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Character individuation: functional, descriptive, and developmental

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Abstract: Characters—parts, properties, or activities of organisms—can be individuated in multiple, non-equivalent ways. This paper aims to show how these differences matter, to frame the problem of character individuation methodologically, and to outline a path to resolving it. I describe the main scientific roles for the character concept, and analyze three broad approaches to character individuation: functional, descriptive, and developmental. I explore which approaches are appropriate for which roles, and propose two evolutionary hypotheses to explain why functionally and developmentally individuated characters diverge.

1. Introduction

One of the characters that distinguishes modern humans from our hominin ancestors is the chin. While primate jaws generally slope upwardly toward a protruding mouth, human jaws have a bony protrusion at the base. Like other human-specific characters, the chin has attracted numerous adaptive hypotheses as to its evolutionary origin. Researchers have explained it as a mechanical support for mastication or speech, as an ornament for the sexual selection of males with high androgen levels, and more (Pampush and Daegling 2016; Meneganzin et al. 2024). In their famous criticism of adaptationism, Gould and Lewontin (1979) made the chin the paradigmatic example of a biological trait that seems real to human observers—thus seeming to call for an adaptive explanation—even though, according to them, it possesses no biologically meaningful unity or independence as a trait in its own right. Their argument was that the chin arises as a by-product of changes in the differential growth rates in different jaw regions. In human evolution, the whole jaw diminished in size, but the alveolar region (where the bottom teeth are located) shrunk more than the basal (lower) region, leaving an outcropping of bone as a result (Pampush and Daegling 2016). From this Lewontin (1978, 217) had concluded that the chin is not a real character: “in an evolutionary

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sense the chin does not exist […] the chin is a mental construct rather than a unit of evolution."

This line of argument raises deeply puzzling questions: what is a biological character? How can we know if the traits that appear salient to scientific observation and measurement genuinely carve the organism at its joints? As Lewontin (2001, xvii) poses the problem: "How are we to recognize the 'true' characters of organisms rather than imposing on them arbitrary divisions that obscure the very processes that we seek to understand? […] No issue is of greater importance in the study of biology".

Despite such enthusiastic pronouncements, there have been few direct investigations of this issue.[1] Character delimitation is not just an empirical problem, but inescapably depends on theoretical and philosophical commitments regarding individuality, genetic reductionism, and the relationships between levels of biological organization. "The question—what is a character?" is therefore one where "philosophers could have been of some service to biologists" (Hull 1969, 262).

The aim of this paper is to begin answering this question. Because characters must be concretely singled-out, counted, and tracked on organisms, as opposed to merely being defined in the abstract, the question "what is a character?" ultimately commutes to the problem of *character individuation*. In this respect, the situation is closely analogous to the evolution of theorizing about the organism into the problem of biological individuality (Clarke 2011).

To address the problem of character individuation, I propose a general methodological frame. First it is necessary to explicate the roles that the character concept plays in biological investigation. I then hypothesize that there are three distinct approaches to character individuation (functional, descriptive, and developmental), examine their inter-relationships, and evaluate how they differentially map onto the investigative roles for the concept. These character concepts often pick out distinct units of phenotype. Rather than halting at a pluralistic view of characters, I suggest that there may be an integrative biological explanation for why different kinds of characters overlap or diverge when they do. I close in this vein by considering the evolutionary basis of divergences between developmentally and functionally individuated characters.

[1] The major exception is the essay collection by Wagner (ed.) (2001). Recognition of the problem can also be found in Richards (2003); DiFrisco and Ramsey (2023), Figdor (2024), Cortés-García, et al (2024), Fábregas-Tejeda (2025), and elsewhere

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2. Methodological framing of the problem

What sort of method should be used to get a handle on the issue of identification and demarcation of biological characters? A common philosophical strategy for treating concepts like "character" (or function, species, organism)—those that are fundamental but not well-defined—is conceptual analysis based on definition and counterexample reasoning (e.g., Neander 1991). A conceptual analysis is generally considered successful when a proposed definition fits some descriptive data—e.g., scientific or everyday usage of a term—without yielding counterexamples, which may be supplied by actual data or by thought experiments. The character concept lacks a stable descriptive basis for such an analysis, however. Scientific usage of the term is often loose and inconsistent. "Character" or "trait"[2] can refer to any property or part of an organism singled out for any purpose, however arbitrary.

More productive would be to examine how scientific practices of character individuation work, with attention to how different practices and associated character concepts may fulfill different aims of investigation (e.g., Love and Brigandt 2017; Waters 2018). For example, "functional" trait concepts may be more common in ecology and evolutionary biology, whereas "structural" trait concepts fit the comparative aims of developmental biology and morphology. An advantage of this type of approach is that revealing the investigative aims and roles at play with the character concept establishes the conditions of a successful explication of a concept. An analysis is successful when the proposed version(s) of the concept can fulfill the aims latent in biological practices that use the concept.

In line with this second methodological approach, we begin below by enumerating major roles for the character concept in biological investigation. However, analysis of scientific practice and investigative aims alone has little utility for understanding the *biological* conditions that make different kinds of character overlap or diverge. This will require understanding the basis for different kinds of characters in biological systems, as opposed to in biological investigation. Attention to investigative roles and description of practices should thus be combined with the development of biological theory and hypotheses, which can then usefully influence scientific practice (see section 5). This third methodological approach may be called "theoretical biology."

[2] In this paper I take "character" and "trait" to be equivalent terms.

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2.1 Roles for character individuation in biological investigation

The following is a (non-exhaustive) list of stereotyped situations where the outcomes of biological investigation actually depend on the way characters are singled-out, demarcated, counted, and/or tracked across time. These constitute roles for character individuation in biological reasoning.

(R1) Characters distinguish taxonomic groups. In phylogenetic research, where the aim is to map the genealogy of life, rival phylogenetic hypotheses are assessed by the number of characters that are congruent with rival hypothetical trees. But different subdivisions of the organism yield different counts of characters. Including arbitrary characters or double-counting the same character under different descriptions can generate faulty phylogenies (Richards 2003; Winther 2009).

(R2) Basic biological concepts are defined in terms of characters. A pleiotropic gene is one that affects multiple characters (Zhang 2023), and the complexity of an organism can be measured by the number of distinct characters it has (Riedl 1978, 126; McShea 2000; McShea and Venit 2001). Both pleiotropy and complexity play into explanatory generalizations in evolutionary theory. For example, the "cost of complexity" (Orr 2000) refers to the hypothesis that as the number of dimensions of variation for a population increases, it will be harder for natural selection to optimize each dimension simultaneously. The "cost of pleiotropy" (Wagner and Zhang 2011) refers to the hypothesis that it is pleiotropy rather than complexity *per se* that imposes a cost on adaptability or evolvability. In either case, measurements of pleiotropy or complexity clearly depend on how we individuate characters. Similar conceptual dependencies affect notions like polygeny and morphological disparity.

(R3) Characters are bearers of function and adaptation, and respond to selection. Clearly the truth of function ascriptions and claims of fitness advantage and adaptation depend on accurately identifying the character that performs the relevant function. More subtly, in evolving populations, the traits that change in response to selection can be different from the traits that are actually targeted by selection. These kinds of traits need to be individuated differently in order for researchers to understand how selection affects organismic architecture.

(R4) Most fundamentally, characters are units of comparison across organisms and species. Within populations, characters are the descriptive bases for tracking demographic

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change. Across species, they underwrite our ability to make inductive projections from the few model organisms that are actually studied to the vast diversity of life. For such comparisons to be informative and generalizable, it is necessary to identify characters that are genuinely comparable. This role applies to comparisons as diverse as identifying homologies, describing convergent adaptations, and defining phenotypic measures of rates of evolution.

2.2 Character individuation and homology

The theme of homology in (R4) raises the essential preliminary question of how character individuation and homology are related. Specifically, is character individuation just the problem of homology framed in different terms? Homology is broadly understood as the relation characters stand in when they descend from the same character in a common ancestor. Understanding and explaining this relationship is a deep and active biological problem, and different authors have different views on the link between homology and character individuation (DiFrisco 2023). It could be argued that character demarcations are set by homology relationships, so that the criteria used to establish homology also establish what the relevant characters or phenotypic units are (e.g., Griffiths 2006). However, even though homology and characters are intimately connected, they are not the same problem. Criteria of homology do not suffice to fulfill roles (R1)–(R4).

It is helpful to separate the criteria of homology into those used to establish "primary homology" and "secondary homology" (De Pinna 1991). Primary homology is based on classical morphological and anatomical criteria such as the relative topological position of a character in a body plan. Secondary homology concerns the phylogenetic relationship between characters identified as potential homologues, and confirms or disconfirms hypotheses based on primary homology. Developmental approaches to homology (Roth 1984; Wagner 1989; 2014; DiFrisco et al. 2020) can be interpreted as contributing additional developmental criteria to supplement primary homology, but candidate developmental homologues still need to be confirmed by phylogenetic relationships. Primary homology, broadly construed, contributes criteria of individuation for characters, as we will see, but there are other legitimate criteria sometimes used to identify and classify characters (such as function) that are orthogonal to homology (although see Love 2007). Secondary homology, as established by congruence tests in cladistics for example, may confirm which characters are homologous with which, but is not informative about which characters to subject to phylogenetic tests in the first place.

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Whatever one's views on homology, character individuation should be understood as epistemically prior to judgments about homology (Ramsey and Peterson 2012; Figdor 2024). Assessing whether two characters are homologous depends on prior determinations about what the characters are that are being compared. As in the roles (R1)–(R4) above, changing the boundary of the characters can change the truth of the homology statement. If the characters are only vaguely defined, it can be impossible to give a determinate answer as to whether they are homologous (Patterson 1982). Conversely, success in establishing homology provides indirect evidence that the characters involved are sufficiently distinct and cohesive to serve as units of phenotypic description (Franz 2014). Several authors have highlighted the dependency of homology on character identification and noted that this latter issue is sorely neglected (Colless 1985; Scholtz 2005; Wiley and Lieberman 2011).

2.3 Individuation

An important task for getting clear on character individuation is to disambiguate the notion of individuation. "Individuation" can refer to (1) the cognitive process by which an item is singled out from its surroundings and tracked through time, as well as to (2) the definition of a class of items that allows such singling-out. "Individuation" can also refer to (3) the natural causal process by which something in the world becomes an individual—i.e., a unit or module with some appreciable degree of coherence and independence. For clarity I will reserve the term "individuation" for (1) and (2) together, since they are mutually required and reinforcing, and "individualization" for (3).

Like organisms, characters are complex, evolved, natural systems. To individuate a character, it is not sufficient to merely formulate a definition, unlike with formal objects like numbers, sets, or axioms. Instead, it is an iterative cognitive process akin to hypothesis-testing: some initial object is defined, detected, singled-out, and evaluated as to whether it is a unit of generalization or a unit of some process of interest (Wagner 2001; Meneganzin et al. 2024). For example, for a given observable arthropod segment, we may ask whether it can vary quasi-independently of other segments, or whether all segments covary as a single character, and at which developmental stage this is the case. The hypothesis that larval segments are units of developmental and evolutionary processes can be revised in light of empirical investigation in favor of other units. Parasegments, for example—internal segments that are spatially offset from the more visibly salient cuticular segments—organize the major organ systems into compartments (Clark et al. 2019) and are more determinative for arthropod development after segmentation. This knowledge may change how segments are

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individuated—i.e., changing the definition together with the cognitive process of detecting the unit—but not how they are individualized.

2.4 Ontological categories for characters

A further task is to clarify the ontological categories that characters belong to. Characters or traits can include body parts (a wing), masses (neural tissue), the properties of body parts (size or color of a wing), and processes or behaviors (segmentation, flying). It is customary to focus attention on morphological characters (cell types, tissues, organs, and organ systems) and molecular characters (nucleic acids, proteins, and signaling pathways), but many of the central issues are reiterated for other categories as well. Characters can be qualitative (wing, red) or quantitative (size of wing, shade of red). Quantitative characters can be single variables or multivariate systems with complex spaces of variation (e.g., morphometric shape). Unlike the generic notion of a "part," "character" is almost always comparative: a character is not a particular, but a type or kind (of part, property, or process).

3 Character individuation

A criterion of individuation is a principle, test, or definition that allows one to single out something from its surroundings, subsume it under a kind, count the number of instances of the kind in a given region, and/or track them across time. The following three sections (3.1–3.3) identify three kinds of criteria of individuation for characters: functional, descriptive, and developmental. These are not proposed conceptual analyses, but correspond to distinct theoretical perspectives, sets of biological principles, and "partitioning frames" (Winther 2006) drawn from evolutionary biology, descriptive morphology, and developmental genetics. Each is evaluated as to its relative strengths and limitations with a view toward ultimately assessing their implementation in roles (R1)–(R4).

To classify the different approaches, it is useful to distinguish criteria in terms of the level of organization of the individuating factor relative to the focal character. This allows the same criteria to be shifted and re-applied to any level. In *top-down* or functional approaches, characters are individuated by factors that lie at a higher level than the character. In *same-level* or descriptive approaches, the factors are roughly at the same level as the character. Finally, in *bottom-up* or developmental approaches, the factors are at a lower level. "Levels of organization" are to be understood as general part-whole or compositional relations, including molecules, cells, tissues, organs, organisms, populations, etc., as well as the activities they are involved in (Salthe 1985; Brooks et al. 2021).

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3.1 Top-down approaches: functional traits

In top-down approaches, the status of some phenotypic feature as a trait is determined by its relationship with factors at a higher level of organization than the character, i.e., within some encompassing system. The contribution of the trait to the higher level can be considered the function or functioning of the trait, and thus the top-down approach supports a *functional* conception of traits. The level above the character may be represented either as the organism, an ecosystem, or a population of conspecifics. The latter, population-based functional perspective is at work in frameworks that identify and distinguish traits in terms of their contribution to fitness differences in a population.

A prime example of this form of top-down or functional trait individuation is the influential "morphology, performance, and fitness" framework developed by Arnold (1983). Originally motivated by concern with how to measure fitness, this framework pictures morphological traits as contributors to fitness via intermediate "performance" variables. The simple idea is that Darwinian fitness is typically determined by grades of performance or function (e.g., fertility, locomotory speed, or photosynthetic rate), and that these grades of performance are based on variations in morphology in a broad sense (e.g., gamete number, limb morphology, or leaf area). Arnold showed that the measurement of fitness could be broken down into two distinct problems: measuring the effect of morphological traits on performance, and measuring the effect of performance on fitness.

Arnold's (1983) framework yields a hierarchical picture of morphology, performance, and fitness variables as ordered in causal graph (Fig 1). In this picture, functional morphological traits are treated as phenotypic variables that can make a distinct contribution to fitness by affecting performance (Geber and Griffen 2003; Violle et al 2007). The connection between morphology and performance is often complicated because key performance traits are influenced by entire suites of morphological characters. For example, the locomotory speed of a tetrapod may be determined by very many aspects of limb morphology, respiratory physiology, and muscular capacities. Similar functional hierarchies have been proposed and depicted in other theoretical work on traits from the perspective of selection, adaptation, and evolvability (e.g., Houle 2001; Altenberg 2005; Violle et al. 2007).

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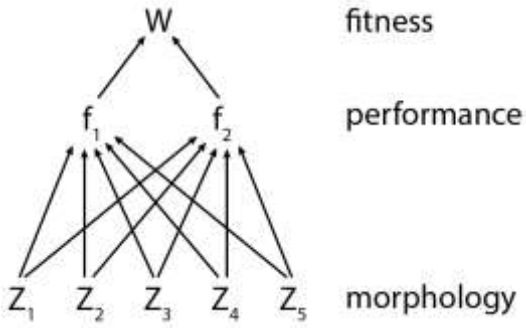


Fig. 1. Functional traits in the "morphology, performance, and fitness" framework (Arnold 1983, 353) are conceptualized as causally distinct contributors to fitness via performance.

The main contribution from top-down or functional frameworks to the theme of trait individuation is the following principle: it is only insofar as a trait influences fitness that it can be "seen" by selection, and thus only to this extent is it a "real" trait from the perspective of selection and adaptation. This principle can be seen in a different functional approach explored in Orr's (2000) discussion of the "cost of complexity." Building on Fisher's (1930) geometric model of adaptation, Orr hypothesizes that the rate of adaptation declines as the number of independent phenotypic dimensions, or characters, increases. This is largely because, assuming potentially universal pleiotropy, as the number of characters increases, a mutation of a given magnitude is more likely to have deleterious effects on more characters. Organisms that are more complex, in the sense of having a greater number of characters that can vary independently, therefore pay the high evolutionary cost of being less adaptable than simpler organisms. Orr then shows how the relationship between mutational effect size and present fitness relative to the optimum allows one to deduce the "effective dimensionality" of an organism by measuring the fitness effects of various classes of mutational effect size. Such a procedure is acknowledged to be impractical, but the claim is that in principle this would yield a correct decomposition of the organism from the point of view of natural selection. As Orr writes, "The fact that we are free to define an arbitrary number of (linearly independent) characters does not mean that natural selection 'sees' a similarly arbitrary, and thus undefinable, number of characters" (Orr 2000, 18). The effective dimensionality of an organism relative to fitness thus gives an (in-principle) answer to the problem of character individuation.

To assess how well functional approaches work for roles (R1–R4), we must consider their general limitations. The main rationale for a functional view of characters is a screening-off argument (Orr 2000; cf. Altenberg 2005): roughly, it is only insofar as a trait influences

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fitness, via some grade of performance, that it can participate in selection-driven evolutionary dynamics. Thus, to understand the latter we only need functional characters. This screening-off argument faces both practical and principled difficulties, however. We often have less epistemic access to fitness and to high-level performance variables than to more directly observable and measurable traits like body size or camouflage pattern (Arnold 1983). When the contrary is the case, performance traits generally *underdetermine* their phenotypic and genotypic causes (see Fig 1). Yet it is the phenotypic and genetic architecture of the organism that establishes the constraints and potentialities for evolutionary change—including change in performance.

The difficulty can be appreciated by contrasting selection and the response to selection (R3). It is a familiar fact from artificial selection experiments that virtually any organismic feature can undergo selection (Charlesworth et al 1982). But the response of a population to a selection regime depends on its underlying variational structure (Lande 1979). For example, the process of domestication involves selection for a behavioral trait (tameness). But in mammals, domestication also tends to produce a suite of seemingly unrelated morphological changes, such as depigmentation on undersides, shortened muzzles, smaller teeth, floppy reduced ears, and curly tails. A leading hypothesis to explain this "domestication syndrome" is that, during domestication, tameness is primarily increased through deficits of neural crest, which give rise to smaller adrenal glands that produce less stress hormones. In tandem, neural crest deficits cause reductions in many other neural crest derived structures, such as melanocytes and craniofacial cartilage and bones (Wilkins et al 2014). Mammals thus respond to domestication with changes that can only be understood in light of the developmental pleiotropy of neural crest. This difference between selection and response to selection can be captured in the following general way: there is "selection for" the trait that is proximally targeted by natural selection, but "selection of" any traits that actually change in response to selection (Sober 1984). Functional traits decomposed under hierarchies of performance variables capture "selection for," but there is no way of capturing the underlying "selection of" traits without some understanding of the internal organization of the phenotype, organismic development, and the genotype–phenotype map. Functional characters alone, then, will often be unable to accurately describe the response to selection (R3).

Functional approaches will also have difficulties decomposing the organism into unique, non-overlapping characters. A given biomass contains very many different, partially overlapping morphological subdivisions that can be targeted by selection at different times.

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Again, artificial selection experiments provide an instructive extreme, but selection regimes can also change rapidly in the wild (Van Valen 1973), where the causal role of the experimenter is replaced by a predator or mate. In experiments on fly wings, Weber (1992) found that a tiny (<0.2 mm), arbitrary region of wing responded locally to selection for shape. He concluded that this suggests an underlying genetic potential for "dense, fine-grained, autonomous and localized adaptive change" (Weber 1992, p. 345; see DiFrisco and Ramsey 2023). To the extent that these results generalize, they imply that an organism's functional traits potentially include many nested, partially overlapping and diverging units (e.g., the wing as well as indefinitely many subdivisions of it). This is a problem if we want criteria of individuation that can tell us "how many" characters an organism has (R1), or how much more "complex" one species is compared to another (R2). With a functional trait concept, there is only a determinate answer to these questions in a local microevolutionary context with a fixed environment and known selection pressures—an epistemically demanding condition. Different populations of the same species located in different environments and experiencing different selection regimes (e.g., different predators) will have different functional traits even if they are developmentally, physiologically, and morphologically the same.

The restriction of top-down or functional trait individuation to microevolution leads to a final limitation on the role of defining characters that are units of generalization for comparative biology (R4). If trait identity is sensitive to specific selection regimes, the resulting functional traits will have low projectibility except to populations with a similar body organization *and* selection pressures. This is likely to be narrowly useful for some comparative studies of convergent evolution between closely related taxa (McGhee 2011). For the rest of comparative biology, a different character concept is needed (most comparative studies rely on homology, Wake 1994).

For all of the above reasons, top-down or functional trait concepts are best viewed not as providing a foundational account of what the characters are in given organism or species, but rather as providing some additional conditions that characters that have already been identified must meet in order to causally operate in processes of selection. None of the functional approaches surveyed enables determinate demarcations of characters in the absence of any other biological information. A more basic descriptive approach is needed for the task of identifying candidate functional (or other) characters.

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3.2 Same-level approaches: descriptive morphology

In same-level or descriptive approaches, characters are individuated by intrinsic features or relations to other characters at roughly the same level of organization rather than by causal connections to a higher or lower level. The establishment of "primary homology" (De Pinna 1991) is based on descriptive morphological criteria. For example, a skeletal element such as a thoracic rib is recognizable as a character by histological differences with its surroundings and comparisons with rib-like characters in other species, without knowing its genetic basis, how it develops, or how it contributes to fitness. Descriptive approaches to character identification can be found in comparative anatomy, morphology, histology, systematics, and elsewhere.

The rationale for a descriptive approach is based on three main principles. First, in practice, character identification must start from observation, measurement, and description of the objects that are perceptually salient to human scientists. Even if these initial demarcations are ultimately to be revised in the direction of functional or developmental trait concepts, the initial descriptive step is necessary to pick out candidate characters to subject to further tests and criteria. Second, character identity possesses some causal autonomy from higher and lower levels of organization (Love 2006). Third, many of the investigative roles for characters demand that character identification should be independent of biological theory or hypotheses in order to be able to serve as stable evidential tests of theory and hypotheses.

The third principle is the most pertinent for understanding the relationships between functional, descriptive, and developmental characters since it requires that descriptive individuation can and should be practiced independently of the others. One area where this ideal of independence has been articulated is phylogenetic testing in systematics. Several authors have argued that character identification should be independent of homology (Vogt 2008; Vogt et al. 2010; Richter and Wirkner 2014; although see Franz 2014). Richter and Wirkner (2014) term these neutral descriptive characters "morphemes." Since homology depends on hypotheses about phylogenetic descent, a set of characters can only be used as evidence for adjudicating between rival phylogenetic hypotheses if the description of characters is not already wedded to a specific hypothetical phylogeny. Otherwise, rival hypotheses may circularly depend on different sets of "characters," making it difficult to evaluate evidence for one or the other. A related idea can be found in the philosophy of "total evidence" in systematics (Rieppel 2009), which maintains that descriptions of characters should not be tainted with proposed mechanisms or causal linkages between them, and instead

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phylogenetic hypotheses should be evaluated based on the sheer number of characters that are congruent with one or the other. This position supports a highly permissive view of characters as anything that can be used to "characterize" a species. A different view (Padial et al 2010) is that, given the aim of mapping phylogeny, taxonomists should give extra weight to functional traits that may have caused speciation, e.g., speciation through sexual selection on male coloration or courtship songs. In this case, phylogenetic inference would involve a descriptive step followed by tests of selection for certain characters.

To assess how well descriptive character individuation can satisfy roles (R1)–(R4), it is necessary to determine its capacity to operate autonomously from other approaches. The aim of describing morphemes *entirely* independently of theory and hypotheses is likely unrealizable. There are indefinitely many ways to group cells and tissues into higher-level phenotypic units. Decisions about which groupings to treat as units and what to measure must rely on background knowledge and hypotheses about how the system works and how it evolved. If this narrowing-down is based only on direct observation and perceptual salience, it will not provide a procedure for resolving differences of opinion when they arise. An example of the limits of observation and description can be found in the Lepidopteran wing color pattern system (Fig 2).

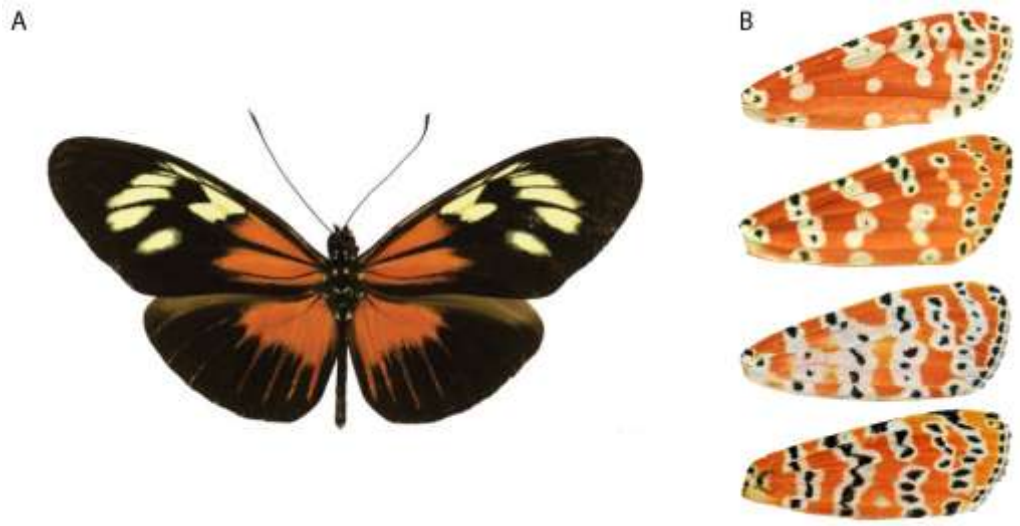


Fig 2. Direct observation alone does not establish whether some phenotypic feature is a distinct character (see text). (A) Color patterns in a *Heliconius* butterfly. Photo by Didier Descouens, modified and reproduced under license CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0/). (B) Spots grading into bands in *Utetheisa ornatrix*. Photo by Richard Gawne, from the collection of the Smithsonian National Museum of Natural History.

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Looking at the *Heliconius* butterfly in Fig 2A, most human observers would probably describe spots of yellow and orange pigment against a black background. Some investigators have thought the same (Sheppard et al. 1985). Developmentally, however, the yellow and orange areas appear when there is an *absence* of black pigment (Nijhout and Wray 1987). The black pigment arises from point sources that fuse together. This sort of revision of units is made possible by understanding how the spots form developmentally. Similarly, wing color patterns in Lepidoptera are often characterized by different visual elements such as spots and bands (Fig. 2B). From a purely descriptive-morphological viewpoint, it is not clear whether spots should be counted as distinct characters based on color boundaries, as contrasted with groups of spots, nor whether spots and bands should be counted as distinct characters or variations on the same character (see Gawne and Nijhout 2020). Although morphological comparisons between clades can reveal variational structure in the color pattern system, the issue is only firmly resolvable through mechanistic investigation of how the color patterns develop.

Without sound criteria for *confirming* characters that have been descriptively identified, such as criteria provided by conceptual schemes for secondary homology, units of selection, or developmental individualization of characters, there are no guidelines for reaching consensus on what an organism's characters are. While this is not necessarily disruptive to species discrimination, it leads to uncertainty about how much evidential weight specific morphemes should carry. In congruence testing in cladistics, any character that is congruent with a given phylogenetic tree can be thought to add an independent piece of evidence in favor of that tree. In the Lepidopteran wing color system, Gawne and Nijhout (2020) argue that bands are nothing more than groups of spots that have expanded enough to fuse together. If this is correct, then bands are not a distinct character over and above spots, and they do not add evidence to a phylogenetic tree that already includes spots.

More generally, our ability to describe phenotypic features as distinct does not guarantee that they are actually causally dissociable in development and evolution. The latter is partly discoverable through comparison of many phenotypic variations but inevitably requires understanding the developmental mechanisms underlying the variational structure of the phenotype (see Wagner 1989, 2014; Brigandt 2007). Practical limitations nonetheless prescribe a wide application of descriptive-morphological methods where experimental interventions are unavailable, tedious, or costly.

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In summary, descriptive individuation should thus be regarded as an initial step that is necessary for all roles (R1–R4), but it requires supplementation by functional and developmental testing in many cases and where possible (see section 4).

3.3 Bottom-up approaches: genetics and development

In bottom-up approaches, the status of some phenotypic feature as a character is determined by the underlying causal mechanisms that produce it. Character individuality is therefore based on the modularity of an underlying developmental or genetic mechanism. Gould and Lewontin's claim that the chin is not a "real" trait, but that the growth fields of the jaw are, can be read as a criticism of top-down and same-level individuation of characters in favor of a bottom-up approach. Bottom-up approaches can be found in developmental biology, developmental genetics, and genetics broadly.[3]

There are two main rationales supporting a bottom-up perspective. First, functional and descriptive approaches can easily fail to identify important units of phenotypic variation. As we saw, functional individuation captures traits selected-for but not traits selected-of. The latter is essential for accurately describing how a population responds to selection (R3) as well as a population's longer-term constraints and potentialities for evolutionary change (evolvability), which may be shared across species (R4). Moreover, the traits that are salient to observation in descriptive approaches can also fail to be distinct and cohesive units of variation, creating limitations for all roles (R1–R4). These lacunae can in principle be filled by models that demarcate phenotypic units as outputs of the causal structure of development.

A second rationale is that the vast majority of body parts—from limbs to liver tissues to neurons—do not directly replicate but must be re-built anew in every generation from what is transmitted through the germline (Wagner 1989). From this Weissmanian observation it is natural to suppose that developmental-genetic factors largely determine what the character boundaries are. Any apparent individuality of characters in the adult should be reflected in some underlying modularity of genetic causes in order to be repeatable across generations and species. This idea can be used as a criterion for the reality or genuineness of a trait: a "pseudo-

[3] There is also a family of *non-developmental* bottom-up approaches based on the following principle: a part or module is a set of components that interact more strongly or frequently with each other than with their environment (see, e.g., McShea 2000; McShea and Venit 2001; Collier 2004; Simon 1962; see Wimsatt 1976; Girvan and Newman 2002; Hintze and Adami 2008). Detailed examination of this principle will have to be reserved for future work.

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trait" would be any phenotypic feature that fails to align with any underlying genetic or developmental module (e.g., the chin), being either a subset or superset of "true" modules.

From here we can define a developmentally individuated character as one whose individuality is grounded in modular underlying factors. While this may seem straightforward in the abstract, filling it in with more concrete models quickly reveals difficulties.

There are two broad ways of filling in the idea of modular underlying factors. The first is in terms of statistical genotype–phenotype maps in quantitative genetics, and the second is in terms of causal mechanisms like gene regulatory networks operating in dynamic cell-biological conditions. In the former case, modularity is often understood as "restricted pleiotropy" (Wagner and Altenberg 1996; Winther 2001; Wagner and Zhang 2011). This means that when genes affect more than one trait (pleiotropy), these effects are mostly restricted to features within the same trait complex—e.g., different aspects of the limb rather than the limb and heart and eyes. If modularity is explicated in terms of pleiotropy, however, it would be circular to suppose that modularity is a pre-condition for trait identity. This is because, again, measuring pleiotropy depends on already having a background notion of where one trait ends and another begins. Same-level methods of trait identification are therefore needed that are independent of genetics and genetic modularity.

Another problem with basing bottom-up character individuation in genetics is that the relevant genes may be diffusely spread across the entire genome rather than forming neatly demarcated modules. Recent models of the genetic architecture of quantitative traits suggest that variances in many traits are not only "polygenic" (being influenced by many genes) but even "omnigenic" (being influenced by virtually all genes) (Boyle et al. 2017; Sinnot-Armstrong et al. 2021). Many of these genes will also be pleiotropic (Hansen and Pélabon 2021). If most traits are statistically influenced by virtually all genes, then genetic association alone can lack the contrastive resolution needed to demarcate quantitative traits. Again, a stable same-level description of a trait is necessary and prior to the mapping of its genetic architecture.

These problems might be circumvented by basing the bottom-up individuation of characters on the more proximal developmental mechanisms that produce the character. What is needed is a way of establishing when in development the relevant character is *individualized* (see section 2.3), and a way of demarcating a specific underlying mechanism for it. One framework that addresses this issue is the mechanistic model of character identity

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developed by Wagner, Love, and DiFrisco (Wagner 2007; 2014; DiFrisco et al. 2020). This model differentiates morphological traits into characters, understood as anatomical body parts, and character states, or properties of those body parts (size, shape, color, etc.). It hypothesizes that the identity of characters, including cell types, tissues, and organs, is controlled and maintained by modular mechanisms known as "Character Identity Mechanisms" (ChIMs) (DiFrisco et al. 2020). Characters at different anatomical levels have different kinds of ChIMs, which represent a subset of the total developmental mechanism involved in generating a determinate phenotypic trait. This subset possesses a specific causal profile—including causal necessity and non-redundancy in switching on downstream developmental processes—that makes it especially likely to be conserved in evolution, as long as the corresponding character is maintained. The ChIM model proposes that these mechanisms can explain the traceability of morphological characters across generations and species (homology), while also explaining the developmental individualization or modularization of characters that contributes to their evolvability (Wagner and Altenberg 1996). These proposals serve the two main rationales for bottom-up approaches to character individuation.

How does this model contribute to the character individuation problem? Importantly, it does not obviate the need to start from same-level descriptive criteria. Although ChIMs are not functionally individuated by characters, they are also not identified entirely independently of the character, and homology of the overlying character is required to confirm homology between ChIMs (DiFrisco et al. 2020). At the same time, the discovery of a ChIM can lead to revising the character initially identified in descriptive terms, in an iterative process of reciprocal demarcation. Another relevant attribute of the ChIM model is that it is designed to apply only to *morphological* characters or body parts—i.e., cell types, tissues, and organs—as well as body plans (DiFrisco and Wagner 2022). It is an open question whether other kinds of characters, such as behaviors, developmental processes, or physiological attributes can be covered with the same model, or whether they require a different developmental model or a non-developmental approach (descriptive or functional). Similarly, morphological character *states* such as the shape, size, color, and number of a body part can be characters in systematics and bearers of phylogenetic signal, even though they are not individuals, entities, or parts. Developmental individualization is therefore not necessary for characters to be used in mapping phylogeny (R1).

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One key limitation of developmental approaches generally pertains to characters involved in natural selection. Whereas top-down or functional approaches can fail to identify characters that are "selected-of," developmental approaches can fail to identify characters that are "selected-for." This is because there are many traits that can be targeted by selection without being strongly developmentally individualized—including superficial attributes, pleiotropically correlated characters, aggregates, and other alleged "pseudo-traits." For example, even if a developmental perspective would indicate that the human chin is an aggregate of two distinct body parts, the configuration of the two constitutes a shape trait that can be subject to selection (and likely has been, Pampush 2015; see Meneganzin et al. 2024). Even when the trait is a "mental construct" (Lewontin 1978), if that construct corresponds to *some* property of the organism with underlying heritable variation, it can be subject to selection-for. This is what occurs in sexual selection, predation, and mimicry, where the identity of a trait is not only fixed by the way it develops, but by the way it is perceived and acted upon by other organisms. If there is a disconnect between the feature that is acted upon and the underlying variational structure of phenotype, then the phenotype will respond to selection by also changing traits other than the traits selected-for (see section 3.1, 5). This is why *both* developmentally and functionally individuated characters will often be necessary for capturing what is happening during a selection process (R3).

4. Prescriptions: mapping criteria onto investigative roles

The three broad approaches described above generate distinct criteria of individuation that can be used for demarcating, counting, and tracking characters across life cycles and species. The further problem is to map these criteria onto the major scientific roles of the concept, in order to prescribe which criteria should be used in which situations. This mapping as elaborated here is not definitive or complete, and further work on the character concept may add or refine criteria as well as roles.

Figure 3 shows a proposed mapping relationship between roles (R1)–(R4) and the three approaches. As argued above, both functional and developmental criteria are dependent on an initial stage of same-level character description to identify a candidate character, which can then be studied as to its contribution to fitness or underlying developmental-genetic mechanism, respectively. This same-level description is akin to an initial hypothesis used to frame and guide an empirical investigation, which can be confirmed or disconfirmed by developmental, functional, or phylogenetic tests. Same-level approaches, even practiced in a comparative mode on a large number of similar characters, can pick out units lacking

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functional or mechanistic significance, and so should not be viewed as evidentially fully self-sufficient. The main exception is for the role of mapping phylogeny (R1), where the sheer number of characters included in a typical phylogenetic analysis makes it practically impossible to test and confirm many of them (although see Rieppel and Kearney 2007; Rieppel 2009).

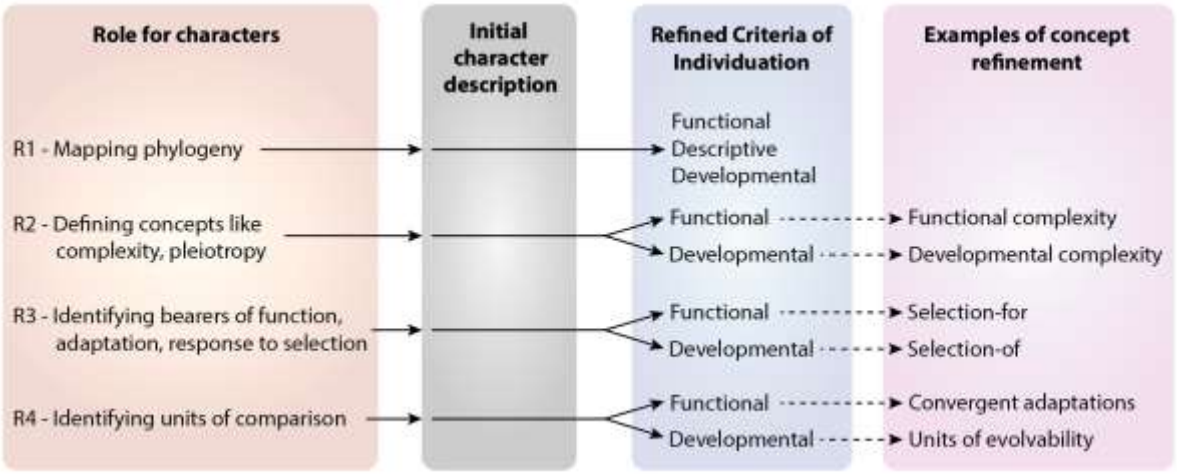


Fig 3. Mapping four investigative roles for characters onto different criteria of individuation, with examples of resulting concept refinement. See text for details.

The fact that developmental and functional criteria will often pick out different units of phenotype is a key insight with ramifying consequences for the roles of the character concept. For example, when biological concepts like complexity and pleiotropy are defined in a way that requires some way of counting characters (R2), developmental and functional criteria can give the same organism different degrees of complexity and the same gene different degrees of pleiotropy. If these criteria are mixed and applied haphazardly, then complexity and pleiotropy become imprecise and less useful concepts. Which kind of complexity or pleiotropy places a "cost" on evolvability, for example? (Orr 2000; Altenberg 2005; Wagner and Zhang 2011) Distinguishing character concepts allows us to see that limits on *adaptability* come from functional complexity or pleiotropy, whereas limits on *variability* come from developmental complexity or pleiotropy. This suggests that other concepts inter-defined with the character concept may also need to be split into developmental and functional versions.

Similarly, for identifying bearers of function or adaptation and describing the response to selection (R3), *both* developmental and functional criteria should be used but not conflated. Suppose, following Gould and Lewontin (1978), that the human chin we pick out with descriptive criteria is not a "real" developmental character. A sound description of hominid

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mandibular evolution nevertheless should not reduce the chin to the underlying growth fields of the jaw (developmental character), if it is true that aspects of chin shape underwent selection (functional character). At the same time, the developmental basis for allometric shifts between these growth fields is necessary for understanding the constraints and evolvability of the mandible in connection to change in other characters such as teeth, cranial bones, lingual musculature, and the respiratory airway (Coquerelle et al. 2013). Functional traits are selected-for, whereas developmental traits are selected-of (see section 3.1, 3.3).

Finally, the different criteria of trait individuation yield different units of comparison with different projectible properties (R4). Developmentally individuated characters share variational properties and can thus be considered phenotypic units of *evolvability* (see Brigandt 2007; Wagner 2014; Hansen et al. 2023). Developmental characters like the vertebral column, the tetrapod limb, or the insect thorax are built by conserved mechanisms that are the source of developmental constraints on body plan evolvability across wide phylogenetic distances (see section 5). Functionally individuated characters share causal roles and contributions to fitness. Since these functions can have heterogenous developmental realizations, and they are defined relative to potentially labile selection gradients, functionally individuated characters are more relevant when sameness of functional role is in focus and its mechanistic basis doesn't matter. This is more often the case in comparative studies of adaptation and convergent evolution (Harvey and Pagel 1991; McGhee 2011) and in ecology (Violle et al 2007).

The proposed mapping between criteria and roles yields prescriptions for the meaning and use of the concept of a biological character. The implementation of functional, descriptive, and developmental characters is differentiated according to different investigative roles. At the same time, each character concept integrates across multiple roles. For example, the effort to describe adaptive processes (R3) that lead to speciation may reveal functional characters that are particularly informative for phylogenetic inference (R1) (Padial et al 2010). Using developmental criteria, one can ask about how developmental complexity (R2) impacts the evolvability of body plans (R4), in the effort to understand macroevolutionary trends like body plan complexification (McShea and Brandon 2010). Similarly, the neural crest deficit hypothesis for mammalian domestication syndrome is based on the idea that developmental pleiotropy (R2) causes a developmentally integrated response to selection (R3) that is also general to mammals (R4) (Wilkins et al 2014) (see 3.1).

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With these prescriptions for concept use in hand, the deeper challenge is to understand why these different kinds of characters diverge. One approach to this sort of problem is to analyze how different individuated units (such as gene, species, or individual) serve different interests, epistemic goals, questions, or values on the part of scientists (see section 2). Following a theoretical biology methodology, however, we are interested in what makes biological systems the way they are. Why do developmental and functional characters diverge, when they do?

5. Explaining divergences between functional and developmental characters

The preceding investigation puts us in a theoretical position to propose new hypotheses for explaining divergences between functional and developmental characters.

The basic source of divergence lies in the fact that high-dimensional standing genetic variation enables populations to respond to selection in functional traits that do not correspond to strongly demarcated developmental-genetic modules (Weber 1992; Pavličev and Wagner 2012; Boyle et al 2017; Hansen et al. 2023). With persistent selection, however, the genetic architecture can be expected to adjust, as described by Riedl's (1978) hypothesis of the "imitative epigenotype" (see also Wagner and Altenberg 1996; Wagner et al. 2007; Zelditch and Goswami 2021; Schlosser 2023). This is the idea that patterns of pleiotropy evolve in such a way that functionally and developmentally related traits come under a common genetic control that is distinct from the genes affecting other character complexes. In other words, over evolutionary time, genetic modularity will tend to "imitate" (align with) the units of development, and these with units of function. Concretely, this capacity for *alignment* will depend on the genetic system's ability to counteract deleterious forms of functional pleiotropy, either by tuning it down directly (Pavličev and Wagner 2012) or through indirect compensatory change (Paaby and Gibson 2016).

Rather than describing an unconditional evolutionary trend, Riedl's hypothesis would more likely hold when selection pressures are stable over long time scales. We can thus formulate a modified version as follows:

> **Hypothesis 1:** the degree of divergence between developmental characters and functional characters depends on the speed of change in the selective environment experienced by a population, relative to the population's capacity for genetic alignment.

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In addition to the *alignment* of modules, there is a contrary process of *entrenchment* (Riedl 1978; Wimsatt 1986). Namely, when developmental complexity increases in evolution, certain developmental mechanisms can become causally necessary for setting up further developmental processes, and become incapable of changing even in spite of shifting ecological demands (e.g., vertebrate notochord signaling). This process is thought to give rise to the phenomenon of stable body plans (Raff 1996; DiFrisco and Wagner 2022). Greater developmental entrenchment means that developmental characters are less likely to re-align with novel units of function. When combined with adaptive radiation, developmental entrenchment promotes dissociation of developmental and functional characters. For example, vertebrates and arthropods each have highly conserved body plans despite using overlapping part complexes for different functions. Birds, bats, and pterosaurs possess the same tetrapod limb (developmental character), but use different parts of it (functional character) for flying. Likewise, the proximal leg segments (developmental character) of ancestral crustaceans were functionally incorporated into the body wall in insects (Bruce and Patel 2020).

> **Hypothesis 2:** the degree of divergence between developmental characters and functional characters depends on the degree to which a historical lineage undergoes developmental entrenchment combined with adaptive radiation.

Shifting combinations of alignment and divergence in evolutionary history appear to have given the genotype–phenotype map the character of a "palimpsest"—a Medieval manuscript with multiple texts partially superimposed over one another and partially erased with time (Hallgrímsson et al. 2009). This may explain much of the pleiotropy and covariance that exists among developmental modules and functional modules.

The above hypotheses are testable using comparative methods, as long as concepts like entrenchment can be operationalized for purposes of measurement. In the present context, they illustrate how the character concepts described above can aid in generating scientific theory and hypotheses about the evolution of the genotype–phenotype map.

6. Conclusion

The question "what is a character?" points to a fundamental unsolved problem of biological theory. This paper answers this question roughly as follows. A *hypothetical* character is a described property, activity, or part of an organism. A hypothetical character may be confirmed or validated as a genuine character by the fact that it either (1) undergoes natural selection by causing differential reproduction in a population (see 3.1), or (2) is produced by a

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modular developmental-genetic mechanism (see 3.3). We have seen how individuating characters based on these criteria is typically an iterative process that must be differentiated according to different roles for characters in biological investigation.

Descriptive identification of hypothetical characters is always a necessary initial step. For roles other than phylogenetic testing (R1) (see 3.2), hypothetical characters should be validated or revised via investigation of the character's causal contribution to fitness, or its underlying developmental mechanisms. Much biological science, but especially phylogenetic research, proceeds in a hypothetical descriptive mode due to practical limitations. Developmental approaches are inherently more demanding to formulate and implement than functional approaches because they typically require a higher-dimensional description of a phenotype that can be compressed when we consider only its effects on fitness. Accordingly, understanding developmental individuation of characters is arguably where further conceptual development is most needed. At the same time, both functional and developmental criteria are necessary for understanding the characters involved in selection-driven evolutionary processes. The units picked out by these approaches do not necessarily overlap or align, they are differently suited for different roles of the character concept, and they have different projectible properties. Mapping the interplay between these character concepts and its implications for biological investigation constitutes the main constructive insight of the preceding analysis.

The attempt to hypothesize how developmental and functional characters align and diverge in evolution outlines a theoretical biology methodology that can be applied to other concepts exhibiting the same pluralistic pattern of cross-cutting units, such as biological individuality and levels of organization. In this approach, the plurality of kinds of character, individual, or levels is not only explained as resulting from different scientific practices and aims. It can be explained as arising from the evolved complexity distinctive of biological systems.

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