HYPOTHESIS

What is a trait? Lessons from the human chin

Andra Meneganzin[1] | Grant Ramsey[1] | James DiFrisco[2]

[1]Institute of Philosophy, KU Leuven, Leuven, Belgium

[2]The Francis Crick Institute, London, UK

Correspondence
James DiFrisco, The Francis Crick Institute, London, UK.
Email: james.difrisco@crick.ac.uk

Abstract

The chin, a distinguishing feature of *Homo sapiens*, has sparked ongoing debates regarding its evolutionary origins and adaptive significance. We contend that these controversies stem from a fundamental disagreement about what constitutes a well-defined biological trait, a problem that has received insufficient attention despite its recognized importance in biology. In this paper, we leverage paleoanthropological research on the human chin to investigate the general issue of character or trait identification. First, we examine four accounts of the human chin from the existing literature: the mandibular differential growth byproduct, the bony prominence, the inverted T-relief, and the symphyseal angle. We then generalize from these accounts and propose a three-stage framework for the process of character identification: description, detection, and justification. We use this framework to reinterpret the four accounts, elucidating key points of contention surrounding the chin as well as other morphological characters. We show that debates over the chin carry broad and important biological implications that extend beyond this trait and that are not mere semantic issues of definition.

KEYWORDS
adaptation, biological character, biological trait, chin, human chin, measurement

1 | INTRODUCTION

When thinking about what makes humans unique, having a chin would hardly be the first thing that comes to mind. Yet, since the first morphological description of *Homo sapiens* (Blumenbach, 1969), the possession of a chin has featured as one of the defining traits of our species (Meneganzin & Bernardi, 2023; Schwartz, 2016; Schwartz & Tattersall, 2000; Stringer, 2016). No other primate displays a bony protrusion extending from the lower jaw beyond the inferior teeth.

However, no consensus has been reached on the chin's evolutionary origins. None of the adaptive or spandrel-based hypotheses are particularly well supported on either theoretical or empirical grounds (for a full summary of the proposed chin hypotheses, see Pampush & Daegling, 2016a). Adaptive explanations focus on masticatory stress (Daegling, 1993), sexual selection (Thayer & Dobson, 2010), or the evolution of speech (Ichim et al., 2007). Nonadaptive or spandrel-based accounts take the chin to be an artifact of reduced dentition and shrinkage of the alveolar region hosting the lower teeth (Gould, 1977; Gould & Lewontin, 1979; Waterman, 1916; Weidenreich, 1936), the prevention of airway constriction (Coquerelle et al., 2013, 2017), or the reduction and retraction of the mid-face due to self-domestication (Cieri et al., 2014).

What makes the chin an interesting case is its resistance to an agreed-upon definition or status as a character (Pampush & Daegling, 2016a; Pampush et al., 2018; Schwartz & Tattersall, 2000). What a chin actually *is* and what is understood by chin-having in extant hominin taxa has received multiple, nonequivalent answers from different authors. Far from being an idiosyncratic issue within

paleoanthropological discussions, difficulties in chin characterization are just one example of a much wider and underappreciated problem —that of character identification in biology (Wagner, 2001). Despite characters, traits, or phenotypes (we use these terms equivalently) being basic units of analysis in biological research, the criteria that should be used for demarcating them are less clear than criteria for comparable concepts like genes or species (Houle et al., 2010).

This paper will focus on studies of the chin to make some headway on this problem. Given that it will not be possible to cover all important aspects of trait individuation in this commentary, we focus on a central cluster of issues, including the relationship between trait description and measurement, how to tell whether a given trait is "real" or genuine rather than an artifactual description, and how the adaptive status of a trait depends on how it is described and measured.

We begin by first reviewing existing ideas about what the chin is, highlighting overlaps and differences in what is taken to be the relevant character, and how it is individuated from surrounding features. We propose a distinction between three steps in the process of character identification—its description, detection, and justification—and show how this distinction can clarify existing disagreements about the chin and other characters. These disagreements, we show, are not merely about definitions or semantics, which can be resolved just by being clear about what one means. They often have deeper theoretical implications. We conclude by drawing general lessons for the problem of character identification in biology.

2 | FOUR ACCOUNTS OF THE HUMAN CHIN

There are in principle indefinitely many ways of partitioning an organism (or a structure) into characters. In biology, a key problem is how to identify characters in a way conducive to phylogenetic reconstructions, comparative analyses, and developmental and adaptive explanations. Unfortunately, there is no simple solution to this problem, as the human chin illustrates.

The preponderance of approaches to understanding the human chin in the evolutionary and anthropological literature of the past century has focused on providing answers to *why* we have chins. Some of these approaches also provide answers to a more basic and often overlooked question: *what* is a chin? These answers provide accounts of what trait is in focus and which anatomical features should be referred to when identifying chins. We describe four historically distinct strains of characterizing the human chin: the mandibular differential growth byproduct, the bony prominence, the inverted T relief, and the symphyseal angle (Table 1; see Figure 1).

Some of these accounts (such as the bony prominence) emerged in the earliest stages of *H. sapiens* characterization, while others developed later in response to dissatisfaction with existing accounts (such as the inverted T relief account being offered as an improvement on that of the bony prominence). One of the accounts even challenges the idea that the chin is a trait of its own, implying that it is wrong to ask adaptive questions about its form. At this stage, our discussion of these accounts is purely illustrative, and we do not take a stance on whether some of them are mutually exclusive or whether they simply provide different descriptions that ultimately refer to the same structure. None of these options is a priori obvious. The matter can only be assessed via an explicit framework for character identification, which we aim to outline. Let's now consider these accounts in more detail.

2.1 | The mandibular differential growth byproduct

Foundational work for understanding the ontogenetic integration of the human mandible has identified five major quasi-independent skeletal units (Figure 1): the basal, alveolar, coronoid, condyloid, and angular regions (Moss & Rankow, 1968). Gould's and Lewontin's criticism of the "adaptationist programme" (1979) famously presented the chin as a *structural artifact* arising as a necessary byproduct of the interaction between two of the five domains of growth: the basal region (where the chin is located) and the alveolar. Elsewhere, Gould (1977) characterized the human chin as the outcome of differential

TABLE 1 Four accounts of the human chin and their respective characterizations.

| Chin account	Characterization
The mandibular differential growth byproduct	The byproduct of the interaction between two growth fields (alveolar and basal, see Figure 1) (Gould, 1977; Gould & Lewontin, 1979; Marshall et al., 2011; Weidenreich, 1936)
The bony prominence	An outgrowth of bone tissue protruding from the front of the human mandible (Daegling, 1993; DuBrul & Sicher, 1954; Enlow, 1982)
The inverted T relief	A composite upside-down T-shaped structure formed by a vertical midline keel, a triangular protrusion at the inferior margin of the mandible (*trigonum mentale*, composed of the central mental protuberance and the lateral mental tubercles), and the attendant depressions on each side of the keel (*mental fossae*) (Schwartz, 2016; Schwartz & Tattersall, 2000)
The symphyseal angle	The angle formed between the horizontal alveolar/occlusal plane and vertical plane cutting through the midline of the mandible (defined by the landmarks *infradentale* and *gnathion*) (Pampush, 2015; Pampush et al., 2018)
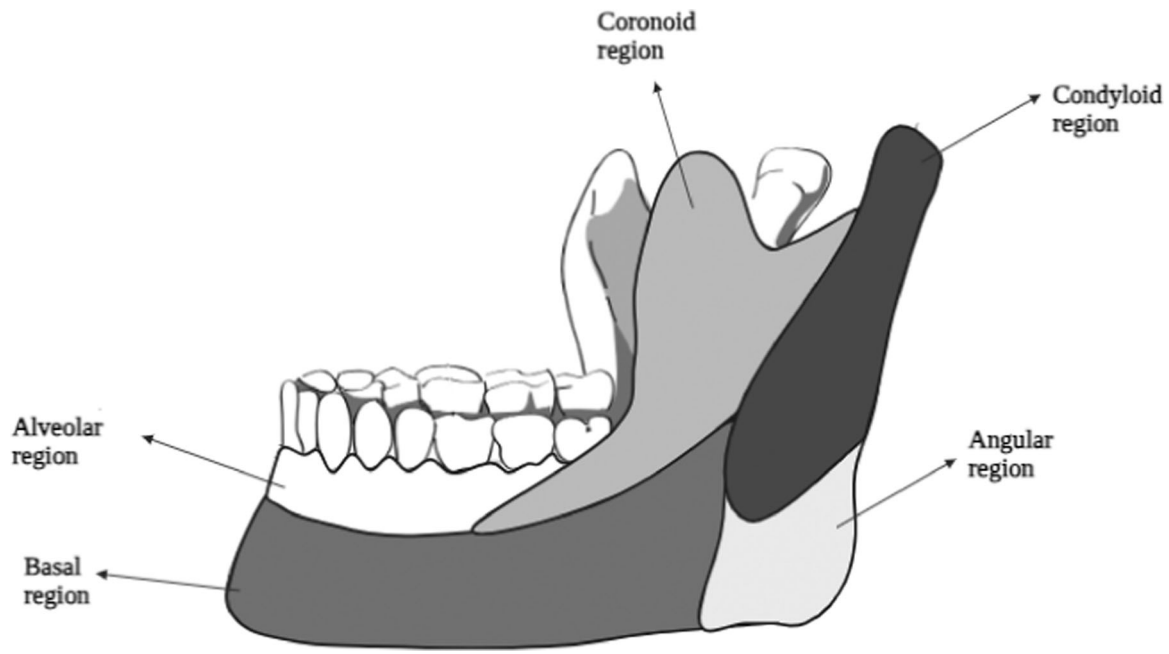
FIGURE 1 The five skeletal modules of the human mandible, adapted from Pampush and Daegling (2016a), drawn after Moss and Rankow (1968). Created with biorender.com. Original image made available under the Creative Commons CC0 1.0 Universal Public Domain Dedication.

slowing (heterochrony) in the development of different parts of the human jaw, with the alveolar portion being far more slowed-down than the basal. This is linked to evidence of differential bone remodeling activities in the two modules. After the appearance of the first deciduous teeth, the alveolar area becomes an area of bone resorption (a pattern unique to modern humans) and thus follows a different growth trajectory from the basal, which becomes developmentally stable after the initial phase of deposition (Enlow, 1966; Pampush & Daegling, 2016a; Weidenreich, 1936) Although the study of the integration of the human mandible remains an active area of research (Polanski, 2011), the ontogenetic interaction between mandibular modules is no doubt crucial for explaining the formation of the chin. Under this account, the chin is the *morphological byproduct* of the differential growth rates of the basal and alveolar modules, due specifically to the different bone metabolism in those modules, which results in their different relative positions.

2.2 | The bony prominence

The chin is frequently defined as the bony prominence or bony boss at the front of the mandible (or, as DuBrul & Sicher, 1954 called it, a "blob of bone"). Indeed, what has captured the interest of many biological anthropologists, and has inspired many functional explanations (see Section 4), was the projection of the lower border of the mandible beyond the anterior dentition. The human chin has thus historically been identified based on protrusiveness alone, with its absence or presence considered as character states (Enlow, 1982; Lieberman, 1995). Under this more general perspective, the chin can

be seen as an *outgrowth of bone tissue* or bone mass that can be explained with reference to analogous masses, blobs, or processes that can be found in human skeletal anatomy (Daegling, 2022; DuBrul & Sicher, 1954).

2.3 | The inverted T relief

Other authors, most notably Schwartz (2000, 2010, 2016) have looked for more stringent criteria for chin-having than a mere protrusion. They suggest that only the constellation of discrete features present from fetus to adult should be referred to as the chin, proposing that the "inverted T" relief or raised "falsum" ("⊥") and its lateral depressions are the "true chin." Under this account, the chin is not the mere outgrowth at the base of the mandible but is a *composite structure* characterized by these specific morphological details (see Figure 2).

2.4 | The symphyseal angle

While acknowledging that the chin is a complex feature, others have proposed the "symphyseal angle" as a key feature for establishing chin possession (Pampush, 2015; Pampush et al., 2018). The symphyseal angle is formed by the horizontal alveolar plane and the vertical plane cutting through the midline of mandible. An obtuse symphyseal angle, although not complete, would be sufficient to assess the presence of a chin—a continuous, quantitative trait allowing for examinations of evolutionary trends and the historical
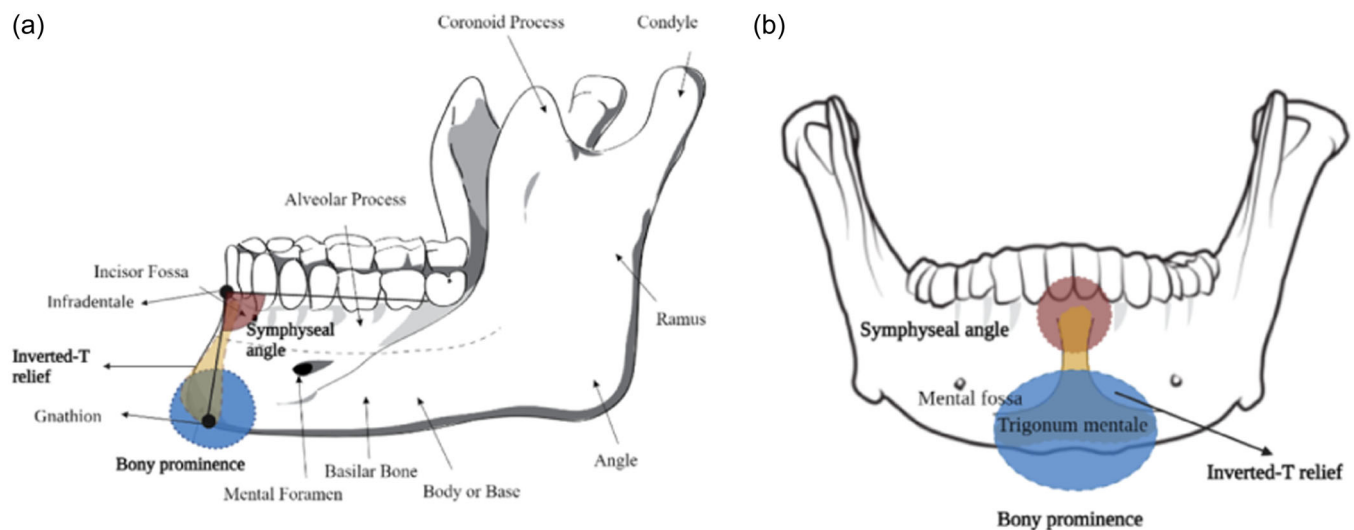
FIGURE 2 Anatomical structures and terminology of the human mandible. (a) Lateral view of the human mandible. (b) Frontal view of the human mandible. Created with biorender.com. Original image made available under the Creative Commons CC0 1.0 Universal Public Domain Dedication.

timing of morphological changes (Pampush et al., 2018). Under the symphyseal angle account, the chin is defined as a *property* or *quantity* (an angle) instead of an object (a bony boss). This property can be measured in the alveolar area of the human mandible by taking the distance between the lower border of the mandible and a frontal plane passing through the midpoint of the lower incisors (Figure 2a).

3 | THREE ISSUES OF CHARACTER IDENTIFICATION

The overview provided above reveals a disagreement over what a chin is that is arguably not just a matter of terminological preference. Instead, the various ways the chin is characterized display substantially different views about what matters in identifying a biological character.

To see what this different understanding comes down to, we propose a distinction between three steps in character identification:

(i) *Description*: *what* is singled out from a broader anatomical region as the relevant character.
(ii) *Detection*: *how* the character is singled out and measured in practice.
(iii) *Justification*: *why* treating the character as a biologically meaningful entity is justified; what grounds the identification of a morphological item as a genuine biological character.

As it'll become clearer later in the paper, these "steps" are not tied to a single logical or chronological order, as investigative progress at each stage iteratively affects the others. Let us discuss them in turn.

3.1 | Description of characters

In *describing* a morphological character, practitioners use a verbal description or a name to delimit an area from a broader anatomical region or single out one of its observable properties (size, shape, color). A description can be viewed as an initial hypothesis that some feature or part in the organism plays a role in a biological process (selection, development, metabolism, etc.), and the description is revisable in light of empirical investigation. That initial hypothesis serves as an important starting point for subsequent research, and as such it should not be viewed as a "definitive" descriptor for the focal character: research advances will provide the ground for testing that hypothesis, potentially leading to revised or new descriptions.

In the case of the human chin, debate on its possible attribution to nonmodern human specimens or other mammals (i.e., whether or not they possess a legitimate chin) has partly emerged as a straightforward consequence of the different approaches to defining or describing the chin discussed above. Most obviously, from the perspective of character description, the bony prominence and the inverted T relief are not coextensive and hence not interchangeable descriptors of the chin, showing instead only a partial degree of overlap (Figure 2). The documented presence of "incipient chins" among some Neanderthals and the suggested presence of a chin-like structure among elephants (Enlow, 1982) are based on particular ways of describing chins. Specifically, whether any outcropping of the surface of the inferior mandible will do or whether the morphological detail of the inverted T relief must be present, determines whether the chin is unique to *H. sapiens* or a possible homology or homoplasy (Schwartz & Tattersall, 2010).

The inverted T relief has been defended as a neutral, hypothesis-free descriptor, "apart from a phylogenetic and functional

interpretation" and from subsequent discussion of the "systematic interpretation of the data" (Schwartz & Tattersall, 2000, p. 403). Although there is room for discussion on what providing a good (and theory-free) descriptor of a character amounts to, the inverted T account prioritizes features that are present consistently across all members of a taxonomic group. This has been proposed *contra* the "simple" focus on the anterior protrusion of the bony prominence, which would make some modern humans seem to lack chins due to intraspecific variation (cfr. Lieberman, 1995, p. 174; Schwartz & Tattersall, 2000, 2010).

That the bony relief versus inverted T approaches are genuine alternatives is further made clear by Schwartz and Tattersall's claim that morphologically, under their view, "a bulging symphyseal region is not equivalent to a chin" (2000, p. 402). If both humans and elephants can be described as having chins, the term "chin"—they suggest—should be dropped. But if "chin" is to be retained, "it should be restricted in usage only to extant *H. sapiens* and those fossils displaying the constellation of symphyseal features of this species [that is, the inverted T structure]" (2000). It should also be noted that while elephants have a forward-jutting part in their lower jaws that may resemble a chin-like structure, they lack lower front incisors. So even when the focus is on bony bulges, the protrusions in human and elephant jaws exhibit quite different morphological configurations. Enlow himself, attributing a "chin" to elephants, remarks that the correspondence is a loose one (1982, p. 87).

However, focusing merely on the descriptive step and the delimitation of the relevant morphological item alone misses much about the biological intuitions implicit in divergences over what the chin is. In fact, the four chin accounts are not all concerned with descriptive matters only—they are not exactly four independent ways of specifying what a chin is.

3.2 | Detection of characters

It is often the case with scientific concepts that the definition of the thing differs from the ways we detect or measure it. Examples include temperature (Chang, 2004) and biological fitness (Arnold, 1983; Endler, 1983). In such cases, the detectable property is not a competing definition of the concept but is a proxy for making the original definition operational or measurable, which may be needed due to practical limitations. Despite temperature being defined as mean molecular kinetic energy, to measure temperature, we do not attempt to measure the kinetic energy of individual molecules. We instead observe phenomena such as the rise of alcohol in a tube or the deformation of a bimetallic strip. In the same way, the chin's symphyseal angle may be understood as a way of detecting or measuring chins rather than as a distinct, competing description of what a chin is.

In general, when we have an initial trait description and a detectable or operational (measurable) version of the trait, there can be three possible relationships between them:

(a) One is as a way of measuring the other;

(b) Each is a distinct trait in its own right; or

(c) The operational trait can be viewed as replacing the initial trait, perhaps if the latter is not well defined.

Situation (a) seems to best characterize the relationship the symphyseal angle has with the bony prominence and possibly also with the byproduct description of the chin. Focusing on the bony prominence, it is not obvious that the symphyseal angle provides an independent description of what a chin is. Rather, the angle is meant to capture the degree of protrusion of the lower border of the mandible, or the degree of "bony prominence." As a proponent of the symphyseal angle measure writes, "The challenge for researchers in explaining the chin is to demonstrate the evolutionary path to this unusual protrusion, not necessarily all of the minor peculiarities of its form" (Pampush, 2015, p. 134). The protrusion can be usefully measured and quantified: under this view, angles above 90° would less ambiguously establish the presence of a projecting chin than the assessment of the degree of expression of specific subcomponents of the T (Pampush et al., 2018).

Situation (b) describes the relationship between the symphyseal angle and the inverted T. The inverted T is qualitative (though composite), whereas the symphyseal angle is a quantity and does not include the morphological detail of the T. Although the two are not as biologically independent as, say, the eye and the kidney (a more pronounced basal portion of the T will likely coincide with a more obtuse symphyseal angle), the symphyseal angle would not be a good measure of the inverted T.

Even when one trait is a measure of another (a), it can still sometimes be useful to treat the operational trait as a distinct trait in its own right (b). The symphyseal angle can be seen in this way as a way of both measuring the bony prominence and defining a new quantitative trait from an initial qualitative description. This seems to be suggested by proponents of the symphyseal angle measure when they refer to it as an "abstract, continuous trait" (Pampush et al., 2018, p. 85). While qualitative traits are important for inferring phylogenetic patterns, they are obviously limiting for tracing evolutionary processes like selection on quantitative traits (Walsh & Lynch, 2018). Thus, although the inverted T may be a way of defining a chin-trait that all and only *H. sapiens* possess, it may have limitations when it comes to studying variation and population dynamics of the chin region.

Different character descriptions obviously affect what is an appropriate measurement of the character. But different measurements and means of detection can also lead to delineating different characters of interest. For instance, studies testing the hypothesis that the chin is a sexually selected character have aimed at quantifying chin surface variation by using various outlines (tracings) of the external contour of the inferior mandible (Thayer & Dobson, 2010). This treats specific aspects of *shape*—a property of the chin, viewed here as a composite structure (Thayer & Dobson, 2010)—as a multivariate quantitative trait that can be used to distinguish and test adaptive hypotheses. Here again, we have a

measurement that defines a new, additional quantitative character that can be investigated.

Situation (c) occurs when the operational version of the trait is viewed neither as describing an additional trait nor a way of measuring an existing trait, but as an alternative or replacement for the original. Though this situation has not, to our knowledge, occurred in the case of the chin, it has occurred elsewhere. In morphological studies, qualitative descriptions of shape traits like "round," "elongated," "curved," and so on have been increasingly displaced by the quantitative traits of geometric morphometrics, which are based on arrays of measured points ("landmarks") that can be studied using statistical and computational techniques (Bookstein, 1991; Mitteroecker & Schaefer, 2022). Similarly, animal vocalizations that have been described and compared qualitatively by the human ear for "calls" or "songs" can now be quantitatively analyzed and compared in terms of acoustic parameters that humans may be unable to discriminate (Erbe & Thomas, 2022). Operationalization need not always involve quantification and can also sometimes combine qualitative and quantitative aspects—for example, measuring the behavioral trait of aggressiveness in terms of rates of "aggressive" encounters. What is common to these examples is that the original trait is either not sufficiently well-defined by itself to be empirically studied or is fully captured by the operational trait. In such cases, the original trait description does not survive its operationalization.

Few today would contest the claim that operationalization—linking the meaning of concepts to empirical operations of detection and measurement—is an important part of the development of scientific concepts and theories. *Operationalism*, by contrast, is the idea that the meaning of a concept (like "trait" or "chin") is *exhausted* by the operations of measurement and detection (Bridgman, 1927; Chang, 2021). Perhaps the most explicit example of operationalism in biology was the pheneticism movement, which aimed to redefine taxonomic groups in terms of overall similarity in observable characters rather than in terms of phylogenetic relatedness (Sneath & Sokal, 1973; see Ehrlich, 1961; Ehrlich & Holm, 1962; Sokal & Camin, 1965). In this framework, "characters" are operationally defined as observable features that vary from one organism to another (Sneath & Sokal, 1973). More generally, operationalism about traits means that there is nothing lying beyond the measured attribute or quantity. Providing a trait description, in other words, should be nothing more than specifying a measurement operation. Must all traits be measurements in this sense? Although pheneticism is no longer considered a viable taxonomic framework, and we know of no other explicitly operationalist proposals about traits, the problems with this view are instructive for understanding the broader relationship between trait description and detection.

One reason why it is useful to maintain a distinction between traits and their measurement, or between trait description and detection, is that it allows asking whether a given measurement operation is a *good* measure of the trait. This is a general problem with operationalist definitions: if temperature were defined merely as the deflection of a bimetallic strip, then we couldn't ask how good this is as a measure of temperature. We can ask this question only if temperature is independently defined. Similarly, we can fruitfully ask whether the symphyseal angle is a good measure of the bony prominence or inverted T, for example: "while not complete, the measure (SA > 90°) does a sufficient job of assessing 'chin possession'" (Pampush et al., 2018). If it is judged to be a flawed measure, this can stimulate development of an alternative measurement operation. By contrast, if the measured attribute just *is* the trait, it cannot be evaluated for fit and significance—it will be automatically valid. While it is important to be able to measure traits, a more measurable (i.e., operationalizable) version of a trait is not necessarily better, and can be worse if the measurement is not biologically meaningful (A measurement is "meaningful" when relationships between numbers can be translated to valid inferences about the empirical entities being measured, as discussed by Houle et al. [2011]).

It makes the most sense to maintain that there is a trait distinct from its measurement when there is an independent basis for thinking the trait of interest has some biological significance, or evidence that the measurement only partially captures it. Examples include cell types as detected by identity marker genes and photosynthetic rate as detected by increase of dry plant mass. This is what is lacking in situation (c). Whether the chin and other morphological traits like it meet this condition is an open question.

To summarize, in different contexts of study, relationships between traits can fit (a), (b), or (c). (a) Sometimes what appear to be two different descriptions of a trait may be a description and a way of detecting it. At the same time, (b) some measured attributes can be well-defined traits to be studied in their own right rather than just being measures of an existing trait. Finally, (c) an initial trait description may sometimes be replaced by an operational version. While the operationalization of trait concepts is often fruitful, operationalism about traits as a general stance is not defensible as it eliminates the important distinction between trait description and detection.

3.3 | Justification of characters

Disagreement over how to define a character like the chin can also be based on different assumptions about what *justifies* some feature having the status of a real, genuine, or biologically meaningful character. According to the differential growth byproduct account, the chin is the mere morphological byproduct of different ratios of bone modeling in two individualized growth fields of the human mandible—that is, a bony mass. However, according to proponents of this view, the morphological outcome should not be "reified" as a trait because it lacks developmental independence. Although Gould and Lewontin did not provide much by way of a constructive account of what should be considered a trait—an omission of a "vital issue" for "lack of space" (1979, p. 585)—they present the chin as a prime example of trait *misidentification*. As Lewontin (1978, 217) wrote, "in an evolutionary sense the chin does not exist."

Without the distinction between trait description and justification, such claims are difficult to interpret. The claim cannot be that the observable bony mass at the base of the mandible does not exist. It is rather that we are not justified in treating it as a distinct "unit of evolution" or as a potential adaptation, to the neglect of the wider allometry of the jaw and dentition. At the same time, this stance about justification has implications for character description—namely, that in studying chin evolution we should refocus more broadly on characters describing the growth process in development to get a better understanding of selection and developmental constraints.

The growth byproduct view is thus not claiming that the chin *is* the differential growth or ratio of bone modeling of the alveolar and basal regions, which would then be a competing description or definition of the chin. Instead, the chin is the bony mass, but the bony mass is just a byproduct of differential growth, and so is not justified as a distinct trait in its own right. The growth byproduct and bony prominence views therefore identify the same structure as being the chin, but the former attaches the definition to a specific explanation of how the trait develops, whereas the latter is neutral with regard to explanations of the chin.

The requirement that the traits we describe and detect must be justified by underlying developmental independence is shared by some chin accounts (Schwartz & Tattersall, 2000) and left undiscussed by others. In what follows, we'll analyze more closely some distinct justification profiles of the chin as a bony prominence or as an inverted T relief to gain further insight into the sources of disagreement over what constitutes an individualized character.

4 | DESCRIPTIVE, DEVELOPMENTAL, FUNCTIONAL CHINS

In Gould and Lewontin's (1979) view, the bony prominence that we call a "chin" would be a pseudo-trait lacking developmental independence and having a composite developmental origin in the different growth rates of the alveolar and basal modules. For this reason, Lewontin (1978, p. 217) considers the chin a "mental construct rather than a unit in evolution," in effect eliminating the need (or possibility) for any adaptive explanation for it (see also Reydon, 2023). In this way, *developmental justification*—assessing the presence of a distinct developmental mechanism grounding the emergence of a character—can be considered necessary for treating a morphological item as a biologically "real" or meaningful entity. The logic behind requiring a developmental justification is that without taking into consideration developmental mechanisms and degrees of independence during ontogeny, any arbitrary morphological item could be picked out as a biological character even if it is merely a part of some larger cohesive trait or an aggregate of distinct traits.

The requirement of a developmental justification is explicitly shared by proponents of the inverted T relief account of the chin. In Schwartz and Tattersall's (2000, 2010) view, the inverted T would provide not only higher morphological detail and a much clearer phylogenetic signal than the simple bony prominence, but it would

justifiably individuate the "true chin" in view of its developmental independence from other features (i.e., the size of the bony prominence region). This assessment was based on a comparative analysis of extant *H. sapiens* and Middle to Late Pleistocene specimens, suggesting that the inverted T relief is established in the human fetus from at least the 5th month of gestation (Schwartz & Tattersall, 2000).

The extent to which a character's proposed justification rests on solid footing can, of course, be subject to debate based on new incoming evidence. Recent results from high-resolution MRI acquisitions of modern human fetuses and geometric morphometrics have been interpreted as suggesting that the development of both the inverted T relief and the breadth of the basilar bone is in fact developmentally integrated with the maintenance of space at the back of the vocal tract and the arrangement of the tongue, the hyoid bone, and attendant muscles (Coquerelle et al., 2017). Coquerelle et al. (2010, 2013, 2017) stress the fact that the patterns of developmental integration in the cranium and vocal tract are well conserved in African apes and modern humans. Interpreted this way, such results cast doubt on the developmental justification of the inverted T relief (however, for a different appraisal of these results, see Pampush et al., 2018).

Aside from developmental justification, the bulk of the discussion has focused on the possibility of a *functional justification*. A functional justification is one in which the status of a morphological item as a *bona fide* trait depends on its serving a distinct function that contributes to fitness.

Functional hypotheses about the chin have, in an obvious sense, been inspired by a focus on the protrusiveness of the bony outgrowth and the related metabolically costly and unevenly distributed cortical bone thickness (or hypertrophy, Daegling, 2012). The bony prominence has been analyzed as a structure apt for countering masticatory stresses generated by chewing or as providing a structural anchor to a speaking tongue. But positive functional justifications like these have been extensively contested on empirical grounds. The case for the masticatory stress hypothesis, for example, was weakened by biomechanical analyses suggesting that actual bone placement is inefficient for that role, coupled with the fact that our diets are relatively soft due to our food preparation, including cooking (cfr. Pampush & Daegling, 2016b).

Another well-known functional justification frames the chin as a sexually selected character, with studies aiming at demonstrating the presence of sexual dimorphism in the expression of some features of the chin (described as a complex structure). Males tend to have more protruding chins with well-developed lateral tubercles (Thayer & Dobson, 2010). More recently, the possibility of region-specific chin shape preferences has been proposed (Thayer & Dobson, 2013). It remains unclear, however, how to infer that chin *presence* was sexually selected from evidence that a property of it (its shape) has been sexually selected (Pampush & Daegling, 2016a). Further, sexual selection theory frequently assumes that sexually selected features must be costly to develop or maintain, and the specific costs in the context of the chin remain unclear. We already mentioned the

metabolic growth or maintenance costs of bone tissue. Immuno-suppressive "handicap models" of sexual selection have also been proposed for the human chin (see discussion in Thayer & Dobson, 2013). These stem from the observation that cortical bone growth is stimulated by testosterone, which is immunosuppressive in high concentrations. Broad chins and a healthy condition would thus signal mate quality. However, consensus on this matter has remained elusive so far.

In support of a selection hypothesis, when the bony prominence is assessed via the symphyseal angle (Pampush et al., 2018), an increase in the angle can be traced back to early members of *Australopithecus*. The increased evolutionary rate, according to Pampush et al. (2018) would exclude a random walk and suggest instead a driven trend (*sensu* McShea, 1994). The case for a driven trend, in Pampush and colleagues' view, would be strengthened by the fact that the hominin symphyseal angle does not appear to be structurally tied to an obtuse configuration (and is therefore unlikely to be drifting away from acute angles, such as those found among great apes). These considerations rest on assessments of the differences and similarities between hominin and African apes' mandibular integration and symphyseal orientation. In this context, the chin detected via the symphyseal angle would have been the result of selection for preoral processing of foods among early members of *Australopithecus* (inferred from reduced rates of wear on the anterior dentition). Specifically, this would have allowed breaking food into smaller chunks, thus alleviating ingestion demands and gradually reducing the anterior dentition. This selective regime would have continued in the hominin clade, with cooking further alleviating chewing demands and permitting the reduction of the posterior dentition. The general reduction in dentition size would have had the effect of retracting the alveolar process, while leaving the basal portion virtually intact.

5 | GROUNDING CHARACTERS MATTERS: CONCLUDING REMARKS

As analyzed in the previous sections, disagreement over the human chin reveals differing views about what makes something a biological character. As we hope to have shown, this disagreement is not superficial and is not readily resolvable by establishing terminological conventions (deciding what should be called a "chin" or dropping its use entirely). It is also not just a matter of definitions or "semantics," or of being clear about what one means with a given trait description, given that disentangling description, detection, and justification is a large part of the problem. Instead, different views on the chin point to deeper issues concerning the proper measurement and biological grounding of candidate characters. Arguably, in paleo-anthropology as well as in many other fields, the step of character justification (iii) has received the least attention. Versions of the chin understood as a bony protrusion have been proposed even before extensive discussions on its possible justification

(Blumenbach, 1969). In other cases, however, issues of detection and measurement tied to specific research questions are prioritized over agreeing on detailed morphological descriptors (Pampush et al., 2018). As we argued, progress in empirical research can create feedback loops among the three steps. What is crucial, however, is that the steps remain distinct and discernible. When it comes to debates on justification, a few lessons relevant to the issue of biological character identification can be drawn. Characters are used in a variety of different analyses and for various research goals. What counts as a "good" character depends on the research question at hand. Merely having some research goal in view for a given trait description, however, is insufficient for justifying that trait biologically. The goal must be legitimate and nonarbitrary, and the trait description must actually satisfy the goal. Perhaps more significantly, the choice of a given trait description may serve "goals" of convenience, simplicity, or ease, without having any biological justification. In that case, more would be needed to justify its status as a real or genuine biological trait.

With the human chin, as we have seen, when the goal is to identify features of significance for systematics, a focus on the degree of the anterior protrusion (the chin as an outgrowth of bone tissue, the second account) might provide poor guidance, as interpretations can be confused by intraspecific variability (Lieberman, 1995; Schwartz & Tattersall, 2000). At the same time, descriptors fulfilling diagnostic purposes (such as the inverted T relief and its accompanying discrete traits) have been deemed less appropriate for tracking long-term evolutionary changes and there-fore also for investigating whether driven evolutionary trends originating at deeper phylogenetic times, tied for instance to the generalized reduction of the alveolar process, might contribute to explaining modern chin appearance.

Disagreement over justification raises important implications precisely about the adequacy of characters for their proposed uses. For instance, Schwartz and Tattersall (2000) suggest that the inverted T relief carries more reliable phylogenetic signal than the bony prominence. But can this still be true if the inverted T relief lacks developmental independence from the prominence (Coquerelle et al., 2010, 2017)? Must a character be developmentally individual-ized to figure in phylogenetic inference?

In many phylogenetic analyses based on morphology, the variational independence of a character—the ability to change quasi-independently of other features—is a major assumption (Wiley & Lieberman, 2011). Underestimating correlations among characters may affect these analyses by numerically overrepresenting single mechanisms or processes (Strait, 2001). If the goal is to map character phylogenies this seems to require some assessment of the ability of candidate characters to vary quasi-independently (an assumption that is explicitly shared by proponents of the inverted T descriptor). This issue has been discussed in debates over "total evidence" in systematics (Rieppel, 2009). In many cases, it may be that phylogenetic reconstructions are not led astray by a lack of established variational independence in the characters analyzed, due

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to the inclusion of other well-defined morphological characters or large numbers of well-defined nonmorphological characters (such as molecular genes). These latter conditions are realized for *H. sapiens* phylogeny, but testing character independence and removing the bias caused by character integration acquire particular importance when morphology and descriptive data are all that is available for recovering phylogeny. Even when these issues are acknowledged, major limitations are of course posed by the availability of sufficient fossil material to test hypotheses of character independence and integration across taxa (but see Strait, 2001).

A further lesson we can derive from the chin case relates to the following question: Can a character that is not developmentally individualized (justified), like the bony prominence, undergo selection? Or, differently put: Can we investigate driven trends and adaptive scenarios for "spandrels"? Spandrels are structures that originated in evolution not to serve an adaptive function but instead due either to "architectural" correlations with adaptive structures or to nonadaptive processes (Gould & Lewontin, 1979). In the correlational case, selection on a specific character not only produces direct effects on the distribution of the target character but also on the distribution of correlated characters (Lande & Arnold, 1983). Pampush et al. (2018) suggest that the chin may be correlated with selective and ecological regimes impacting the anterior dentition. If a case can be made that dentition shrinkage is the result of directional selection for reduced teeth size (and not, for instance, of the relaxation of selective pressures), and that the chin's symphyseal angle is mechanistically integrated with it, then this argues that selection has played an (indirect) role in the evolution of the chin.

In principle, one can make a case for spandrels *also* undergoing direct selection. This would be the case in the hypothesis about sexual selection on the chin (which is not without criticism, cfr. Pampush & Daegling, 2016a). Of course, there is an apparent contradiction in calling one and the same trait a spandrel and an adaptation. This can be resolved by recognizing that the trait has these different statuses at different times—that is, originating by nonadaptive processes but later undergoing selection.

More interestingly for the present discussion, the contradiction can also be resolved by recognizing that the "one and the same" trait that is both spandrel and adaptation may actually refer to two subtly different traits. Research analyzing the protruding chin via the symphyseal angle seems to suggest that a role for selection can be revealed when we choose different means of detecting or measuring a character (Pampush et al., 2018). In the chin case, this would be the outgrowth of bone (a thing) and aspects of its shape (symphyseal angle, a property of the thing). The credibility of finer distinctions among chin traits reveals that the question "is the chin an adaptation?" allows for different answers based on different descriptions of the chin. This starts to indicate how differences in how we describe traits can strongly influence whether those traits count as adaptations or not (in addition to influencing the truth of adaptation*ism* more broadly, DiFrisco & Ramsey, 2023; see Orzack & Sober, 1994).

This leads us to a final consideration. How can we know if traits like the chin really are one trait or several traits? This question asks about the *justification* for trait descriptions. One option is to rely on expert intuition, and in fact, most initial trait descriptions originate with a best guess by investigators studying that system. Although some reliance on expert intuition is likely necessary and unavoidable, we have seen how experts can disagree, and the disagreements can reflect different investigative aims or even different theoretical commitments. It is therefore desirable to have a general criterion in view for what should count as a trait that different investigators can agree on.

With aims as diverse as phylogenetic reconstruction and assessments of adaptation alike, we see a common need to ground trait descriptions in terms of *variational independence* in a broad sense (Brigandt, 2007; Wagner, 2014; Wagner & Altenberg, 1996). This means scrutinizing the ways in which a descriptively identified morphological item can vary cohesively as a unit and quasi-independently of other units (Lewontin, 1978). If some described feature only varies together with some larger trait of which it is a part, or is an aggregate of traits that do not vary cohesively as a unit, then investigators arguably should re-describe the trait in terms of the larger or smaller units. We see establishing variational independence as a necessary condition for a full developmental or functional justification for a given trait description, though it is not always sufficient. A phenotypic feature can have the capacity to vary independently without actually undergoing selection as a unit, for example. In practice, variational independence can be established by a combination of information about development, observed patterns of variation across individuals and/or species, and/or functional relations with the historical environment. Further work on the procedures and operations for establishing variational independence can help to turn intuitions about where one trait ends and another begins, or whether traits like the chin are one or several, into hypotheses subject to empirical test.

This, however, does not make character identification a purely empirical problem. Given the centrality of the trait concept to the life sciences, one would like the problem to be resolvable by ordinary empirical procedures of data collection, measurement, and causal hypothesis testing, rather than being consigned to a priori theorizing. As we hope to have shown, the intermingling of conceptual and empirical matters in the problem of trait identification means that conceptual work is needed before the problem can progress to being a more purely empirical one.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study. No data was generated in this study.

ORCID

Andra Meneganzin https://orcid.org/0000-0003-3641-3803
Grant Ramsey https://orcid.org/0000-0002-8712-5521
James DiFrisco http://orcid.org/0000-0001-9600-1013

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