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Conceituando *espécie*: uma discussão a partir do quadro conceitual de Darwin

Conceptualizing species: a discussion from Darwin's conceptual framework

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Resumo

Este artigo investiga o conceito darwiniano de espécie e suas consequências para a classificação dos seres vivos. Em sua formulação da teoria evolutiva, Darwin (1872) introduz o conceito de espécie enquanto segmentos de linhagens populacionais. Nessa perspectiva, a seleção natural atua de forma gradual e produz ligeiras variações nos indivíduos através do tempo. O autor vincula o componente evolutivo com a ideia de que a *espécie* consiste numa classificação taxonômica, na qual variações bem demarcadas são o critério central para classificar as linhagens descendentes. Formulações posteriores do evolucionismo mantiveram tais componentes, mas buscaram substituir o critério de classificação por bases mais objetivas. O resultado foi uma proliferação de definições e consequente controvérsia sobre o tema. Argumentar-se-á que inadequações históricas sobre a definição de Darwin contribuíram para o surgimento dessa discussão. Em conclusão, será desenvolvido um argumento a favor do princípio de seleção natural com base na discussão entre fisiologia e morfologia enquanto mecanismos para o surgimento de novas espécies.

Palavras-chave: Darwin; espécie; evolucionismo; morfologia; fisiologia.

Abstract

This article investigates the Darwinian concept of species and its consequences for classifying living beings. In his formulation of evolutionary theory, Darwin (1872) introduces the concept of species as segments of population lineages. In this perspective, natural selection acts gradually and produces slight variations in individuals over time. The author links the evolutionary component with the idea that the species consists of taxonomic classification, in which strongly marked varieties are the central criterion for classifying descendant lineages. Later formulations of evolutionism maintained these components but sought to replace the classification criterion with more objective bases. The result was a proliferation of definitions and consequent controversy on the topic. The article argues that the historical inadequacies of Darwin's definition contributed to the emergence of this discussion. In conclusion, an argument in favor of natural selection will be developed based on the discussion between physiology and morphology as mechanisms for the emergence of new species.

Keywords: *Darwin; species; evolutionism; morphology; physiology.*

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Darwin (1872) establishes that the principle of natural selection is a constant factor in the preservation of species through the preservation of variations useful to individuals in the face of their living conditions. In other words, the author collected convincing evidence that species were not created, but evolved from a common lineage. In the face of the debate of his time, he proposed natural selection as the scientific alternative to the principle of the creation of species, according to which they would exist as they are from their beginning and no new species could exist without a supernatural cause. The problem is that the concept of species was, until then, culturally ingrained as referring to individuals belonging to definitive groups. In other words, all members of a species had ancestry through kinship with each other, but none descended from members of another species.

A supernatural argument defended by Buffon (1764) was that interspecies sterility consisted of a protective mechanism instilled by God to preserve his purity. In this vein, Owen (1858) presented a succinct definition in his treatise on primates, in which orangutans and chimpanzees maintained their primitive distinction by obstructive generative peculiarities. The difference between these positions and the Darwinian argument for the emergence and differentiation of species lies in the defense of the existence of small variations among the descendants of the same lineage. It is emphasized that the idea that species evolved through descent with modification is broader than the concept of species itself, permeating it and encompassing all forms of life. In fact, this point has central importance in explaining how new species can arise in nature and how others become extinct over time.

Regner (2006) points out that, in Darwinian evolutionism, the characteristics of an individual are selected for the benefit of the one who possesses them. The selection of these characteristics occurs through gradual variation and their fixation occurs slowly, but always varying in favor of the individual in its relationship with the environment in which it lives. The advantages of the best-adapted forms lead to an increase in offspring and the consequent propagation of these characteristics, resulting in the emergence of new species based on the differentiation criterion. Therefore, the Darwinian explanation has the following formulation: (i) the classification of living beings occurs in a genealogically subordinate way; (ii) the subordination occurs in a genealogical way; (iii) the genealogy of classification allows us to affirm that different species have a common originating lineage; (iv) the common descent with the demarcated modification originates a new species.

> I believe that, in order to be natural, the arrangement of the groups in each class, according to their relations and their degree of mutual subordination, must be strictly genealogical; but that the quantity of differences in the various branches or groups, although allied in the same degree of consanguinity to the different degrees of modification that they have undergone;

> and this is expressed by the arrangement of the classified forms in different genera, families, sections or orders (Darwin, 1872, p. 369).

The problem is that the definition of common descent is not simply interchangeable with the concept of species. After all, since species evolve, hybrid sterility is expected to provide evidence of continuous evolution across species boundaries. It was precisely this conceptual issue that did not receive much attention from Darwin (1872), as there are few pages where he discusses the topic. Perhaps the exception is the aforementioned hybrid sterility, but even in later editions of his main work, to which a glossary was added, there is no formal definition of this issue. Nevertheless, Darwin (1872) presents evidence of his conceptualization of species, which was recognized as useful for its purpose: to present evidence of transmutation. According to Ruse (1987, p. 229), "evolution establishes that you can take virtually any property you want, and if you go back (or forward) far enough in time, then the ancestors (descendants) who did not have it (will not have it)." The Darwinian definition is simple, but it aligns with the idea that different species originate from a common ancestor.

> From now on, we will be obliged to recognize that the only distinction between well-defined species and varieties consists only in the fact that the latter is known or supposed to be currently connected by intermediate gradations, while species were previously connected in this way (Darwin, 1872, 426).

In the second chapter of *On the Origin of Species,* Darwin (1872) conducts a brief investigation into the difficulty of distinguishing between species and variety. For the author, when it becomes possible to unite two or more life forms with others through intermediate characters, one is considered a variety of the other. However, in some cases the description refers to the species and, in others, to the variety. In fact, this statement seems to be about varieties and not species, since forms without morphological gaps between them are varieties. Still, a definition of species is implied, since forms that have gaps between them would be considered separate species.

> We have every reason to believe that many of these neighboring and doubtful forms have maintained their own characteristics permanently for a long period; for so long, as far as we know, as being good and true species. In practice, when a naturalist can link two forms by intermediaries, he treats one as a variety of the other; classifying the most common, but sometimes also the first described, as the species, and the other as the variety. But sometimes cases of great difficulty arise, which I will not enumerate here, in deciding whether a form should be classified as a variety of another form, even when they are closely connected by intermediate links; Neither the commonly assumed hybrid nature of intermediate forms will in all cases remove the difficulty (Darwin, 1872, pp. 36-37).

The problem is the qualification added to this passage, in which Darwin (1872) argues that, in difficult cases, the criterion for distinguishing between species and variety is the opinion and common sense of experienced naturalists. The final part of the aforementioned passage is presented as evidence of Darwinian nihilism regarding the concept of species, contradicting other passages in his work. In truth, Darwin (1872, p. 137) wavers in his position, stating that "[...] I believe that species become tolerably well-defined objects, and at no period do they present an inextricable chaos of varied and intermediate links." This position sounds like the opposite of the statements made in the second chapter of the aforementioned work.

From the passages above, it is clear that there is controversy regarding the Darwinian concept of species. However, this does not mean that species do not exist. Mallet (2010b) argues that the Darwinian position does not result in arbitrariness in the definition of this concept. For the author, the position that common-sense naturalists would be the best guides to definition does not imply that they are obliged to make educated deductions. On the contrary, the argument is that species are similar to varieties, but not the same, since the former would not possess morphological intermediates. Apparently, this would be the criterion of distinction, since the task would consist of showing the existence of borderline cases, which would provide evidence of continuous evolution between species.

> Regardless of interbreeding, the complete absence, in a well-investigated region, of varieties linking any two closely related forms is probably the most important of all the criteria for their specific distinction; and this is, in some way, a different consideration from mere constancy of character, since two forms can be highly variable and yet not produce intermediate variables (Darwin, 1871, pp. 124-25).

Mallet (2010b) points out that good evidence for this interpretation is that the most cited passages on species in Chapter 2 of *On the Origin of Species* have the expression "doubtful species" in the heading of the first edition. In other words, Darwin (1872) was showing that, in nebulous cases, it becomes difficult to differentiate species from variety, using this as a prelude to investigations into how species evolve. Therefore, the argument that Darwinian thought considered all species to be mixed in the aforementioned inextricable chaos of varied intermediate links is doubtful.

Inadequacy of the Species Concept

It is undeniable that The Origin of Species is among the most important works in the history of science, and that its author demonstrated that species evolved from varieties, with natural selection being an important process in nature. However, it sounds paradoxical that the central theme of this work is considered inadequate and dubious within discussions about the genesis of evolutionism. For Mayr (1963, p. 14), “in retrospect, it is apparent that Darwin’s failure [...] resulted to a large extent from a misunderstanding of the true nature of species.” Mallet (2008) emphasizes that the difficulty lies in accepting that the English naturalist understood what species were and made an effort to explain their origin through varieties, or that natural selection was involved in the process. It seems that, with the advent of the modern synthesis, this view was rooted in the dogma that Darwin had failed in his attempt.

> Here is evidence of his belief that species within genera and varieties within species obey the same laws and are the same kinds of things, adding further support that his nominalist view of species and varieties makes sense (Mallet, 2008b, p. 6).

The apparent inadequacy of the species concept arises both from the difficulty of its terminological definition and from the practical way of classifying a living being at this level. Darwin (1872) considers such use to be subject to arbitrariness, giving the term a double meaning, since it is defined in the sense of the absence of an objective foundation (which occurs in the definitions of his time); and as being a name and not an entity. It is only in the second case that there is a more objective foundation, which is conferred within the theory of natural selection by the genealogical condition of the natural classification system.

> There is a point related to individual differences that is extremely disconcerting: I am referring to the genera called "proteus" or "polymorphs," in which the species vary in a disordered way. With respect to many of these forms, hardly two naturalists agree on classifying them as species or as varieties (Darwin, 1872, p. 35).

Mayr's (1963) critique is based on the concept of biological species in the modern synthesis, that is, its negation as populations isolated from one another by mechanisms of reproductive isolation. The author's argument is that Darwinian evolutionism did not understand the central importance of reproductive isolation in speciation intrinsic to the concept of species. In fact, Darwin (1872, p. 237) points out that "it can thus be demonstrated that neither sterility nor fertility provides any certain distinction between species and varieties." Mayr's (1963) main argument lies in the inadequacy of the Darwinian argument concerning the concept of species, in particular in its position on hybridism. In this part, Darwin (1872) argues against the relevance of hybrid sterility as capable of providing a useful definition or, at least, an explanation of speciation and its distinction from variety.

> From these notes it will be observed that I perceive the term species as arbitrarily given, for the sake of convenience, to a set of individuals similar to each other, and

> that it does not differ essentially from the term variety, which is applied to less distinct and more variable forms. The term variety, again, in comparison with simple individual differences, is also applied arbitrarily in order to be more convenient (Darwin, 1872, p. 42).

In contrast, Mayr (1963) highlights hybrid sterility and other isolation mechanisms as the central differences between species and variety, the elucidation of their origin constituting an understanding of speciation. The isolation mechanisms of hybrid sterility can be understood from a Darwinian perspective as an accidental byproduct of other evolutionary changes among species. In this case, the term mechanism would be inadequate, as it could not be directly explained by natural selection[1]. Mallet (2010b) emphasizes that Darwinian evolutionism is not oblivious to how the intersterility of species and the reluctance to mate enabled coexistence among them. Indeed, there is discussion in *On the Origin of Species* about how such characteristics were strongly associated with what taxonomists recognized as separate species. Still, the difficulty that direct natural selection has in explaining the evolution of hybrid sterility, the fertility of many hybrids between well-adapted species, and the existence of some types of infertility within the species themselves is credited with Darwin's abandonment of the idea that species could be relegated via reproductive isolation.

> Darwin managed to convince the world of the occurrence of evolution and [...] he found (in natural selection) the mechanism that is responsible for evolutionary change and adaptation. It is not so widely recognized that Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species over time, he never seriously attempted a rigorous analysis of the problem of species multiplication, the division of one species into two (Mayr, 1963, p. 12).

This point does not resolve Darwin's (1872) position regarding the arbitrariness in the classification of living beings, since the Darwinian perspective remains without an objective criterion for distinguishing between species and variety. The result is arbitrariness in the application of these concepts and, consequently, in the way individuals are classified. In this sense, both the classification methodology and the very definition of species remain inadequate due to their arbitrary classification. This arbitrariness allows Darwinian evolutionism to consider its practical application and reconceptualization in such a way as to make the concepts of species and natural selection mutually dependent without the existence of more precise empirical markers.

The English naturalist argues favorably about the inadequacy of the concept of species. In fact, he brings case studies in which individuals are classified differently by different specialists. In other words, the same individuals are classified as species by some researchers, and as varieties by others.

[1] Mallet (2010a) points out that Mayr (1963) agrees with the Darwinian position that there is insufficient evidence that sterility evolved through natural selection. However, his critique converges on the point that isolation mechanisms were adaptive and therefore useful to species as a means of keeping them separate from one another.

It is precisely this lack of consensus in the practical application of the criteria for classifying living beings that weakens the Darwinian concept of species.

> It cannot be disputed that varieties possessing this dubious nature are far from uncommon. Compare the various floras of Great Britain, France, or the United States, described by different botanists, and see the surprising number of forms that have been classified by one botanist as species and by another as mere varieties (Darwin, 1872, p. 37).

The problems in understanding the Darwinian concept of species go back to discussions beyond the 20th century. In this way, this misunderstanding precedes the discussion carried out by Mayr (1963) based on the modern synthesis. The seeds of this issue can be found in one of the most positive reviews of The Origin of Species at the time of its publication. Considered one of the most fervent and laudatory defenders of Darwinian theory, Huxley (1887, p. 52) writes that the concept in question is "one of the greatest, or perhaps we may say the greatest, of all the difficulties in the way of accepting the theory of natural selection as a complete explanation of the origin of species". Previously, Darwin's Bulldog had already expressed his criticism after a long discussion about Darwin's evidence regarding the nature of species.

> There is no positive evidence at present that any group of animals, through variation and selective breeding, has given rise to another group that was, even to the slightest degree, infertile with the first. Mr. Darwin is perfectly aware of this weak point and presents a multitude of ingenious and important arguments to diminish the force of the objection [...], but still, as the case stands, this "little crack in the lute" must not be masked or forgotten (Huxley, 1860, p. 309).

Lovejoy (1968) highlights the notable difference between varieties and species with respect to fertility as one of the main inadequacies of these concepts in Darwinian evolutionism[2]. It does not follow from this point that the theory of evolution failed to present a new perspective on the natural processes from which well-marked varieties arose in living beings. However, theorists contemporary to the publication of *The Origin of Species* did not immediately accept the possibility of individuals accumulating small variations over time. After all, until then the term species was adopted almost exclusively as applicable to the special act of creation.

In general terms, the creationist position defended that all living beings present in nature result from a special act of creation carried out by a superior being. In this way, individuals would arise on the

[2] The cited article was originally published in 1909 and subsequently revised for the centenary of the publication of *On the Origin of Species* in 1959. In this study, the author documents not only the context that led Darwin and Wallace to formulate the theory of evolution, but also the reason why other biologists did not. Huxley (1887, p. 197) comments that "my reflection, when I first grasped the central idea of the 'Origin', was how utterly stupid it had been not to have thought of it!". This point reinforces, by contrast, the argument about the concept of species, since much of the Darwinian approach can be considered quite objective when analyzed in retrospect.

material plane independently and abruptly. Contrary to this position are the empirical evidences collected by science. In the natural environment, it is possible to observe numerous transitional variations in different forms of life. In fact, such variations are so marked that it is not simple to establish a classification pattern for these individuals. Ultimately, since they possess such a capacity to acquire them, the very concept of species related to the special act of creation is flawed in classifying them, even at a semantic level, as species.

> A few naturalists maintain that animals never exhibit varieties; while the same naturalists attribute a specific value to the slightest difference; and, when the same identical form is found in two distant countries, or in two geological formations, they believe that two distinct species are hidden under the same covering. The term species thus becomes a simple, useless abstraction, implying and affirming a separate act of creation (Darwin, 1872, p. 39).

Owen (1859) synthesizes the nature of the discussion by arguing that species, as a result of the special act of divine creation, maintain their primitive distinction through obstructive generative peculiarities. At this point, Darwin (1872) argues against defining species based on reproductive isolation, since creationists like Buffon (1764) proposed hybrid sterility as evidence for their theoretical position. Owen (1859, p. 272) reinforces this point, arguing that "the sterility of primary crosses and hybrids [...] is not a special gift, but is incidental and slowly acquired, more specifically, in the reproductive systems of the forms that have crossed." It is plausible that the English naturalist understood that he needed to demonstrate that sterility was a rhetorically attractive argument to counter the position of his critics. However, for both defenders and detractors of Darwinian evolution who considered the explanation of hybrid sterility fundamental to the theory of speciation, the argument presented in The Origin of Species seemed to mitigate its importance and, consequently, offered an insufficient partial explanation.

> The rules and facts set forth above [...] seem clearly to indicate that sterility, both in primary crosses and in hybrids, is simply accidental or dependent on unknown differences, mainly in the reproductive systems of the species that crossed. The differences are of such a peculiar and limited nature that, in backcrosses between two species, the male sexual component in one will frequently act freely upon the female sexual component of the other, but not in the reverse direction (Owen, 1859, pp. 260–61).

Darwin (1872) seemed not to fully understand what caused hybrid sterility, although some causes could be ruled out. However, this fact was far from universal among species, being so dispersed and incidental that it seemed more improbable that it was either a naturally selected adaptation or a divine attribute to preserve its purity. Instead, it is closer to an incidental factor in slowly acquired modifications, that is, a byproduct of evolutionary divergence in general or, in contemporary genetic terms, a *pleiotropy*[3]. The correspondence between Darwin and Wallace themselves indicates that the English naturalist was dissatisfied with his partial explanation, even though this point was considered more problematic by some of his main interlocutors.

The concept of species and the question of hybrid sterility

The question of hybrid sterility was also the focus of correspondence between Darwin and Wallace between March and April 1868. The English naturalist was asked whether this characteristic could arise through natural selection. Kottler (1985) points out that the focus of the Darwinian position was at the individual level of selection. By pointing to the case of Primula veris and Primula vulgaris, both moderately sterile with the ability to occasionally produce hybrids, he admits that these characteristics are the result of natural selection. However, Wallace (1916, p. 170) received the following response from Darwin: "[...] as I believe, that Natural Selection cannot result in what is not good for the individual, including in this term a social community". The reply touched on the argument that the rejection of copulation could result from natural selection. Again, Kottler (1985) emphasizes that the Darwinian response was that there would be no necessary connection between sterility and lack of inclination to copulate. Darwin's reply to Wallace (1916, p. 171) was that he did not see "why it would not have been sufficient to prevent incipient species from mixing simply to increase the lack of sexual inclination to mate." At this point, the Darwinian argument concerning the role of natural selection in the origin of pre-mating reproductive isolation becomes clear[4].

Romanes (1886) states that natural selection would not be capable of causing the differentiation of species. He published a lengthy article in which he argues that the classification of species based on physiology and separated by hybrid sterility could be based on what he called physiological selection. This point is consistent with that of another critic of the Darwinian argument. Wagner (1868) emphasizes that, if populations were geographically isolated, there would be no interspecies crossing in divergent variations and, therefore, the modification that would lead to the separation of species

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[3] Pleiotropy is identified when a single gene affects two or more traits. In an evolutionary context, Curtsinger (2001) points out that this phenomenon occurs when a single gene affects an organism's fitness at different stages of life. For example, if a new mutation improves the fitness of young and old individuals, this trait is likely to be preserved by natural selection. However, a gene that decreases an organism's fitness in the same way tends to become extinct through the evolutionary process. The author highlights interesting cases in which the effects of fitness in young and old organisms are negatively correlated, known as negative pleiotropy or antagonistic pleiotropy. In this case, mutations that favor early fitness over late fitness tend to be favored.

[4] In his reply, Wallace (1916, pp. 172-73) laments the trouble Darwin had to go through in responding to him, writing further that "[...] in fact, I was only half convinced of my own arguments – and now I think there is an equal chance that Natural Selection may or may not be able to accumulate sterility." As Kottler (1985) correctly points out, Wallace's position that hybrid sterility would be a source of controversy proved true. In the decades following the publication of On the Origin of Species, both critics of natural selection and many of its defenders opposed the Darwinian position.

would occur within the groups themselves. The difference between the two lies precisely in this point, since the latter does not argue that all speciation originates from geographic isolation, with physiological selection having the same effect in preventing gene flow. According to Romanes (1886, p. 352), if a variation occurs but does not have an effect within an emerging variety to the point of generating hybrid sterility, "in such a way that the reproductive system [...] continues to be fertile within the limits of the variety form, in this case the variation would not be flooded by crossing, nor would it die because of sterility." On the contrary, in this case the author states that the variation would be perpetuated with more certainty than one of any other type.

> Thus, I repeat, what we require in a theory of the origin of species is a theory to explain the first and most constant distinction between species, or the distinction by virtue of which they exist as species. This distinction, as we have now seen so many times, is one that belongs exclusively to the reproductive system; and it always consists in comparative sterility in relation to related forms, with continued fertility within the varietal form (Romanes, 1886, p. 370-71).

Wallace (1889) recognized an apparent similarity between physiological selection and his position in letters exchanged with Darwin regarding the evolution of sterility by natural selection. This point motivated the author to argue against Romanes' (1886) assessment. The main criticism is that the importance of the concept of physiological selection is only stated, without presenting a convincing mechanism by which this selection would occur or providing empirical evidence for its operation. The author refuted this position with a mathematical argument, in which he demonstrates that a new and scarcer variety that produces sterile hybrids with the most common wild type would eventually die out. He points out that, firstly, two individuals of the opposite and complementary sexes would have to survive to reproductive age, and the odds against this encounter are measured by the infertility of the species. In short, if such individuals produced 10 offspring per year, the probabilities of an encounter would be nine or ten to one against the possibility of one of them surviving[5].

> However, there is not a single passage in Mr. Romanes' article to show that he recognizes this difficulty; on the contrary, he always speaks as if any number of physiological variations within a species should necessarily form a variety [...] The chances of survival of the two complements are about ninety to one; and then there remain the chances against the two meeting at breeding time, for, supposedly, there is nothing to bring them together except chance, and that could be any number from thousands to one (Wallace, 1889, p. 131).

[5] Wallace (1889) posits that individual **A** is infertile with most of its species, except for individuals of the opposite sex **a**, **b**, and **c**. A second individual **E**, born in a different geographical region, is fertile only with individuals of the opposite sex **e**, **f**, and **g**. Individuals **K, P, R**, and so on may have similar relationships, each being fertile only with some individuals of its species, referred to here as its physiological complements. Separately, each of these individuals constitutes a physiological variety, but the entire set **A**, **E**, **K**, **P**, and **R** are, in fact, five distinct varieties. To form a variety, they would all have to be fertile with an identical group of individuals of the opposite sex. According to the author, this is so highly improbable that it should not be assumed until rigorously proven based on empirical evidence.

Moving away from the Darwinian approach to natural selection at the individual level, Wallace (1889) establishes group selection as his main argument in defense of an evolutionary basis for hybrid sterility. The author emphasizes that varieties exhibiting greater hybrid sterility would have greater evolutionary success due to the greater genetic purity resulting from better adaptation to the conditions that gave rise to the divergence. For example, if a part of a species' distribution area has two varieties with different degrees of hybrid sterility, the one with the higher degree should outcompete the other in cases where competition occurs between them. This is a complicated argument, as it is directly countered within the ecological niche by the aforementioned Darwinian argument used against Romanes. In other words, this argument is based on the idea that populations with greater sterility leave more descendants due to greater genetic purity and better adaptation to local conditions compared to those with lower sterility and, consequently, lower purity.

Johnson (2008) states that contemporary biology accepts that circumstances in which group selection in the manner described above overcomes a selective compensation force within populations are rare. Kotler (1985) points out that understanding sterility for what it is, that is, a problem for the individual, can lead to the perception that sometimes a beneficial adaptation that also causes sterility will remain despite it, since the benefits of the adaptation would outweigh the inability to generate offspring. In this case, one could defer to Wallace's first hypothesis (1889), in which hybrid sterility would arise as a byproduct of natural selection. However, Wilson and Wilson (2007) argue that, by defending this characteristic as a direct potential advantage for populations, the author ends up developing a *naive group selection.*

> In biological hierarchies that include more than two levels, the general rule is that "adaptation at any level requires a process of natural selection at the same level and tends to be weakened by natural selection at lower levels." All students of evolution need to learn this rule to avoid the errors of naive group selection (Wilson and Wilson, 2007, p. 338).

Hybrid sterility was defended both as a byproduct of divergent environments and as an adaptive modification inherited from two emergent varieties. Wallace (1889, p. 176) reinforces this point by arguing that such a characteristic could arise "in correlation with the different ways of life and the small external peculiarities that exist between them." Here we have a primary formulation of the pleiotropy argument: a selective adaptation to living conditions can evolve if it overcomes the indirect disadvantage of the negative side effects of the same genes on hybrid sterility. According to Drès and Mallet (2002), this hypothesis for the evolution of hybrid sterility is more widely supported contemporaneously.

A similarly based argument is that new varieties would exhibit a correlated aversion to mating. Wallace (1889) posits that adaptation to different ways of life would result in a reduction in the tendency to mate between divergent varieties, since organisms specialized in different resources would encounter each other less frequently. In fact, several contemporary models have examined how quickly habitat preference can evolve. Rice (1984) establishes a scenario in which niche preference has a quantitative genetic basis, with the environment being unevenly distributed between two habitat types. In this case, natural selection favors individuals who prefer the same location over those who do not exhibit this preference. As a result, the probability of mating decreases as differences in habitat preference increase simply because individuals become less likely to encounter each other. However, Gavrilets (2004) points out that supporting this position would be like defending what has become known as the magic trait: a pleiotropic effect that automatically aids speciation. However, Hendry et al. (2007) argue that pleiotropic effects on the ecological adaptation of mating provide a plausible pathway for speciation.

> The speed of this [mating] process appears to have been greatly accelerated by the fact that a single locus determines both adaptation and selective mating. More generally, a variety of models have shown that speciation will be easier and faster in these "one-trait" or "magic-trait" scenarios, where selected loci have pleiotropic effects on reproductive isolation (Hendry et al., 2007, p. 456).

Wallace (1916) mentions a final Darwinian position on the subject. In their correspondence, Darwin argues that the lack of inclination to form pairs could be potentiated by natural selection, as the selective process would reduce the number of offspring that could become sterile. This argument was taken up by Dobzhansky (1937) in his study on fruit flies (*Drosophila pseudoobscura*). The Ukrainian naturalist established the discussion on heterosis[6] by highlighting the importance of studying natural populations. This occurs because the crossing of inbred lines produces an increase in hybrid vigor, since deleterious recessive traits are masked by variable dominant traits. Later, Blair (1955) defined this process as reinforcement, while Grant (1966, p. 99) called it the Wallace effect, which occurs "more readily in short-lived organisms, such as mayflies or annual plants, in which the loss of reproductive potential is especially disadvantageous". Johnson (2008) points out that this phenomenon is generally accepted as a possibly common means by which reproductive isolation is acquired via natural selection in specific situations.

Coyne & Orr (2004) emphasize that, whatever the contemporary view on the ideas presented in The Origin of Species, there is consensus that hybrid sterility itself is not an adaptation. In retrospect, it is possible to accept that central Darwinian conceptions do not satisfactorily explain it, since its causes have only recently been understood. Broadly speaking, sterility represents a failure in hybrids of normal beneficial interactions between genes that have differentiated into varied populations over a sufficiently long period. Orr (2009) states that, although these genes are generally known as speciation genes, there is sufficient consensus that many differences responsible for negative interactions in hybrids evolved after speciation was complete, rarely causing species differentiation.

[6] Birchler et al. (2010) define heterosis as the phenomenon in which the offspring of different varieties of a species or crosses between species exhibit greater biomass, growth rate, and fertility than their predecessors.

One way to begin a better conceptual definition of species in Darwinian terms is to consider its correlation with the process of natural selection. As seen previously, the Darwinian concept of species is flexible, which can be identified by the difficulty in finding a pattern for classifying living beings that make up varied populations. Individuals are classified as belonging to different species using plural and often anachronistic methods. In general, the methodological diversity in the classification of living beings as species occurs based on characteristics peculiar to each group. Such pluralism in the identification and classification of individuals as belonging to a particular species may constitute an argument in defense of the apparent imprecision of the aforementioned concept in Darwinian theory. If its conceptualization is directed towards a genealogical organization of life, then the interrelation between the concept of species and the principle of natural selection is necessary, because without this mechanism speciation through the accumulation of slight variations would be impossible, just as the existence of life is a prerequisite for natural selection to occur.

Although it is possible to observe the existence of well-marked varieties within the same group, this does not directly lead to the conclusion that the accumulation of these variations can lead to the emergence of new well-marked varieties. Darwin (1872) establishes that natural selection acts in favor of preserving well-adapted individuals, leading them to accumulate slight variations advantageous to survival. This accumulation is what allows the emergence of varieties and, consequently, of incipient species. After a long period and considering the accumulation of a greater number of variations, a variety acquires well-marked characteristics. To delve deeper into this point, it is necessary to better understand Darwin's argument of species, followed by the distinct focuses on the physiology and morphology of living beings.

Reconstruction of the Darwinian Species Concept

The Darwinian species concept is based on the argument that the functional aspects of organisms did not arise so suddenly. In fact, Darwin (1872, p. 33) states that "almost all the parts of every organic being are so admirably arranged in relation to the complex conditions of life, that it seems improbable that any of these parts should have suddenly attained perfection." The English naturalist makes clear his opposition to creationism, while at the same time opening the door to a practical classification of species through the process of natural selection. In general terms, the argumentative structure in favor of a Darwinian species concept can be structured as follows: (i) exposition of the inadequacy of applying the species concept to the classification of living beings; (ii) emergence of variations in living beings; (iii) emergence of intermediate forms through the accumulation of small variations;

(iv) emergence of well-marked varieties through the accumulation of small variations; and (v) emergence of species through the accumulation of variations.

In Darwinism, the definition of species is related to well-marked varieties, since the author himself does not present an infallible criterion that can differentiate them. The differentiation process occurs through the principle of natural selection, as presented in items iii, iv, and v.

The point is that, if intermediate forms of these individuals are not found, the differential characteristics that will serve as central factors in their classification into a particular species or variety will be arbitrary. However, it should be noted that no living being is static in its form, and all offspring have variations in relation to their progenitors. Darwin (1872, p. 34) states that "the numerous small differences that appear in the offspring of the same progenitors [...] because they are observed in individuals of the same species inhabiting the same restricted locality, may be called individual differences." In this sense, when distinct variations arise in members of the same species confined to the same space, these mutations will be called individual differences.

> We have seen that there is no infallible criterion by which to distinguish species and well-marked varieties; And when intermediate links were not found between the doubtful forms, naturalists are compelled to decide on the amount of difference between them [doubtful forms], to judge, by analogy, whether this difference is sufficient to raise one or both to the species level. Therefore, the amount of difference is a very important criterion for defining whether the two forms should be classified as species or varieties (Darwin, 1872, p. 45).

One of the criteria for determining what a species is at the time of the publication of The Origin of Species was that the individual be visibly different. As presented above, small variations can arise in individuals of a species restricted to the same environment, and it is possible to affirm that this differentiation arises independently of environmental pressure. Darwin (1872) emphasizes that it is natural for all living beings to develop these small variations. If they are beneficial to their possessor, then they can be accumulated over time by the process of natural selection. Their successive accumulation, over a long period, can lead to the emergence of well-marked varieties. In turn, these variations consist of organic forms that have previously accumulated mutations that make these individuals different from their original species. If the process continues to occur, it will lead, in this way, to the emergence of a new species in nature.

> The forms that possess to some notable degree the character of species, but which are so similar to other forms, or so closely linked to them by intermediate gradations, that naturalists do not like to classify them as distinct species, are in several respects the most important to us. We have every reason to believe that many of these doubtful and closely linked forms have permanently retained their characters for a long period; for as long as we know, for as long as there are good and true species (Darwin, 1872, p. 36).

It is important to note that the criteria for classifying species are not standardized, since, in many cases, there is disagreement about where to allocate individuals with specific variations. This disagreement opens the door to identifying the interrelationships between species and variety, in order to standardize the classification of organisms at the species level. On the one hand, standardization through the common link between an ancestral species and a new one presents itself as a position compatible with the principle of natural selection. However, it can be rendered unfeasible by the need to fill every gap in the geological record, particularly with regard to the preservation of fossils – a herculean process impossible to complete. Therefore, it is necessary to establish a classification of living beings that is not necessarily governed by the presence of intermediate forms between species. Focusing on the discussion between morphological and physiological aspects points to a sufficiently standardized classification, which takes into account the emergence of distinctive characteristics in different groups based on their natural structure.

The Concept of Species in the Discussion Between Morphology and Physiology

Huxley (1860) points out that Darwin's use of the term species was indeed useful, but it had a markedly morphological basis. A competing proposal was that physiology also constituted a relevant foundation in the differentiation between species. In fact, the author establishes that individuals incapable of reproducing should be classified as physiological species. However, it is unclear whether he coined the aforementioned concept, since the term does not appear in Darwin's work, or whether he co-opted it from the effervescent discussion of the time. Regardless of its origin, the idea of physiological species became the touchstone of the discussion about the concept of species[7]. Indeed, the preference for physiological aspects over morphological ones was one of the main reasons for the contemporary rejection of the Darwinian definition of species.

> If a male and a female, selected from each group, produce offspring, and these offspring are fertile with others produced in the same way, the groups are races and not species. If, on the other hand, no results occur, there is no result, or if the offspring are infertile with others produced in the same way, they are true physiological species (Huxley, 1860, pp. 552-53).

[7] In his writings on butterflies (*Heliconius*), Bates (1863) alludes to Huxley's critique of the morphological concept of species. The author understands a physiological species as a group of individuals that will not reproduce with those from which it derived, even when given opportunities to do so, and will not exhibit signs of returning to a previous condition even when placed in the same conditions as its ancestors. The controversy established since the publication of Darwinian theory lies in the lack of empirical evidence to demarcate species based on their physiology from the above definition. However, Bates (1863, p. 388) tends to show that "a physiological species can be and is produced in nature from the varieties of a pre-existing close family". The example used to support the argument is that, although the mail butterfly (*Heliconius melpomene*) and the passionflower butterfly (*Heliconius thelxiope*) hybridize in certain locations, they are found in other locations where this process does not occur. The point is that, although contemporary taxonomy does not support Bates's position, it helps in understanding Huxley's critique of Darwin, particularly his need to explain the role of physiological species as a relevant topic of discussion.

Darwin (1871) responds to Huxley apparently by adding a physiological dimension to the concept of species. The author points out the need to be guided by the amount of differences between distinct groups to verify whether they should be classified as species or varieties. In fact, the number of differences may be related to different degrees of disparity and, in that case, may have physiological importance. Darwin (1871, p. 93) states that "even a slight degree of sterility between any two forms when first crossed, or in their offspring, is generally regarded as a decisive test of their specific distinction [...]". However, this argument does not in itself exclude the question of the morphological gap in the Darwinian position, nor does it give physiology the weight given by Huxley.

> In determining whether two or more closely related forms should be classified as species or varieties, naturalists are practically guided by the following considerations; that is, the amount of difference between them, and whether such differences relate to few or many points of structure, and whether they are of physiological importance; but more especially whether they are constant. The constancy of characteristic is what is primarily valued and sought by naturalists (Darwin, 1871, p. 93).

At the beginning of the 20th century, Jordan (1905) revived the discussion that species should be classified physiologically based on their reproductive isolation. With the rediscovery of Mendelian heredity, Bateson (1913) addressed the understanding of species under the new perspective of experimental genetics, since hybrid sterility could be investigated in the laboratory. The author reiterated the argument that the Darwinian definition of species ignored a central characteristic of the selective process, which was its physiological tendency to produce sterile hybrids. Chetverikov (1926, p. 208) states that "the true source of speciation, the true cause of the origin of species is not selection, but isolation." The Russian geneticist echoes Bateson (1922) in arguing that the Darwinian concept of species was incomplete, as it does not explain the importance of species specificity in nature.

Krementsov (1994) highlights the influence that discussions about physiological species in Europe and North America between the late 19th and early 20th centuries had on the development of later naturalist ideas about the speciation process. By turning to the concept of race as variation, Dobzhansky (1937) explicitly shifts his focus away from morphology itself. However, it should be noted that the evidence points to the genetic basis of heredity and the nature of mutation as based on the occurrence of morphological attributes. The point is that, up to this point in his investigation, he was concerned with the distribution of mutations and allelomorphs in general within populations and species.

His argument gains greater relevance when the focus shifts to a specific ontological question: what is a race (or a variation within a species)? Dobzhansky (1937, p. 62) states that "the fundamental units of racial variability are populations and genes, not the complex characteristics that connote a racial distinction in the popular mind." His answer is consistent with how he would later establish the concept of species from the notion that a race is not a particularly clear entity. Thus, variation does not consist of a static entity, but a process with different stages of development. His work results from an amalgamation of Mendelian genetics with Darwinian evolutionism, supporting the idea that species are classifiable through *mechanisms of physiological isolation*.

> If we allow differentiation to proceed unimpeded, most or all individuals of one race may come to possess certain genes, while those of the other race do not. Finally, mechanisms that prevent interbreeding can develop, dividing what used to be a single collective genotype into two more separate selves. When such mechanisms have developed, and the prevention of crossbreeding is more or less complete, we are dealing with separate species. A race becomes increasingly a "concrete entity" as this process progresses; what is essential in races is not their state of being, but their state of becoming. But when the separation of races is complete, we are no longer dealing with races, for what has emerged are separate species (Dobzhansky, 1937, pp. 62-63).

Dobzhansky (1937) establishes that phenomena such as hybrid sterility and sexual or psychological isolation could operate in a system of mutual reinforcement. As a consequence, subsequent isolations could be adaptive in specific circumstances. A first analysis might suggest that applying this hypothesis to hybrid sterility and inviability could constitute a case of the previously mentioned naive group selection. However, the author himself accepts the argument that hybrid sterility should be considered a byproduct of divergent evolution, rather than a directly selected influence on speciation. Therefore, what seems to occur is an acceptance of the relevance of the Darwinian approach to understanding the definition of species, even though both authors have differences in their views on the subject.

Mayr (1942) highlights this definition of reproductive isolation of species and renames it the biological species concept. The author does not refute the argument that this new species concept differs from the original argument presented in *On the Origin of Species*, requiring a new understanding of the work. In short, this new view of the speciation process is representative of the modern synthesis of Darwinism with Mendelian genetics. It is in this new light that we intend to return to Darwin (1872) and present the current relevance of his proposal to answer the central question of this article: what is a species?

Reinstatement of the Darwinian concept of species.

As previously presented, Darwin (1872) criticizes the then-current concept of species in favor of a new conceptualization compatible with the evolutionary argument he proposed. Based on the process of natural selection, the author indicates that speciation occurs through the preservation and accumulation of small variations beneficial to the individual, which lead to the emergence of well-marked varieties or incipient species. In this sense, naturalists began to arbitrarily adopt a diversified concept based on three central criteria: (i) perception of visible differences between individuals; (ii) use of links between two forms, with the first or most common being classified as a species and the others as variations; and (iii) classification of one form as a variety of another by analogy with the already documented form, whether current or extinct.

The problem with this diversification was precisely that there was no semantically unifying concept. It should be noted that, in practical activities, there are major disagreements regarding the classification of living beings at the species level, and the result is the impossibility of reaching a consensus on how to classify them. The step taken by Darwinian theory was precisely to develop an argument based on a widely accepted process, namely, natural selection.

Given the inadequacy of the concept of species and the intense debate that followed the publication of *On the Origin of Species*, it is now necessary to emphasize the positions that converge on a common point and that have opened up space for the compatibility between Darwinism and Mendelian genetics. Possibly the central argument is that all organisms exhibit slight variations[8]. Darwin (1872) states that it is a mistake to consider that variations only affect characteristics that are not important to organisms. Previously, case studies were presented in which it is possible to verify the presence of variations in relevant structures, including among individuals of the same species. The author emphasizes that those who refute his statement fail to verify the numerous occurrences of these variations in nature. His concern is emphasized in the weight he gives to this phenomenon as one of the pillars supporting his explanation of the natural emergence of new life forms.

> These individual differences are of the utmost importance to us, as they are often inherited, as should be familiar to everyone; and thus they furnish materials for natural selection to act upon and accumulate, in the same way that man accumulates individual differences in his domesticated productions in any direction. These individual differences generally affect what naturalists consider unimportant parts; but I could show by a long catalogue of facts, that the parts which must be considered important, whether viewed from a physiological or classificatory standpoint, sometimes vary in individuals of the same species. I am convinced that the most experienced naturalist would be surprised at the number of instances of variability, even in important parts of the structure, that he could collect with good authority, as I have collected, over the years (Darwin, 1872, p. 34).

Darwin (1872) shows remarkable interest in emphasizing the existence of cryptic species. The author defines these groups as forms that possess some considerable degree of characteristics of a given species, but which, at the same time, are similar to other forms or are closely linked through intermediate

[8] Faria (2011) establishes that parental DNA replication is impregnated with repair and proofreading enzymes. The function of these enzymes is to correct differences that occur in the copy, with some modifications remaining after correction. In this sense, a mutation consists of a persistent difference that is not corrected by the enzymes and remains after cell reproduction. Then, a new DNA sequence emerges capable of encoding a new protein, with properties different from the original. Note that this occurs both in vertical gene transfer (in the generation of gametes in the transmission of parental genetic material) and in horizontal transfer (the process by which an organism transfers genes to a non-descendant cell). The important point is to emphasize that the concept of variation is compatible with genetics, since all forms of life exhibit observable variations due to the chemical similarity of their genetic code.

gradations. In general, naturalists are reluctant to classify groups of this type as a distinct species. The Darwinian argument is based on the analogy between a species and other forms, which are classified as a result of the observed distinctions and can be listed as subspecies or varieties. At this point, there is a tendency to assume that the life form already exists somewhere or has existed in the past. The issue is that cryptic species possess a considerable degree of shared characteristics. The complicating factor in the use of analogy is that they have such similarity to other forms – or are even closely linked to these forms through intermediate gradations – that they will hardly be classified as distinct species.

> In many cases, however, one form is classified as a variety of another, not because the intermediate links have actually been found, but because the analogy leads the observer to assume that they now exist somewhere, or may have existed previously; and here a wide door opens for the entry of doubts and conjectures (Darwin, 1872, p. 37).

The peculiarities presented by cryptic species serve as an argument in favor of genetics based on natural selection. After all, this principle allows one to understand the degrees of similarity and differentiation through the selection of genotypes over time, originating variations that gradually become the well-marked varieties that define the formation of new species. The cryptic factor portrays the complexity of the process that involves both the similarity originating from common descent and the differentiation through modification resulting from the replication of parental DNA. In this way, the system is viewed from the understanding of the common link that is provided by genealogy plus the modification by natural selection. Well-marked varieties possess their own characteristics, even though they share common traits with distinct groups. In short, it is through the process of natural selection that it is possible to explain the emergence of variations and well-marked varieties.

> The forms that possess in some considerable degree the character of a species, but are so similar to other forms, or are so closely connected with them by intermediate gradations, that naturalists dislike classing them as distinct species, are in several respects the most important to us. We have every reason to believe that many of these doubtful and closely allied forms have permanently maintained their characteristics for a long time; for so long, as far as we know, as good and true species (Darwin, 1872, p. 36).

Darwin (1872) presents a materialist explanation for the emergence of new species. The author emphasizes that the exposure of an organism for a long period can undergo gene mutations from the process of natural selection circumscribed in complex laws of variation. This principle tends to favor the modified form to the extent that it presents adaptive advantages. Natural selection operates in such a way that small modifications are accumulated genetically over time, leading organisms to adapt in different ways to the environment.

> The passage from one stage of difference to another may, in many cases, be the simple result of the nature of the organism and the different physical conditions to which it has long been exposed; but with regard to the most important and adaptive characteristics, the passage from one stage of difference to another may be safely attributed to the cumulative action of natural selection [...] (Darwin, 1872, p. 42).

As previously presented, Huxley (1860) was not convinced by the Darwinian argument that species should not be defined based on reproductive isolation. He coined the term physiological species to conceptualize the thesis that reproductive isolation constituted the fundamental nature of species, an idea that resurfaced strongly in the mid-20th century. The strong disagreements regarding the argument that species should be fundamentally distinct from varieties based on their physiology led to a search for the reintroduction of fundamental concepts to define what a species is. Thus, Cracraft (1989) states that a phylogenetic species is a distinct form that retains stable morphological or genetic differences, whether or not it is reproductively isolated. Yang and Rannala (2010) advance this point, emphasizing that it is necessary to infer from genetic data at least a minimum separation time between a pair of populations in order to classify them as distinct species. In turn, Hilário et al. (2021) presents a recent version of this perspective, employing Bayesian statistical analyses of genealogical coalescence to determine the presence of phylogenetically separate species in a dataset of individual genomic sequences.

Mallet (1995) establishes that a Darwinian delimitation of species is contemporaneously valid from the synthetic theory. For the author, species are separate genotypic groups when considered in the molecular genetic sense. Note that arguing in favor of two species based on genetic data is equivalent to defending the possibility that two sets of individuals, each originating from a population with genetic frequencies, may differ from each other. In other words, it means refuting the hypothesis that there is a single population in the set of individual genetic and genomic datasets to prove that the presence of two populations is a better hypothesis, with the advantage that this method can be extended to multiple populations. Pritchard et al. (2000) points out that, when plotting the distribution of individuals along axes representing multilocus gene frequencies, the distribution will be bimodal if there are two species or single-peaked if there is only one.

Huelsenbeck and Andolfatto (2007) reinforce this argument by stating that the data can be statistically treated using a Bayesian-Markov-Chain-Monte-Carlo approach. This procedure became known as the assignment test, as it determines the appropriate number of distinct populations to which it is possible to assign each of the genotyped individuals in a sample. Zeng et al. (2010) state that assignment tests are useful for delimiting cryptic species in low plants. This position is corroborated by Pinzón and LaJeunesse (2011), with regard to corals; Dasmahapatra et al. (2010), to butterflies; and Weisrock et al. (2010), to primates such as lemurs (Lemuriformes primates). Peccoud et al. (2009) points out that this method is useful for identifying genetically distinguishable taxonomic units that are usually considered below the species level, such as aphids (Toxoptera citricidus). Similarly, Hoelzel et al. (2007) establishes the usefulness of this approach for classifying forms of social groups in mammals, taking the orca (Orcinus orca) as an example. In Darwinian terms, these ecological groups represent exactly the dubious cases that the English naturalist uses in his argument that species evolve from varieties.

> All the previous rules, aids, and difficulties in classification can be explained, if I am not very much mistaken, by the view that the Natural System is founded on descent with modification; – that the characters that naturalists consider as showing true affinity between any two or more species are those that were inherited from common parents, all true classification being genealogical; – this community of descent is the hidden link that naturalists have unconsciously sought, and not some unknown plan of creation, or the enunciation of general propositions, and the mere joining and separation of more or less similar objects (Darwin, 1872, p. 369).

The Darwinian concept of species arises associated with the principle of natural selection, interrelated in such a way that one does not exist without the other. The focus of divergence demonstrated that, in practice, each naturalist uses different methods for identifying a species and, as long as there is no objective foundation for the natural system that is unconsciously used, there will be classificatory divergences. If it becomes evident that the natural system is based on descent with modification, then it will be possible to understand subordinate genealogy and the relationship between groups where similar organisms share common ancestors. In light of synthetic theory, gene frequencies can differ if populations are spatially isolated without this necessarily implying speciation. Finally, the Darwinian position is corroborated in cases where distinguishable populations occur together in the same region and yet retain differences in several gene loci. As a result, these groups tend to be classified as different species. In fact, hybrid individuals can occur, but unless they are rare in overlapping areas, these populations can also be considered as separately delimited species.

Conclusion

The Darwinian concept of species proves to be dynamic and paves the way for the thesis that a permanent classification is only possible if one carefully observes the intermediate forms that link the ancestral species to its descendants. Natural selection explains everything from the accumulation of variations, through the emergence of intermediate forms, to the separation of groups into new species. This principle allows for the natural emergence of new species, providing an evolutionary explanation for the variation in the composition of populations of living beings over time.

The concept of species formulated by Darwin (1872) completed a cycle that went from general disregard to the use of statistical methods that employ a clear Darwinian notion of species. However, it is important to emphasize that the advancement to the theory of extended synthesis added to the evolutionary perspective the use of genetic data instead of a strictly morphological approach. In this sense, the genetic and morphological bases can be seen contemporarily as explanations for the scarcity of intermediate links between species. Thus, genotypic bimodality makes practical sense for naturalists who support both approaches, from those who more strongly defend phylogenetic approaches to those who maintain that the Darwinian perspective was correct from the beginning. The point is that, from a contemporary perspective, genetics and morphology are not necessarily antagonistic. This seems to offer a solid path to end what the English naturalist defined as a vain search for the undiscovered essence of what a species is.

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