but they do not constitute a part if they are also interacting strongly with other guests outside the subset. Both integration and isolation may vary continuously, and therefore the extent to which a system is a part—its degree of partness—is likewise a continuous variable.

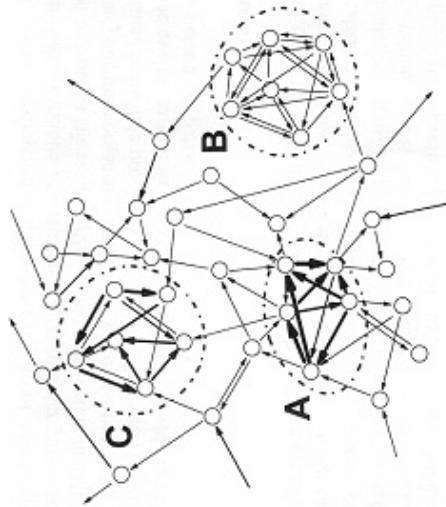


FIGURE 1 Parts. Small circles are components. Arrows show interactions among them; the thickness of the arrows corresponds to the strength of interactions. Parts are enclosed by dashed lines.

In the discussion and examples just given, it is understood that the patterns of integration and isolation which constitute parts are stable. Of course, stability is relative to some chosen time scale. Over the adult life of a multicellular organism, the structures we call organs tend to be fairly stable. Certain patterns of neural activation, such as might be responsible for a behavior, are also stable—and therefore parts—but on much shorter time scales.

Figure 1 shows parts abstractly. In the figure, the small circles are components and the arrows show interactions among them. The thickness of the arrows corresponds to the strength or intensity of the interactions. Parts are enclosed by dashed lines. What characterizes each part is the large number of interactions and/or their greater intensity relative to the number and/or intensity of interactions with the surround. Part A has few internal interactions, but they are strong relative to its weaker interactions with external components. Part B has weaker internal interactions, but they are many relative to interactions externally. Part C is intermediate.

B. Relationship to Other Terms

1. Characters

Colless (1985) distinguishes character-parts from character-variables and character-attributes. Variables and attributes refer to descriptions or measurements of aspects of organisms (Frstrup, 1992), while parts refers mainly to the physical structures that constitute organisms. Importantly, Colless notes that character-parts can be construed to include processes, or patterns of interaction, such as behaviors and metabolic cycles, as well as objects. Thus, parts as used here correspond well with Colless's character-parts.

2. Individuals

Parts are close to "individuals." Mishler and Brandon (1987; see also Hull, 1980; Ghiselin, 1997) list four criteria for individuality—spatial localization, temporal localization, integration, and cohesion. Parts meet some of these criteria. Like individuals, they must be integrated. Some parts will also be cohesive; more generally, the requirement is that they must be stable, as discussed. Also, parts are located in space, and therefore have boundaries, or at least limits of some kind; however, parts may also be spatially distributed and therefore not highly localized in the usual sense. Mishler and Brandon point out that biological entities meeting some but not all of the criteria may nevertheless behave as individuals in certain respects, and in certain contexts. Parts seem to fit this description fairly well, and therefore might be called individuals.

In many contexts, however, the term individual is applied exclusively to organisms. For example, it has been used to distinguish a well-integrated multicellular organism from a mere colony or aggregate of independent cells (e.g., Buss, 1987); only the organism would be called an individual. However, by the present definition, both could equally be parts.

3. Modules, p Groups, and F Groups

Our understanding of a part is also close to what Wagner and Altenberg (1996; see also Wagner, 1996), Raff (1996), and others have called a "module." The difference is that modules are internally integrated and externally isolated units in the development of an organism, in its generation or manufacture. On the other hand, parts are units in what might be called the "operation" of an organism, which is limited to processes occurring within the organism once it has been generated, such as adult physiology. Mittenthal *et al.*'s (1992) "dynamic modules" include both developmental and operational entities. In organisms, the distinction is not perfectly clean, but it is sufficiently so to make the use of different terms appropriate.

There is also some connection between parts and the entities that Olson and Miller (1958) call *p* groups and *F* groups. *P* groups are developmental entities, like modules. *F* groups are functional entities; parts may be functional but need not be, and therefore part is a more inclusive term.

4. Difficulties

Our choice of the term "part" is somewhat problematic. For one thing, as the term is used colloquially, it would not include most spatially distributed systems, such as a chirping cricket population or a hormonal regulatory system. For another, we usually think of parts as entities within larger wholes, entities that are "part of" something, but our technical definition includes many entities that we normally think of as standing alone, such as crystals and whole organisms. (Although arguably, all entities—except perhaps the universe itself—actually are parts of some larger whole, whether or not we choose to think of them that way.) On the other hand, almost any entity that would qualify as a part in colloquial usage would also qualify under the technical definition. In any case, other terms that might have been chosen instead of part, such as entity, thing, component, or system, would also have been problematic. In the present discussion, we use these other terms in their colloquial senses, in cases where a technical term is unnecessary or where ambiguity is helpful.

C. Part Hierarchies

Here, hierarchy refers to the physical nesting of parts within parts, or what Valentine and May (1996) called a cumulative constitutive hierarchy. Wimsatt (1994) described as "compositional levels of organization," and what Sathe (1985, 1993) called a scalar hierarchy (see also McShea, 1996a,b).

The parts occupying a given level in a hierarchy consist of internally integrated and externally isolated sets of components (often, subparts) from the level below. These may also be integrated with other parts at the same level to produce parts at the next level up. Notice that the level in a hierarchy at which a part occurs is purely a function of the topology of the system, not of the part's absolute size. Figure 2 shows a hierarchy in which C and D are parts of the whole, and A and B are parts of C. Thus, A and B occupy the hierarchical level below D, even though A, B, and D are all about the same absolute size. Indeed, if E is a part, it occupies the same level as C and D, although it is smaller in absolute terms than either. Further, notice that the hierarchical level at which a part is placed will be very sensitive to changes in our decisions at higher levels. For example, suppose that we discovered upon closer examination of the system that, contrary to Fig. 2, A and B are not highly connected, and therefore that part C does not exist. In that case, parts A and B would be promoted to the next higher level and would become parts on the same level as D.

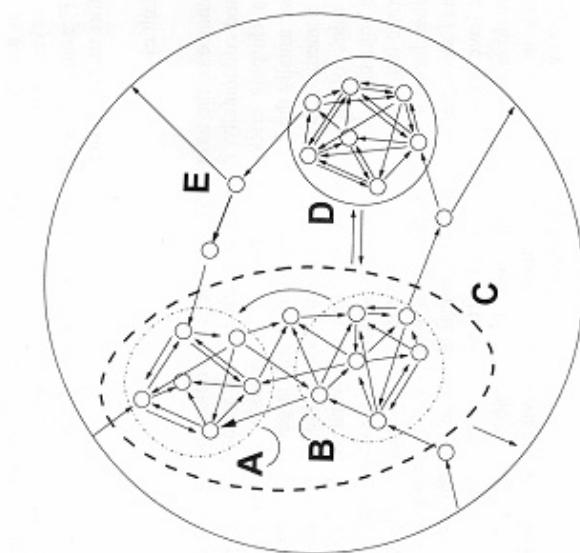


FIGURE 2 Hierarchical relationships among parts. Circles and arrows are as in Fig. 1 caption, except that strengths of interactions are not shown. D and E are parts; see text for discussion of the status of A, B, and C.

In Fig. 2, the occupation of hierarchical levels by parts is discrete, in that each part occurs exclusively at one level. In organisms, however, occupation of levels is often continuous in that parts may cross levels, existing simultaneously partly at one level and partly at another. For example, suppose that in Fig. 2, A and B were only weakly integrated, so that C would be only weakly a part. In that case, A and B would occupy two levels at once, the higher level at which D occurs and the lower level just below D. More precisely, they would occupy each level only to some degree. Alternatively, suppose that A and B were well integrated with each other but only at certain times, or in certain functional contexts. In that case, A and B might shift back and forth between levels. This crossing of hierarchical levels is undoubtedly quite common in organisms, and one of the main reasons for their apparent complexity (Wimsatt, 1974), for the difficulty we have in parsing them into their component parts at each hierarchical level.

Because level occupation may be continuous, we have no *a priori* reason to think that discrete levels will be identifiable at all in organisms. However, some

levels do seem to be occupied more or less discretely, in particular those levels which have experienced especially intense selection (Maynard Smith, 1988). In multicellular organisms, for example, cells would seem to be parts at a single hierarchical level, presumably as a result of selection in the past, and to occupy that level fairly discretely, for the most part. Similarly, in most metazoans, the entire multicellular individual is a part, and individuals seem to occupy that level discretely. However, parts at levels between cells and multicellular individuals—parts at roughly the tissue, organ, and organ-system levels—have presumably not been selected at their own level, but instead seem to have been interpolated by selection at the individual level. Thus, they are more likely to cross levels and therefore to occupy any given level more ambiguously.

In the discussion of bryozoan parts in the next section, we assume that in bryozoans, selection occurs or has occurred in the past at the level of the zooid, and we take advantage of that fact to anchor the analysis hierarchically. In other words, we assume that all zooids in bryozoans occupy the same hierarchical level, and therefore that all parts one level down from the zooid occupy the same level. However, because parts are not expected to occupy the hierarchical level just below the zooid especially discretely, counting part types at that level in a consistent way is expected to be a rather uncertain undertaking.

Notice that the hierarchical structure of organisms based on this conceptual scheme need not accord with the classic object hierarchy in biology, also called “levels of organization” [not to be confused with Wimsatt’s (1994) more precise “compositional levels of organization”]. Conventionally, these include: ... organelle, cell, tissue, organ, organ system, multicellular individual, Despite the intuitive appeal of this list, the identity of the structures that occupy each level is an empirical issue, one on which—for most levels—we have little solid evidence. For example, it is not obvious that all of the structures we call organs occupy the same hierarchical level in any organism.

D. Parts and Function

In the present scheme, functionality and partness are independent notions. Parts can be functional, as a bicycle tire is, but a nail that punctures and becomes buried in the tire is also a part. Likewise in organisms, an essential organ might be a part, but nonfunctional structures, or even deleterious ones, can also be parts. Indeed, a system of components with a randomly configured pattern of interactions—a random “wiring diagram,” so to speak—would likely be entirely functionless, but would probably contain a number of internally integrated and externally isolated subsets of components, i.e., parts (Kauffman, 1993).

However, this is a conceptual separation only. Arguably, in organisms, functions are expected to be very closely associated with parts. Briefly, the reason is that in order for a system to function, it requires a certain amount of internal coordination, and therefore integration to achieve that coordination, and also some

degree of isolation, to limit interference from other systems. Thus, for example, to the extent that an organism must be able to move and feed at the same time, and to the extent that these functions require different activities, components involved in locomotion are expected to be isolated from those involved in feeding. More generally, selection for function is expected to have isolated functions to some degree in parts. However, the relationship between number of different functions and number of part types is not expected to be simple, not one to one, for example. See McShea (in press) for a longer treatment of this issue.

This argument is a modification of a similar one by Wagner and Altenberg (1996). They suggest that selection for evolvability is expected to produce developmental modularity; the present argument is that selection directly for function itself is expected to produce a kind of operational modularity, i.e., parts, regardless of developmental organization. (Of course, this too is only an in-principle separation; in organisms, developmental modules may correspond closely with parts.)

The hierarchical level occupied by a part is, like partness itself, independent of function in principle. However, also like partness, there is reason to suspect that function is relevant in fact, in particular, that the hierarchical organization of parts in organisms is partly a consequence of selection. The argument is based on the notion of "screening off," a concept which has proved useful in analyzing levels of selection. [See Brandon (1996) for a more formal treatment; see also Roth (1991).] For present purposes, what is significant is that in organisms, higher-level functions often screen off lower-level functions. For example, in vertebrates, the malfunction of one or a small number of nephrons (possible "subparts") in a kidney (possible part) is screened off by, and would not interfere with, the function of the kidney as a whole. Likewise, the malfunction (e.g., occlusion) of a single small blood vessel ("subpart") is partly screened off by the function of the circulatory system as a whole (part), which has some capability to revascularize tissues deprived of sufficient blood supply. To the extent that upper-level functions are insulated from lower-level variation in this way, a hierarchical arrangement of functions is presumably advantageous. Thus, to the extent that parts organization follows functional organization in organisms, a hierarchical arrangement of parts is also expected.

instead be a subpart in a larger part that includes the adrenal medulla, the hypothalamus, and other systems. Parts are also expected to vary in absolute time; the parts in a sea urchin larva change dramatically during metamorphosis. Thus, any attempt to decompose an organism into parts must first specify a temporal scale and a range of absolute time over which parts will be identified.

2. Unique Decomposition

In the present scheme, the parts organization of a system is a function solely of the number, intensity, and configuration of interactions within it. It follows that—at a given temporal scale and range—every system has a single, unique decomposition into parts, subparts, and so on. (Granted, that decomposition may be difficult to discern in practice.) A possible objection is that, as Wimsatt (1974) has pointed out, the decomposition of organisms into parts varies with theoretical perspective. For example, viewed as a device for locomotion, a tetrapod limb is decomposable into one set of components, but viewed as a device for thermoregulation, it has a different set, and the two sets have noncoincident boundaries (Wimsatt, 1974). Actually, this insight raises no problem for present purposes. Different theoretical perspectives amount to different functional decompositions, and the fact that a system has many functional decompositions does not deny that it has a single wiring diagram like that in Fig. 2, or in other words, a single pattern of parts, subparts, and so on at each timescale.

Interestingly, it is not obvious that a tetrapod limb would, by itself, count as a part in the present scheme. A limb might amount to little more than a group of components which various parts share, perhaps with some overlap. For example, the bones, muscles, and other components associated with locomotion might constitute one part, while the circulatory system, sweat glands (if present), and so on constitute another. Another way to say this is that the relative reductions in integration at the boundaries of the locomotory and temperature-regulatory parts might be more significant than the reduction that occurs at the mechanical joints near the proximal end of the humerus or femur. Whether or not this is true is an empirical matter; in any case, the partness of a limb is not problematic in principle.

PARTS: IN PRACTICE

We propose a general strategy and a series of protocols for constructing a partial list of part types in an organism (i.e., a sample of all part types), in particular, the part types occupying the hierarchical level just below that of the whole organism. The temporal scale and range of interest is that portion of an organism's (presumably, adult) life over which its internal structure is relatively stable.

The protocols were devised for organisms that seem to be structurally fairly simple (at the level just below the organism), that is, for organisms containing only

E. Two Clarifications

1. Temporal Scale and Range

Just as stability is time-scale relative, as discussed, degree of integration and isolation—and thus partness itself and the hierarchical level of parts—are also time-scale relative. For example, a circulatory system might be a part in some very short time-scale process like respiration. However, in a (facultatively) longer time-scale process, such as a fight-or-flight response, the circulatory system might

a small number of loosely packed objects, readily distinguishable from each other, in a fluid matrix. In particular, they were designed for identifying part types just below the zooid level in bryozoans. Applying them to more complex organisms and to other hierarchical levels might be possible, even straightforward, but it is also possible that difficulties not addressed here would arise.

Notice that our goal here is to produce a list of different part *types*, rather than of all parts (including duplicates of the same type). However, for simplicity, we will often refer simply to parts, omitting the word “types.”

A. A Strategy: Object Parts

If we knew the complete pattern of interaction within an organism, that is, its complete wiring diagram (like Fig. 2), all parts would be equally visible and their hierarchical levels apparent. In the absence of such diagrams, we can still identify many parts using morphological boundaries, or physical demarcations, in other words, using objects. In practice, the objects used will be those that are typically visible in dissections, photographs, and anatomical drawings at a magnification that is low relative to the size of the organism. The assumption is that the appearance of an object is usually a consequence of the relatively tight integration among a set of components, and that the limits or boundaries of objects correspond to reductions in integration. Parts identified in this way might be called “object parts” or “structural parts.”

This strategy has certain limitations. First, it cannot identify all parts, because many parts (i.e., the spatially distributed ones) will not be objects. Second, it cannot identify all objects: small objects will not be visible at low magnification, and many methods of specimen preparation will leave some of even the larger objects invisible. Third, on account of these two limitations, the hierarchical level of some parts will be misidentified; for example, some subparts will be identified as parts. Finally, it will produce some errors: some object parts will not be true parts at all, because integration will sometimes cross object boundaries. (Thus, object parts are technically not a proper subset of all true parts.)

However, the method should produce a representative sample of part types, one that should be useful for comparative purposes. At very least, lists of object parts should be useful for comparing part counts in closely related organisms, where the omission of small or invisible parts, and the inclusion of a small number of objects that are not parts, is unlikely to introduce a bias.

The use of object parts as a proxy for true parts is consistent with standard practice in various kinds of morphological analysis, including many phylogenetic analyses. One of its principal virtues is that it allows parts to be identified by direct observation, without elaborate experiments or equipment. It also allows procedures for identifying parts to be made fairly explicit, which minimizes subjectivity.

In the remainder of this paper (as well as in figures and the appendix), we refer to object parts simply as parts, on the assumption that they do represent a reasonable proxy.

1. Three Levels

Saltne (1985) argues that three levels are relevant in the analysis of hierarchical systems generally: the level of interest, or what he calls the focal level, plus one level above and one below. Here, the focal level is that of parts, the higher level is occupied by the organism as a whole, and the lower level by parts of parts, or subparts. Attention to level is crucial here in order to count parts in a consistent way. For example, a parts list that includes the circulatory system, the heart, and the blood vessels as distinct parts in effect counts the circulatory system twice.

Actually, for present purposes, it will not be necessary to establish the precise level at which entities below the focal level occur—that is, to establish whether they are subparts, sub-subparts, sub-sub-subparts, etc.—and it will be convenient to use the term “subparts” more broadly to describe the components at any level below parts. We place the word in quotes to emphasize this deliberate ambiguity.

2. Approximations

The strategy requires certain approximations. Ideally, a list of parts would take into account the fact that the degree to which each structure is a part and the degree to which it occupies the focal level are continuous variables. Perhaps quantitative measures of partness and of level occupation could be devised to assign a “weight” to each part. Lacking measures of this sort, we instead provide standards for making binary decisions, for deciding whether a given structure shall be counted as a part at the focal level or not. In effect, partness and level occupation are discretized, with the consequence that counts of parts are really approximations.

B. Protocols

1. Spatial Relationships and Compositional Differences

The first step is to identify the objects that might qualify as parts, or the “candidate parts,” and for this purpose a liberal and somewhat vague standard is appropriate: a candidate part is an object that is distinct in some way from its surroundings and occupies a localized, definable region within the organism. Then, the partness and hierarchical level of a candidate is evaluated based on two types of spatial relationship: (1) enclosure and (2) contiguity with a difference in composition.

of other structures in contact with the surrounding environment (e.g., the lophophore in bryozoans; see later). Importantly, here the term "outer structure" refers to the set of all structures that are in contact with the surrounding environment.

In the figure, a focal candidate part is drawn as a light gray square (and marked with an arrow in G, H, and I), except in B and F where the candidate is the outer structure itself or a segment of it (also shaded light gray). The darker gray shapes (C and D) are structures that differ in composition from the candidate part. Before turning to the spatial relationships, two preliminary issues need to be addressed. First, we assume that the fluid-filled interior and other fluid-filled cavities are not objects and therefore do not by themselves count as parts. The rationale is that neither the integration among the fluid's components nor the isolation that begins at the edge of a fluid mass is likely to be sufficient to achieve part status. (Of course, if a fluid-filled cavity is bounded by a membrane, then fluid and membrane together might be a part.)

Second, candidate parts are understood to be "contained" within the organism, meaning that they occupy space inside an imaginary line marking the organism's outer perimeter, i.e., marking the limit of the outer structure. Containment is relevant, because a candidate part that is inside this perimeter is likely to interact most directly and strongly with parts in the same organism, and therefore is unlikely to be "outside" the organism in terms of its interactions. To put it another way, a part within the outer perimeter is unlikely to constitute an independent entity on the same hierarchical level as the organism or on a higher level. Therefore, it most likely occupies some lower level, either as a part or "subpart." All of the candidates in Fig. 3 are contained in this sense, including the outer structure (Fig. 3B) which technically lies within the organism's outer perimeter and therefore is itself a legitimate candidate for a part.

Now consider the first spatial relationship, "enclosure." As understood here, enclosure is different from containment; a contained candidate part merely lies inside an imaginary line, the perimeter of the organism, while an enclosed part lies inside a physical structure (e.g., the outer structure), which physically isolates it. The enclosing structure monopolizes the candidate's boundaries, so that all interactions between it and entities outside must go through the enclosing structure; such interactions are likely to be mediated by, and much attenuated by, the enclosing structure. Thus, the candidate part in Fig. 3A is not only isolated by virtue of being contained within the organism, as discussed earlier, but also by virtue of its enclosure within the organism's outer structure. Notice that the outer structure itself (Fig. 3B) does not enjoy this double isolation, but qualifies as a part anyway on account of being contained. The fact that it has a special role in enclosing and isolating other parts does not detract from its partness. Finally, notice that in Fig. 3C, the candidate is further enclosed by another structure, and therefore is a "subpart" rather than a part.

Now consider "contiguity with a compositional difference." Compositional differences between contiguous structures are relevant on the assumption that a

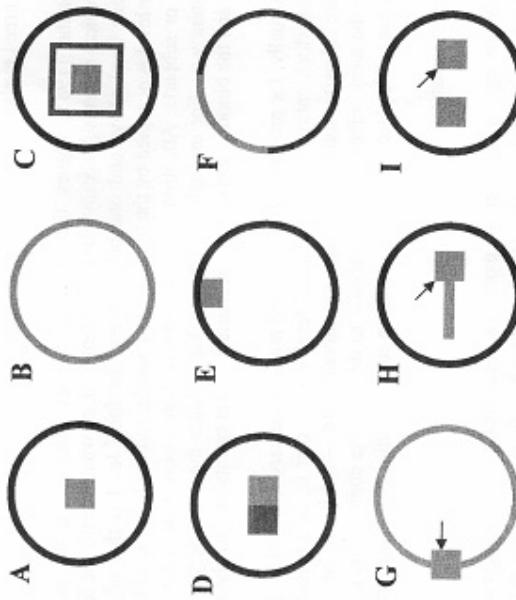


FIGURE 3 Enclosure and contiguity with a compositional difference. Outer structure of organism = dark circle; candidate part (CP) = light gray square (in A, C, D, E, G, H, & I) or light gray circle or arc (in B & F); dark gray = another part, differing in composition. A: CP = part (enclosed by outer structure); B: CP = part (outer structure itself); C: CP = "subpart" (enclosed by another part); D: CP = part (contiguous with another part but different in composition); E: CP = part (contiguous with outer structure but different in composition); F: CP = part (contiguous with the rest of the outer structure but different in composition); G: CP = nonpart (shape differences not considered sufficient for part status; however, entire outer structure, including gray square, is a part); H: CP = part (shape differences not considered sufficient for part status; however, entire gray structure, including gray square, is a part); I: CP = part or duplicate part. See text for further discussion.

Figure 3 will be used to illustrate these relationships. The assumption is that the organism has a mainly fluid interior and that it is enclosed by an outer structure. In some organisms, this is a single structure, a shell, membrane, or wall (shown as a large black circle in the figure), which encloses the organism entirely. In others, however, the shell, membrane, or wall is incomplete, leaving a number

change in the type of components that constitute a structure (i.e., a change in composition) is likely to be accompanied by a reduction in integration among them. In Fig. 3D, the candidate is contiguous with another structure, but differs from it in composition and therefore qualifies as a part. The same is true in Figs. 3E and 3F, except that in E the contiguous structure happens to be the organism's outer structure, and in F the candidate is a segment of the outer structure. In both, the candidate is a part by virtue of its distinctive composition. In cheilostome bryozoans, the operculum and the ocellus muscle that closes it are contiguous but differ in composition (see later).

Of course, composition may vary continuously. In principle, quantitative metrics might be used to discover compositional discontinuities, which in turn might correspond to part boundaries. Here compositional variation is assessed subjectively. Notice that in principle, small-scale compositional differences along structures that are compositionally homogeneous at a large scale would constitute "subparts." However, here we are interested only in the parts level and therefore disregard small-scale variation.

2. Shape Differences

Differences in shape might also be construed to indicate reductions in integration corresponding to part boundaries. A shape difference might consist of a local deformation of an object, one that is not compositionally distinctive (at least at a large scale). On this basis, an amoeba's pseudopod might count as a part distinct from the rest of the membrane. In bryozoans, the stomach is, on account of its shape, distinct from the rest of the digestive tract (see later). The use of shape to identify parts seems reasonable; on the other hand, shape differences also seem to be less substantial indicators of change in integration than compositional differences, and here we have chosen to disregard them. As a result, our protocols will undoubtedly miss some parts, but in any case, for comparative purposes, the main requirement is consistency not completeness.

In Figs. 3G and 3H, the gray square marked with an arrow is not a part, because it differs only in shape from the contiguous structures. There is a part in Fig. 3G, however: it is the entire outer structure *including* the gray square. In Fig. 3H, the entire gray shape, again including the gray square, is a part.

3. Duplicate Parts

As discussed, the goal is a list of distinct part types. Thus, if an arm of an octopus is a part, it has only one part of that type, not eight. In Fig. 3I, only one of the gray squares counts as a distinct part type. In principle, quantitative metrics can be used to search for discontinuities which might correspond to differences among part types; here, we make the evaluations subjectively.

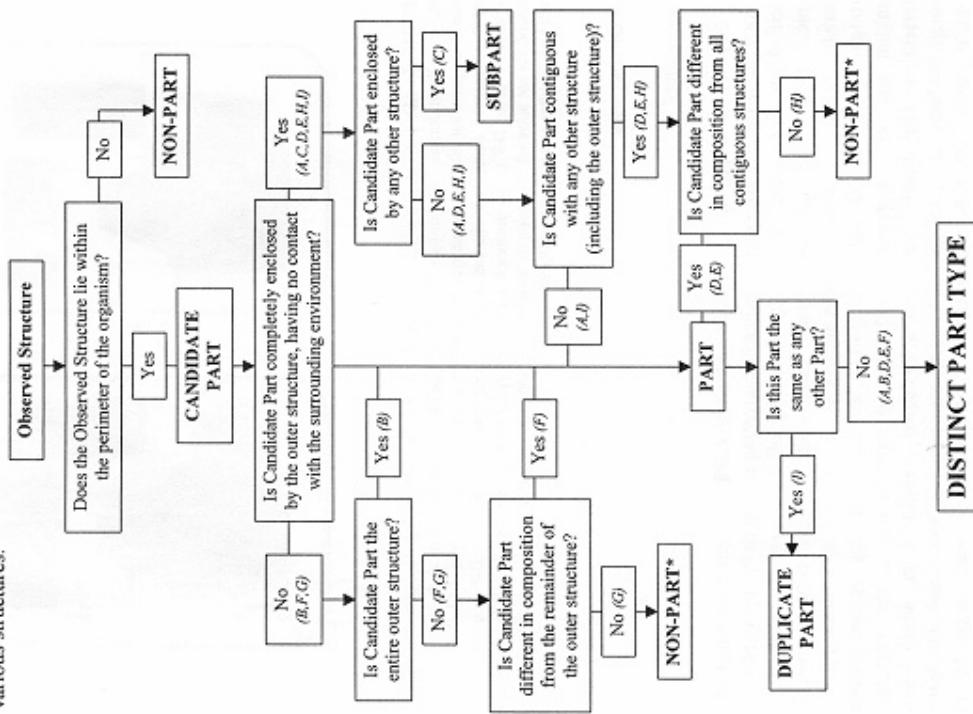


FIGURE 4 A key for identifying parts. A “nonpart” marked with an asterisk marks with an asterisk part, or a region, of some larger entity which is a part (or subpart). Any such larger entities that can be identified are candidates for parts and should be tested using the key. For examples, see “nonparts” and their likely larger parts (in parentheses) in column 2 of the Appendix.

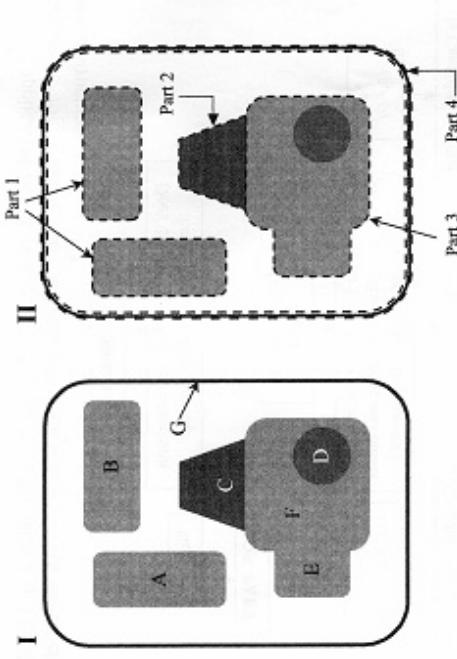


FIGURE 5 Abstract example to illustrate how the key works. Left drawing (I) shows the candidate parts, A–G. Right drawing (II) shows the distinct part types that would be identified by the key (Fig. 4). A, and B are parts but are of the same type and therefore count as one distinct type (Part 1). C is a part (Part 2), because it is contiguous with and different in composition from the entire D–F group (Part 3). D is a “subpart” of the D–F group, because it is enclosed by it. E is distinct in shape from F, but the present protocols do not acknowledge shape differences, so E and F are not parts. G is the enclosing structure, which here qualifies as a distinct part (Part 4).

C. Bryozoa

1. Anatomy

Bryozoa is a phylum of usually sedentary colonial marine invertebrates. Colony morphologies are diverse, typically encrusting or branching, many of them calcified. In all species, the majority or totality of the colony is composed of (typically) box- or cylinder-shaped “autozooids,” which feed, providing nourishment for the colony. In these autozooids, a tentacled lophophore extends through an orifice into the surrounding water, and cilia on the lophophore channel plankton and other suspended food into a mouth located at the tentacles’ intersection. The mouth opens into a U-shaped digestive tract, which loops through the body cavity and terminates in an anus below the mouth and outside the tentacle crown. Lophophore extension is accomplished in various ways, but in almost all species, retraction is effected by a muscle that inserts at the base of the zooid (Fig. 6). Zoid walls are usually perforated in some way to allow interzooidal communication. For further descriptions, see Ryland (1970) and Boardman et al. (1987).

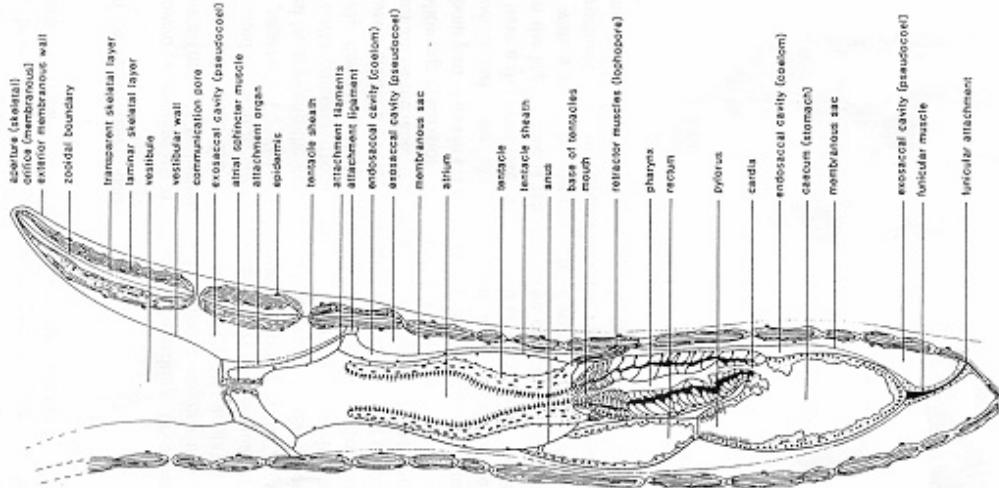


FIGURE 6 Longitudinal section of a *C. elegans* autozooid. (From Boardman et al., 1992, reproduced with permission.)

In addition to autozooids, many species also have one or more other differentiated zooid forms, collectively called heterozooids. In many species of cheilostome bryozoans, the most common type of heterozooids are avicularia, which are armed with claw-like mandibles, perhaps defensive in function.

2. Parts in Two Bryozoan Species

Eminoecia carsonae is a calcified, branching bryozoan in the class Gymnolaemata (order: Cheilostomata). *Cinctipora elegans* is also calcified and branching but in the class Stenolaemata (order: Cyclostomata). Part-type lists for two of the zooid types in *E. carsonae* (autozooids and avicularia) and for the one zooid type present in *C. elegans* (autozooids) appear in the Appendix. The lists were derived by applying the key (Fig. 4) to anatomical descriptions and drawings of *Hippadennella carsonae* (reclassified as *E. carsonae* by Hayward and Thorpe, 1988), mainly from Rogick (1957), and of *C. elegans*, from Boardman *et al.* (1992). Figure 6 shows a *C. elegans* autozooid with many of its structures labeled; many, but not all, of the labeled structures qualify as parts (see Appendix).

The following discussion illustrates how the protocols were used to make decisions about part status in certain cases, some of them problematic.

Eminoecia carsonae. As is common in the cheilostomes, *E. carsonae* autozooids have a trapdoor-like device called an operculum, which closes over the orifice when the lophophore is retracted. The operculum attaches to, and is thus contiguous with, a set of occlusor muscle fibers which provide the closing force. The two structures differ in composition: the operculum is composed of cuticle, while the muscle fibers are made of muscle cells. Thus, each is classified as a distinct part.

Eminoecia carsonae, namely, that they are divided into

11. WHAT IS A PART?

Zooids in *E. carsonae* are arranged in longitudinal series along the colony branches. Adjacent longitudinal columns are offset by half of a zooid length such that the proximal half of any given zooid is flanked on the right and left by the distal halves of its neighbors (Fig. 7, left). Communication between zooids occurs through four openings in the walls of each zooid, two on each side. The two distal openings are sieve-like structures called rosette plates (Fig. 7, right). The two proximal openings are simple holes ringed by a raised annulus. On account of the offset between zooids and their neighbors, the rosette plate from one zooid aligns with the proximal opening of an adjacent zooid, forming a connection between zooids.

The status of the annulus surrounding the proximal opening and of the rosette plate might seem to be somewhat problematic. Both structures present prominent and distinctive gestals, strongly suggestive of parts. However, the annulus seems to be composed of the same calcium carbonate as the zooid wall, and therefore is not a distinct part. Likewise, the rosette plate apparently does not differ in composition from the zooid wall, and therefore is not a part. Finally, the hole in the annulus might seem to qualify as a part, in that its composition differs from that of the annulus itself. However, the hole is not an object, and therefore cannot be a part.

Cinctipora elegans. Figure 6 shows the *C. elegans* digestive tract, consisting of a series of candidate parts: mouth, pharynx, cardia, caecum (stomach), pylorus, rectum, and anus. The cells of the pharynx are inflated and those of the upper pharynx are ciliated (Boardman *et al.*, 1992). The pylorus is also ciliated, while the remaining digestive-tract candidate parts are not.

The mouth and anus are openings, not objects, and therefore are not parts. Cell inflation was deemed a sufficient compositional difference for the pharynx to qualify as a distinct part. If ciliation were also deemed sufficient, then the digestive tract would actually consist of five distinct part types: (1) ciliated, inflated-celled, upper pharynx; (2) unciliated, inflated-celled, lower pharynx; (3) unciliated cardia and caecum; (4) ciliated pylorus; and (5) unciliated rectum. However, ciliation was deemed a minor compositional feature, and thus in our scheme, the digestive tract consists of only two parts: (1) inflated-celled pharynx and (2) the remainder of the tract (cardia, caecum, pylorus, and rectum).

SUMMARY

We have attempted to develop a scheme which formalizes a common intuition about the structural organization of organisms, namely, that they are divided into parts. We show how the scheme might be rendered partly operational, in particular, how it can be used to identify certain kinds of parts—object parts—in a consistent way at a hierarchical level just below that of the organism. The assumption is that, for comparative purposes, counts of object parts can be used as a proxy for counts of true parts.

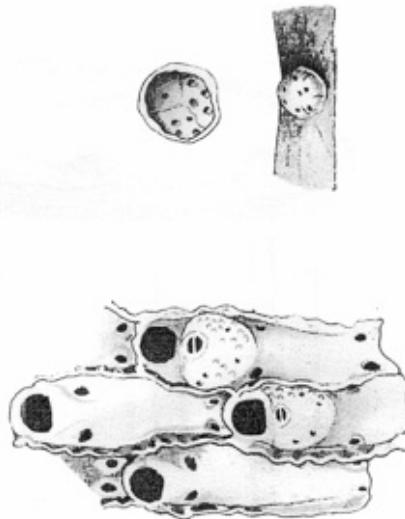


FIGURE 7 Left: arrangement of zooids along a branch in *E. carsonae*. Right: two views of the rosette plate. (From Rogick, 1957, reproduced with permission.)

The goal is to devise methods to enable us to answer evolutionary questions in which identification of parts, and counts of part types, would be useful, such as questions concerning the structural complexity of organisms. The scheme is expected to be especially useful for identifying parts in cases in which our preconative mechanisms are not helpful or are even misleading, cases in which the question dictates the organism and the hierarchical level, and therefore we are not entitled to choose organisms or levels in which the parts are obvious.

Our approach has certain limitations. Although it represents an advance over purely subjective identification of parts, considerable subjectivity remains. Also, our protocols were designed to produce a parts list only for organisms that are apparently structurally quite simple, like bryozoans, and they may need to be modified for other organisms.

Despite these limitations, the approach seems worthwhile, at very least because of the explicitness of the protocols it proposes, and of the assumptions on which they are based. On account of this explicitness, areas where more conceptual work is necessary, or where revision is required, become easier to identify.

Identifying parts in organisms will only rarely be straightforward: part boundaries are often vague, and parts often occupy more than one hierarchical level at once. On the whole, organisms are not organized in cognitively congenial ways, as machines often seem to be, and thus it is not unreasonable to doubt that identification and listing of parts in organisms can be meaningfully done. Still, we are hopeful; we draw our optimism in part from an imaginative study by Schopf *et al.* (1975), who used number of anatomical terms—estimated mainly from glossaries in anatomy texts—as a proxy for morphological complexity, essentially taking a gestalt-based approach to counting parts about as far as possible. Despite the obvious subjectivity of their metric, they documented a correlation between morphological complexity and taxonomic turnover rate. Likewise, for the present scheme, the test of the meaningfulness of the parts list it produces will lie in whether robust correlations can be found with other biologically significant variables.

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APPENDIX

Classification of Various Observed Structures

Organism	Candidate part name	Status (larger part)	Reasons for classification
<i>Cinctipora elegans</i>	annular muscle	part	enclosed, contiguous, different comp.
	anus	nonpart	empty space
	axial sphincter muscle	part	enclosed, contiguous, different comp.
	attachment ligaments	nonpart* (attachment organ)	enclosed, contiguous, not different comp.
	attachment organ	part	enclosed, contiguous, different comp.
	cardia	nonpart* (digestive tract)	enclosed, contiguous, not different comp.
	caecum	nonpart* (digestive tract)	enclosed, contiguous, not different comp.
	communication pore	nonpart	empty space
	digestive tract (excluding pharynx)	part	empty space
	epidermis	part	enclosed, contiguous, different comp.
	funiculus	part	enclosed, contiguous, different comp.
	laminar skeletal layer	nonpart* (skeleton)	outer structure, contiguous, not different comp.
	lophophore	part	outer structure, contiguous, different comp.
	loph, refractor muscle	part	enclosed, contiguous, different comp.
	membranous sac	part	enclosed, contiguous, different comp.
	mouth	nonpart	empty space
	orifice	nonpart	outer structure, contiguous, not different comp.
	peristome	nonpart* (skeleton)	enclosed, contiguous, different comp.
	pharynx	part	enclosed, contiguous, not different comp.
	pylorus	nonpart* (digestive tract)	enclosed, contiguous, not different comp.
	rectum	nonpart* (digestive tract)	enclosed, contiguous, not different comp.
	skeleton	part	outer structure, contiguous, different comp.
	tentacle	nonpart* (lophophore)	outer structure, contiguous, not different comp.
	tentacle sheath	nonpart* (lophophore)	outer structure, contiguous, not different comp.
	transparent skeletal layer	nonpart* (skeleton)	outer structure, contiguous, not different comp.
	vestibular wall	nonpart* (lophophore)	outer structure, contiguous, different comp.
<i>Autozooid total:</i>		11 parts	
<i>Eminiooceria coronaee</i>			
Autopods:			
	part name	class (possible larger part)	Reasons for classification
	anulus	nonpart* (skeleton)	outer structure, contiguous, not different comp.
	anus	nonpart	empty space
	cardia	nonpart* (digestive tract)	enclosed, contiguous, not different comp.
	cecum	nonpart* (skeleton)	outer structure, contiguous, not different comp.
	cardelle	part	enclosed, contiguous, different comp.
	digestive tract	part	enclosed, contiguous, different comp.
	epidermis	nonpart* (digestive tract)	enclosed, contiguous, different comp.
	esophagus	part	enclosed, contiguous, different comp.
	funiculus	part	enclosed, contiguous, different comp.
	lophophore	part	enclosed, contiguous, different comp.

Eminiooceria coronaee

Autopods:

part name	class (possible larger part)	reasons for classification
abductor muscle	part	enclosed, contiguous, different comp.
adductor muscle	part	enclosed, contiguous, different comp.
avicularian gland	part	enclosed, contiguous, different comp.
epidermis	part	enclosed, contiguous, different comp.
mandible	part	outer structure, contiguous, different comp.
mandibular membrane	nonpart* (mandible)	outer structure, contiguous, different comp.
membrane	part	enclosed, contiguous, different comp.
pivot bar	nonpart* (skeleton)	outer structure, contiguous, different comp.
rudimentary polypide	part	enclosed, contiguous, different comp.
skeleton	part	outer structure, contiguous, different comp.
Avicularia total: 8 parts		

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