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Parsimony and consilience: monophyly from a logical-epistemological approach, exemplified with exochorionic morphogeny of Pieridae (Lepidoptera: Papilionoidea)

Parsimonia y consiliencia: monofilia desde un enfoque lógico-epistemológico, ejemplificado con morfogenia exocoriónica de Pieridae (Lepidoptera: Papilionoidea)

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ABSTRACT

A logical-epistemological analysis and a defense of the Principle of Parsimony, based on inductive consilience, are presented to re-evaluate monophyly as the theoretical foundation of phylogenetic systematics; the results are exemplified through a case study of exochorionic morphogeny of Pieridae (Lepidoptera: Papilionoidea). The central epistemology and abductive logic of phylogenetic systematics *sensu* Hennig are expounded, following Fitzhugh's proposal. Sober's philosophical research on parsimony and its use in phylogenetic systematics, reformulated as the 'Extended Parsimony Model,' is reviewed. In conclusion, the 'Principle of Triple Consilience with Intergrades' is proposed as an independent justification for the Principle of Parsimony. In the case study, the model is used to review the contributions of exochorionic morphogeny in the discussion of the 'Klots hypothesis' on the genus *Leptophobia* Butler, 1870. It is shown that: i) exochorionic characters allowed for an improved version of the hypothesis, insofar as being more consilient; ii) morphogeny, reinterpreted through Goethe's 'genetic method', serves as a 'bridge' theory between morphology and phylogeny in explaining synapomorphies through monophyly.

Key words: egg, morphology, abduction, *Leptophobia*, consilience, Goethe, auxiliary principle.

RESUMEN

Se presenta un análisis lógico-epistemológico y una defensa del Principio de Parsimonia, basada en consiliencia inductiva, para reevaluar la monofilia como fundamento teórico de la sistemática filogenética; los resultados se ejemplifican mediante un estudio de caso sobre morfogenia exocoriónica de Pieridae (Lepidoptera: Papilionoidea). Se exponen la epistemología central y la lógica abductiva de la sistemática filogenética *sensu* Hennig, siguiendo la propuesta de Fitzhugh. Se revisa la investigación filosófica de Sober sobre la parsimonia y su uso en la sistemática filogenética ', reformulada como 'Modelo de Parsimonia Extendida'; en conclusión, se propone al 'Principio de Triple Consiliencia con Intergrados' como justificación independiente del Principio de Parsimonia. En el estudio de caso, el modelo se utiliza para revisar las contribuciones de la morfogenia exocoriónica en la discusión de la 'hipótesis de Klots' sobre el género *Leptophobia* Butler, 1870. Se muestra que: i) los caracteres exocoriónicos permitieron obtener una versión mejorada de la hipótesis, en tanto más consiliente; ii) la morfogenia, reinterpretada a través del 'método genético' de Goethe, sirve como teoría 'puente' entre la morfología y la filogenia en la explicación de sinapomorfías mediante monofilia.

Palabras clave: huevo, morfología, abducción, *Leptophobia*, consiliencia, Goethe, principio auxiliar.

Probably one of the most pressing philosophical problems in phylogenetic systematics, situated at its theoretical core, is providing justification for Hennig's (1966: 121) so-called 'auxiliary principle', which assigns evidential value to synapomorphies for monophyly hypotheses. Correctly understood, addressing this problem ultimately amounts to provide an independent justification for the Principle of Parsimony (PAR). In this paper, we approach the issue through a logical and epistemological analysis of the concept of parsimony, and its application in phylogenetic systematics, and propose that its best available independent justification is through a stronger version of inductive consilience, based on gradualist 'triple parallelisms' between form, time, and space. We exemplify these results through a case study of oocytic —exochorionic— morphology, applied to butterfly phylogenetic systematics.

Since Plato's *Theaetetus* ([*c.a.* 369 B.C.E] 1988: 210a–b), justification (*logos*) is considered a necessary —though, following Gettier (1963), not sufficient— component of knowledge. In a broad sense, *reliabilism* encompasses theories of justification that emphasize the role of reliable, 'truth-conductive' processes in belief formation (García-Campos & Vázquez-Gutiérrez 2012: 4,5). In this paper, we adopt two core premises: i) logical analysis is a necessary —not sufficient— component of epistemological research; and ii) the justification of an epistemic tool or content is an argument for its reliability, where its degree of logical strength and the empirical adequacy of its premises serve as gradual truth-conducive properties. We sought to justify PAR, operational in phylogenetic systematics through the auxiliary principle, by proposing an alternative principle X that imposes stricter demands for empirical adequacy and logically entails it (X→ PAR). Given the inherent complexity of scientific research, we propose a gradualist criterion: the use of PAR is justified to the degree that it meets the requirements for the application of X.

The paper is divided into three major sections. In the first section, the core epistemology of phylogenetic systematics *sensu* Hennig (1965, 1966) is outlined, with emphasis on its logical abductive structure following Fitzhugh's (2006a) proposal. In the second section, Sober's (1988, 1989, 1994, 2000, 2008, 2015) line of philosophical research on PAR in general, plus its meaning and particular usage in phylogenetic analysis, is revised and reframed as 'Extended Parsimony Model' (PAR+). The 'Principle of Triple Consilience with Intergrades' (3PCI) is proposed as an independent (non-circular) justification for PAR, insofar as 3PCI imposes stricter demands for empirical adequacy than PAR and logically entails it (3PCI→ PAR). In the third section, an ongoing research program of exochorionic morphology and morphogeny applied to phylogenetic systematics of Pieridae (Lepidoptera: Papilionoidea) is presented as a case study, in which PAR+ is used to review the contributions of the exochorionic morphogeny to the discussion of the 'Klots hypothesis' (Hernández-Mejía *et al*. 2015). It is shown that: i) exochorionic characters allowed for a better-justified version of Klots hypothesis, by making it more consilient *sensu* 3PCI; ii) exochorionic morphogeny, reframed through Goethe's (Goethe [*ca.* 1790] 2009) 'Genetic Method', served as a 'bridge' theory between morphology and phylogeny in the explanation of synapomorphies by monophyly.

PHYLOGENETICS' EPYSTEMOLOGY AND LOGIC: AN OUTLINE

Phylogeny as a foundation for systematics. One of the core epistemological questions in systematics is how systems of characters allow for the delineation of species and other biological groups. Arguably, the answer lies in the concept of *homology* and its historical transformation into the concepts of *homogeny* and *homoplasy*. Owen (1843: 379) defined *homologues* as the same organ in two or more organisms, regardless of their variations in form and function. This concept dominated idealist morphology from its disciplinary demarcation by Gegenbaur (1878) to its post-Darwinian conceptual transformation influenced by Haeckel (Laubichler 2014, Rieppel 2016). Homologues retain their original meaning of 'sameness' as they occupy the same places within a given 'structure'. But, after Darwin, the sort of hypothetical explanation for the occurrence of homologues could be either homogeny (same origin) or homoplasy (different origin, plasticity) *sensu* Lankester (1870). Homogenetic homology, understood as an explanation for the occurrence of homologues due to a common cause, acquired two meanings: 1) *ontogenetic*, when organs or structures originate from the same part or primordium of the embryo; 2) *phylogenetic*, when inherited from a common ancestor.

Haeckel (1866: 22–30) introduced the term *morphogeny* to refer to the post-Darwinian use of the term *evolution*, derivative from the German *Entwicklungsgeschichte*, 'history of development'. He clarified this term by introducing two other neologisms: i) *Ontogeny*, *i.e.,* individual or organismal development, studied by *Embryology*, and; 2) *Phylogeny*, *i.e.,* collective development or descent with modification, studied by *Paleontology*. According to Rieppel (2014, 2016: xvi, xvii, 50), the 'Hennigian revolution' can be considered the culmination of a history that began with Haeckel's coining of the term and concept of phylogeny, driven by two main goals: i) the search for a scientific foundation for systematics; ii) a system to explore the multidimensionality of biology (Rieppel 2014: 299).

Based on Zimmerman (1931, see also Hamilton 2014: 100), Hennig (1965: 97) defined 'phylogenetic relationship' as follows: "species, B, is more nearly related to species, C, than to another species, A, when B has at least one ancestral species source in common with species C which is not the ancestral source of species A." With this relational concept established, the degree of phylogenetic relationship between 'sister species' is the relative age of their exclusive 'mother' ancestral species. The core ideas (Schmitt 2014: 53) of phylogenetic systematics are: i) the natural system is based strictly on phylogenetic relationships; ii) monophyly is the only correct foundation in the formation of natural groups; iii) the degree of phylogenetic relationship between species and monophyletic groups is the relative age of their exclusive common ancestor; iv) monophyletic groups are diagnosable by the presence of synapomorphies. The following sections outline the most relevant epistemological and logical aspects of phylogenetic systematics *sensu* Hennig (1965, 1966) to inform the paper's later discussion.

Semaphoront as empirical unit of phylogenetic analysis. The central task of phylogenetic systematics is the search for sister groups, *i.e.,* unveiling the natural system of species according to their relations of exclusive common ancestry. However, the empirical unit of study in phylogenetic systematics is not the species or even the individual organism, but rather the 'character bearer' or *semaphoront* (Hennig 1950: 9; 1966: 6, 65; *Merkmalsträger sensu* Hennig 1947: 276; see also Havstad *et al.* 2015: 580). The semaphoront is defined as a stable phase during an organism's 'ontogeny' (development), without internal changes among its parts or in its relations with other organisms. The classic Hennigian example is each of the stages in the life cycle of a holometabolous insect, but it can be shorter and applies to all organisms with any type of development.

According to Rieppel (2016: 312), a semaphoront is: "The same yet changing individual through time […] a material (substantial) body extending in the three spatial dimensions and with a variable duration in time, in short, an individual." This point of view aligns with the 'semaphorontic view' of homology (Havstad *et al.* 2015), in which characters, just as the semaphoronts they partake of, are conceived as causally connected temporal parts of ontogenetic, phylogenetic, or in general, morphogenetic processes. It also supports Hennig's conception of apomorphic characters as homologous to their plesiomorphic counterparts, within a 'transformationist paradigm' (Havstad *et al.* 2015: 578, 579).

Despite its original importance, the concept of *semaphoront* is now almost entirely ignored in the phylogenetics literature. This may be due to the ontological neutrality of much contemporary phylogenetics, with its tendency to move away from theoretical–conceptual foundations, toward the instrumentalization using computational algorithms in character analysis (Rieppel 2007, 2014). It can also be so due to the belief that semaphoronts are irrelevant in phylogenetics based on sequence data, as particularly evident in phylogenomic systematics, where: "morphology of butterflies and their life stages (including caterpillar foodplant preferences) are encoded in these genomic sequences. [...] As a result, genome-scale phylogenetic trees [...] represent the entire organism and therefore enable us to judge more accurately about its evolution" (Zhang *et al.* 2020: 2–4, 2021: 3). However, semaphoronts and the semaphorontic view of homology are still relevant in systematic phylogenetics, particularly for morphogeny, as will be stated in this paper.

Monophyly as naturalness and the 'auxiliary principle'. Hennig **(**1965: 102, 103) referred to groups as polyphyletic, paraphyletic, or monophyletic, depending on whether they are outlined by convergence, symplesiomorphy, or synapomorphy. Synapomorphies *sensu lato*, *i.e.,* apomorphies shared by at least two species, are considered the only homogens *sensu* Lankester (1870), *i.e*., possible evidence of monophyly. Hennig's (1966: 73) 'monophyletic group' coincides with Haeckel's 'tribe' (*Stamm*) (Willmann 2003: 458, 459), as comprising all descendant species of an exclusive common ancestor. 'Naturalness' and 'monophyly' are synonymous *salva veritate* in phylogenetic systematics: all and only monophyletic groups are natural, *i.e.,* objectively existing in nature regardless of human detection or interests.

We assume that synapomorphy arose as an autapomorphy in the ancestral species and was inherited by all and only its descendant species. Thus, hypotheses of groups of species' monophyly and apomorphic characters' homogeny occur simultaneously in the production of phylogenetic hypotheses, by means of the same causal theory (Fitzhugh 2006a: 58, 59; see ***Theory of Descent with Modification* (TDM)** section in this paper). The default hypothetical explanation of a synapomorphy by monophyly is the guiding theoretical 'auxiliary principle' of the Hennigian method: "I have therefore called it an "auxiliary principle" that the presence of apomorphous characters in different species "is always reason for suspecting kinship [*i.e*., that the species belong to a monophyletic group], and that their origin by convergence should not be assumed a priori"" (Hennig 1966: 121).

Hennig (1966: 121; see also Mooi & Gill 2016: 259, 264) insisted on this point through an argument that can be called of 'indispensability', on the side of the homogenetic explanation, and of 'burden of proof', on the homoplastic alternative; meaning that without this principle: "phylogenetic systematics would lose all the ground on which it stands." Indeed, Hennig's definition of phylogenetic relationship necessitates the proposal of at least one hypothesis of monophyly. In light of the seemingly ubiquitous nature of homoplasy, the auxiliary principle remains perhaps the most contentious aspect of Hennigian theory; as such, it serves as the focal point of the logical and epistemological analysis in this paper.

Heterobathmy and the 'outgroup' polarization method. 'Heterobathmy' (*chevauchement des spécialisations* in Dollo 1895, *Spezialisationskreuzugen* in Abel 1909, *Heterobathmie der Merkmale* in Takhtajan 1959, adopted by Hennig 1965: 106, 107; see also Takhtajan 2009, Rieppel 2016: 75–77, 320–322) refers to the combination of primitive and derived character states in organisms of one or more species. This phenomenon arises from different rates of character transformation, *i.e., heterochrony sensu lato*. The original Haeckelian neologism referred to different rates of character transformation at the ontogenetic level, *i.e.,* during the life cycle of organisms (McKinney & McNamara 1991: 6, 7, 12). As the main cause of heterobathmy, heterochrony refers to different rates of transformational homology among plesiomorphies, autapomorphies, and synapomorphies at the phylogenetic level. Heterobathmy underpins the Hennigian shift in phylogenetics, by replacing the Haeckelian search for ancestor-descendant species with a search for common ancestry (Rieppel 2016: 75), leading to the search for sister groups diagnosed by shared synapomorphies.

Every synapomorphy of a monophyletic group is homologous to some autapomorphy of its ancestral species, which must have exhibited the plesiomorphic state of that same character before it became autapomorphic. Thus, Hennig (1965: 107) asserts that the group most closely related to the diagnosed monophyletic group should exhibit the plesiomorphic and conserved state of that same character. This reasoning underlies the 'outgroup' method for character polarization, *i.e.,* the outgroup to the studied group provides the relatively plesiomorphic characters or character states.

Logic of producing and testing phylogenetic hypotheses. A crucial —yet often overlooked— aspect of phylogenetics' epistemology, is the types of logical inferences involved along with their respective degrees of strength and reliability. Fitzhugh (2006a) presented a resume of the roles of logical inferences in general scientific methodology *sensu* Peirce (1878: 472; Fitzhugh 2006a; see also Deely 1994: CP 2.776, 2.777), followed by a semi-formal analysis of abduction in phylogenetic systematics. The author also has researched a quasi-nominalistic proposal of definition of 'species' as ontologically neutral explanatory hypotheses (Fitzhugh 2005), character coding (Fitzhugh 2006b) and the impossibility of character data or alternative phylogenetic hypotheses to serve as test evidence (Fitzhugh 2012). For the purposes of this paper, we focus on his account of the logic and epistemology of scientific research, with emphasis on the abduction of phylogenetic hypotheses.

Together with Fitzhugh's own references, especially the works of Cleland (2011, 2013) on common cause explanation, the reader can consult the works of Aliseda (1997, 2003, 2004a,b, 2005, 2006, 2007, 2014) for a broad and in-depth overview of abduction and its creative or inferential functions in both experimental an historical sciences, mathematics, pure logic and artificial intelligence. Although some criticisms of Fitzhugh focus on the application of computerized algorithms to molecular data, his logical-epistemological points of discussion addressed herein apply to any character system, in any semaphoront, and for any recognizable species through an operational concept akin to Hennigian phylogenetic systematics. Reference can be made to the work of Suárez-Díaz & Anaya-Muñoz (2007) for a historical and contemporary overview of the methodological problems inherent in the use of molecular characters in computerized phylogenetic systematics, the common thread of which is a long-standing search for 'mechanical objectivity' *sensu* Daston & Galison (1992, 2007; see also Flores-Gallardo *et al.* 2022). Regarding the 'species problem' and its impact —or oversight— in contemporary phylogenetic practice, the historical and philosophical works of Kitcher (1987), Mayden (1997), Stamos (2003), Wilkins (2009), Richards (2010), and Zachos (2016) can be consulted.

According to Peirce's Aristotelian model (1878), there are three basic types of inference: *deduction*, *induction,* and *abduction*, which are variations of the same basic type of argument, the syllogism, through the permutation of its parts:

$$\begin{array}{ll} \text{Major premise} & (\textit{Rule}) \\ \underline{\text{Minor premise}} & \underline{(\textit{Case})} \\ \text{Conclusion} & (\textit{Result}) \end{array}$$

The third, abduction (*Rule* and *Result*, therefore *Case*), occurs in the production of explanatory hypotheses (*Case*) for particular events (*Result*) using a general law (*Rule*), as in hypotheses of phylogenetic relationships. The basic idea is that to 'explain' something means to subsume it under a general 'rule', understood as a theory of cause-and-effect relations. Hempel (1965: 249, 250) states that explanatory causes (*explanans*) and explained effect (*explanandum*) must be subject to logical strict implication (*explanans* → *explanandum*), and scientific explanation must contain general laws. In Peirce's conception of abduction, sometimes called 'inference to the best explanation', the production of explanatory hypotheses for surprising facts generally does not have deductive validity, *i.e.,* assuming all premises are true does not guarantee the truth of the conclusion. It is only an 'explanation sketch' *sensu* Hempel (1965: 424, Fitzhugh 2006a: 45) insofar: "as presenting the general outlines of what might well be developed by gradual elaboration and supplementation." Phylogenetic hypotheses, in particular, require appeal to mechanisms of speciation and character replacement to obtain a complete —and testable— explanatory hypothesis. The operational relations between types of inference in scientific inquiry are: i) a hypothesis is generated by abduction; ii) potential test evidence is obtained by deduction, under the assumption that the causal conditions presented in the hypothesis occur; iii) a test is performed by induction, leading to the hypothesis' confirmation, refutation, or revision.

Fitzhugh (2006a: 18) mentions that abduction, a.k.a. 'inverse deduction', 'inverse *modus ponens*' or 'retroduction' —not to be confused with Cleland's (2011) 'retrodiction', *i.e.*, a deductive contrastive test for a historical hypothesis obtained by abduction—, is often understood as 'reasoning backwards', from consequent (*Result*) to antecedent (*Case*) conditions subject to causality through strict implication (*Rule*). Beyond the syllogistic account of Peirce and Fitzhugh, abduction of an explanatory hypothesis H given some evidence E is usually formalized as follows in standard propositional logic:

$$\begin{array}{ll} H \rightarrow E & (\textit{Rule}) \\ \underline{E} & \underline{(\textit{Result})} \\ H & (\textit{Case}) \end{array}$$

As such, abduction is indistinguishable from the 'Affirming the consequent' fallacy. This should not be of concern, since the 'fallacious' attribution only means that abduction isn't a valid (*i.e.,* deductive) inference, which was not expected to be the case. However, in the context of hypothetic scientific explanation, abduction says something slightly different: that given an implication taken as necessary (□), *i.e.,* with the strength of a theoretical principle (*Necessary Rule*), together with evidence of its consequent (*Result*), we can infer the possibility (◊) of the antecedent (*Possible Case*). In modal logic, this would be formalized as follows:

$$\begin{array}{ll} \Box(H \rightarrow E) & (\textit{Necessary Rule}) \\ \underline{E} & \underline{(\textit{Result})} \\ \Diamond H & (\textit{Possible Case}) \end{array}$$

In the following discussion, we frame hypothesis testing primarily as *empirical demodalization*: an operation by which a modal possibility (◊A) is compared against empirical data to yield its assertion (A) or negation (¬A), thereby fixing its truth value within a provisional factual framework. This notion of testing is coherent with Fitzhugh (2006a: 14, 95), drawing on Peirce (Deely 1994: CP 5.168) and Hilpinen (2000: 93). Demodalization is a necessary condition for testability in scientific inquiry; accordingly, we will address the alleged testability of phylogenetic hypotheses through the addition of characters or comparison with alternative phylogenies.

***Theory of Descent with Modification* (TDM)**. Fitzhugh (2006a: 51–52) proposed a semi-formal theoretical statement as the core foundation of phylogenetic systematics, to which, in consistency with its original conception by Darwin (1859: 565), he refers to as the *Theory of Descent with Modification* (TDM) and states the following:

TDM: *If character α existed among members of an ancestral species h, which was an effect of an earlier speciation event, and this character was subsequently replaced during tokogeny by character β among members of h, and h later underwent speciation, then members of the descendant species would exhibit character β.*

That is, the explanation for the presence of character β is being a synapomorphy originating as an autapomorphy in the ancestral species *h* from the plesiomorphy α. This theoretical-axiomatic statement underpins Hennig's 'auxiliary principle', *i.e.*, the inference of monophyly from the presence of synapomorphies. TDM states, *grosso modo*, that if X group of at least two species is monophyletic (Mono-X), then X will exhibit at least one synapomorphy (Syn-X). The abduction of hypothetic monophyly by means of TDM and the presence of synapomorphy would be as follows:

□(Mono-X → Syn-X)	(*Necessary Rule* / **TDM**)
Syn-X	(*Result* / **Evidence**)
◊Mono-X	(*Possible Case* / **Hypothesis**)

Thus TDM, taken as theoretical principle, allows for the explanation of synapomorphies as the effect of hypothetical monophyly, *e.g.*, if X = species of Lepidoptera, we hypothesize their monophyly (◊Mono-X) from TDM and the presence of wings with scales as a synapomorphy (Syn-X). However, this inferential scheme is epistemologically problematic and controversial. In its broadest sense, this controversy revolves around the concept of parsimony and the application of its associated principle in phylogenetic systematics.

PARSIMONY IN PHYLOGENETIC SYSTEMATICS

The problem of synapomorphy as evidence of monophyly. Since the first English-language publications of Hennig's work (1965, 1966), phylogenetic systematics has generated polarized reactions. Given that monophyly is the central concept of phylogenetic systematics, one crucial question informing some of these controversies is: what justifies the interpretation of synapomorphy as evidence of monophyly? The discussion of this problem has involved concepts that do not belong to Hennig's original conception but to his later developments by adherents of the so-called 'pattern cladism' (Nelson & Platnick 1981, Patterson 1982, see also Rieppel 2014; Williams & Ebach 2014). One of the most persistent controversies concerns the methodological dispute between parsimony and likelihood as guiding principles for phylogenetic hypotheses production (Suárez-Díaz & Anaya-Muñoz 2007). Elliot R. Sober (1988, 1989, 1994, 2000, 2008, 2015) has dedicated much of his philosophical work to studying the inferential and evidential roles of parsimony and likelihood, both in science in general and in biology and phylogenetic systematics in particular.

Sober (1989: 265–26) emphasizes that the fundamental postulate of phylogenetic systematics is that only synapomorphies constitute evidence of (possible) phylogenetic relations, *i.e.,* of monophyly. Crucially, he attributes the correctness of this reasoning to an issue of parsimony: the homogenetic hypothesis is, in principle, more acceptable than the homoplastic one, because it is the 'most parsimonious' explanation of the observed correlations between homologous characters. For Sober, however, an indispensability argument like the Hennigian one is not sufficient to justify the application of this principle.

Parsimony *sensu lato* (Pa) and its principle (PAR). The concept of parsimony, or 'simplicity,' as economy of expressive or inferential resources with descriptive or explanatory roles, has a philosophical tradition that can be traced back to Aristotle (Sober 2015: 2, 5–9). It is often associated with the so-called 'Ockham's razor' (*novaculam istam Occami*), as formulated by Froidmont (1649: CAP. V, ART. III): *Non sunt multplicanda entia sine necesitate*, *i.e.,* entities or processes —whether descriptive or explanatory— should not be multiplied unnecessarily. What Ockham said *ca.* 1323, in *Summa Totius Logicæ* (Ockham 1675: XII), was that *frustra fit per plura quod potest fieri per pauciora* (Ockham 1675: XII), *i.e.,* 'it is futile to do with more what can be done with fewer'.

In contemporary philosophy of science and influenced by the seminal paper of Kuhn (1977) on the subject, simplicity is often considered an epistemic virtue, understood as an auxiliary tool in the choice between rival scientific theories or hypotheses subject to empirical underdetermination, *i.e.,* when the same body of observations equally serves as evidence. This is usually understood as, *ceteris paribus* ("all else being equal"), the simpler theory or hypothesis should be preferred, *i.e.,* the one that requires the fewest entities or processes to fulfill an explanatory function. Refer to this broad notion of explanatory simplicity as *parsimony sensu lato* (Pa) and its associated principle as the *Principle of Parsimony* (PAR):

Pa: *The most parsimonious theory or hypothesis is the one that minimizes the number of entities or processes required to fulfill its explanatory function.*

PAR: *ceteris paribus, the more parsimonious theory or hypothesis is preferred.*

Parsimony (Pa) is a gradual, extrinsic, and relational property of hypotheses or theories, when comparing them with rival hypotheses or theories. Pa is conceptually distinct from the additional epistemological principle (PAR) stating that, *ceteris paribus*, the more parsimonious hypothesis should be chosen. Below, definitions of parsimony are reviewed along with their respective logical relations; with Pa being the most general and weakest in a logical sense, PAR serves as the basis for all subsequent definitions, contextualized to each of them.

Phylogenetic or 'cladistic' parsimony (PaC). The *ceteris paribus* clause is rarely fulfilled in phylogenetic systematics, since the choice of causal theories and additional assumptions determine the phylogenetic hypotheses that can be obtained as cladograms. For example, if a different evolutionary model is used to analyze the same molecular data, different premises are involved, and the "all else being equal" clause is not satisfied. However, if the meaning of the *ceteris paribus* clause is weakened to 'empirical adequacy,' in this case, preservation of distributive relations among characters in the cladogram with respect to a data matrix, then PAR can be applied in phylogenetic systematics. Sober (1988: x, 27, 31, 2000: 176, 179–181) proposed a precise definition of cladistic parsimony (PaC):

PaC: *The most parsimonious phylogenetic hypothesis is the one that minimizes the number of evolutionary changes required to explain the observed characters altogether.*

Then, he asserts the 'equivalence' of that definition with the following two (PaC1, PaC2):

PaC1: *The most parsimonious phylogenetic hypothesis is the one that minimizes the number of homoplasies required to explain the observed characters altogether.*

PaC2: *Only synapomorphies, not symplesiomorphies, are evidence of phylogenetic relations between groups (i.e., of monophyly).*

His statement of logical equivalence (strict biconditional: α ↔ β; one holds if, and only if the other holds, *i.e.,* α is both sufficient and necessary for β: (α → β) and (β → α)), warrants careful analysis.

Obtaining the 'most parsimonious' cladogram *sensu* PaC involves minimizing the number of homoplasies as much as possible, *i.e.,* logically, PaC → PaC1 (Fig. 1. A, B). The converse, PaC1 → PaC, is not evident: minimizing the number of homoplasy hypotheses might not be sufficient to obtain the cladogram with the fewest evolutionary changes necessary to explain the observed characters altogether. However, the cladistic principle stipulates that groups be formed exclusively based on synapomorphies, not on symplesiomorphies or the number of autapomorphies. In fact, Sober's (1988: 24, 2000: 177, 178) examples illustrating the lack of parsimony in a tree with convergence include evolutionary changes uncoupled from cladogenesis along the same branch, *i.e.,* phyletic changes or anagenesis, which should not appear in a cladogram *sensu stricto* (Fig. 1. B). If the only way to add evolutionary changes to a cladogram is through homoplasy, and these have already been minimized, then parsimony *sensu* PaC1 is sufficient to guarantee it *sensu* PaC; *i.e.,* PaC1 → PaC. Thus, the biconditional (PaC → PaC1 and PaC1 → PaC) is satisfied, and the definitions are logically equivalent: PaC ↔ PaC1.

Sober's claim that the previous definitions and PaC2 are equivalent is unsound. In a later text, Sober (2000: 179) proposes an example where two different hypotheses, both obtained through symplesiomorphy, each require only one evolutionary change, *i.e.,* they are equally parsimonious *sensu* PaC (Fig. 1. C, D). Overall, Sober (1988: 27, 31; 2000: 179, 180) argues that symplesiomorphies lack discriminative power in obtaining the most parsimonious cladogram *sensu* PaC. According to this argument, a failure of PaC2 (by grouping based on symplesiomorphies) leads to a failure of PaC, since the second requires the uniqueness of the most parsimonious hypothesis. In logical terms, we would have: ¬PaC2 → ¬PaC; thus, by logical contraposition (*i.e.,* (α → β) being logically equivalent to (¬β → ¬α)), we conclude that PaC → PaC2. However, the converse (PaC2 → PaC) does not seem to hold. Through analyses based solely on synapomorphies (not symplesiomorphies), different cladograms can emerge that explain all the character observations with equal parsimony *sensu* PaC. Thus, PaC2 is a necessary condition for PaC (*i.e.,* PaC → PaC2), but not sufficient: it is not the case that PaC2 → PaC. Thus, PaC2 is not equivalent to PaC.

The previous analysis shows the relative logical weakness of PaC2 compared to PaC. The cladistic requirement of inferring monophyly only from synapomorphies is too weak by itself to obtain parsimony *sensu* PaC. However, the amendment is immediate considering the proof of PaC ↔ PaC1: it must be prescribed to maximize the hypotheses of homogeny in explaining syapomorphies, which is cladistically equivalent to minimize the number of hypotheses of homoplasy. This is merely a paraphrasing of PaC1, which can be stated as follows (PaC1'):

PaC1': *The most parsimonious phylogenetic hypothesis is the one that maximizes the number of homogenies required to explain the observed characters altogether.*

To be more precise, the most parsimonious phylogenetic hypothesis is the one that maximizes the coverage of TDM over the causal questions about characters encoded in the data matrix (Fitzhugh 2006a: 71–74, 2006c: 338), when explaining the presence of interspecific apomorphies by homogeny given by the species' monophyly. As noted by Fitzhugh (3006c: 327): "homogeny and homoplasy hypotheses are always relational – it is only possible to refer to homoplasy hypotheses relative to homology hypotheses that were produced from the same inference. This accounts for the *ad hoc* nature of homoplasy hypotheses since they are

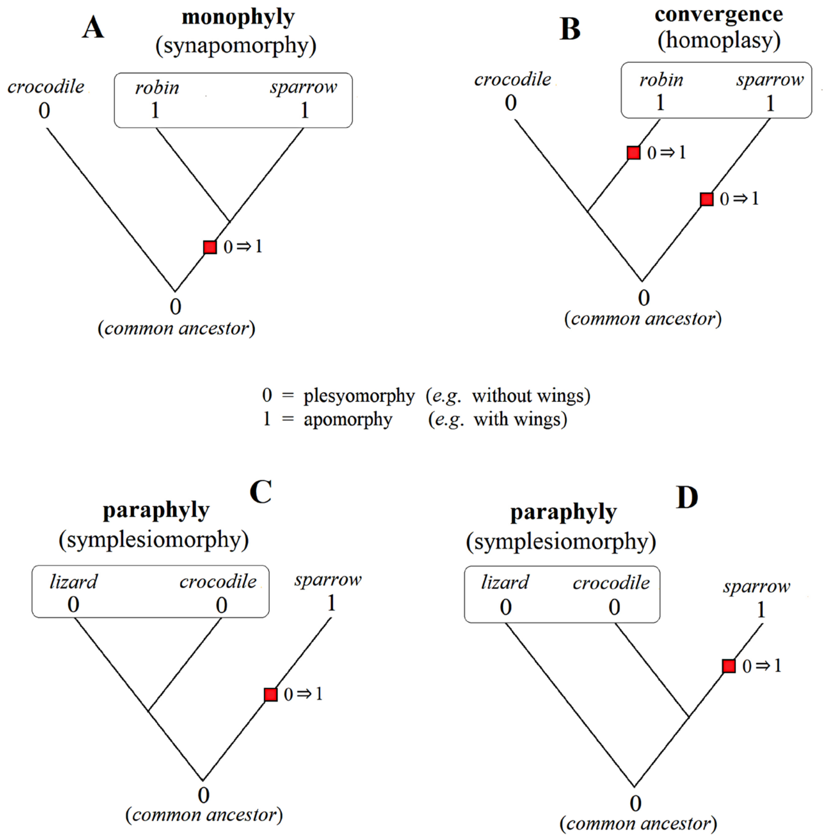


Figure 1. Reconstruction of the examples provided by Sober (2000: 178, 180) in his argument about the equivalence between definitions of cladistic parsimony. The most parsimonious phylogenetic hypothesis is the one that minimizes the number of evolutionary changes required (red boxes) to explain the observed characters altogether. This is achieved through the hypothesis that maximizes the number of homogenies (A), versus those that propose a higher number of homoplasies (B). Hypotheses based on symplesiomorphies (C, D) do not allow discrimination between equally parsimonious trees.

inferred beyond the causal theory applied to homologues." In general, a hypothesis is considered *ad hoc* insofar as it isn't inferred from the leading common-cause theory used in abduction; hypotheses of homoplasy are *ad hoc* insofar as obtained by —implicit or explicit— causal theories other than TDM.

Since PaC1 posits minimizing the number of homoplasies (*i.e.,* the number of entities, causes, or processes required for the hypothesis to fulfill its explanatory function), it is obvious that fulfilling PaC1 is sufficient to fulfill Pa (parsimony *sensu lato*), *i.e.,* PaC1 → Pa. The equivalence of PaC with PaC1 / PaC1' guarantees that PaC → Pa as well. Therefore, a principle of parsimony (PAR) based on PaC will also be fulfilled for Pa.

Principle of Uniformity of nature (PU) and Principle of Common Cause (PCC). Achieving a satisfactory definition of phylogenetic parsimony constitutes only the necessary preliminary step in the search for justification of the corresponding principle of parsimony (PAR). Sober (2000: 178, 181–184) mentions earlier proposals to justify it through Popperian falsificationism; the basic idea is that the most parsimonious hypothesis is preferable because it is the least falsifiable, as it requires the fewest homoplasies. However, Sober dismisses this proposal because, according to Popper's strict deductivism, a single homoplasy would falsify any phylogenetic hypothesis. In phylogenetic practice, even the most parsimonious hypotheses typically require some homoplasies to explain the totality of character data; *i.e.,* the goal is to minimize them, not to eliminate them, in acknowledgment of their apparent facticity. Throughout his research on this topic, Sober (1988, 1994, 2000, 2008, 2015) has repeatedly explored two principles correlated with parsimony: The *Principle of Uniformity of Nature* and the *Principle of Common Cause*.

The Principle of Uniformity of Nature (PU) is part of Hume's skeptical argument, proposed in *A Treatise of Human Nature* in 1739 (see Hume 1998), regarding the rational or empirical —and non-circular— indemonstrability of the Principle of Induction *sensu lato* (PI) upon which science is based:

PU: *Nature is uniform, i.e,, homogeneous across space and time.*

PI: *What has not yet been observed will be like what has already been observed of the same kind.*

As interpreted by Sober (1988: 41, 43), Hume bases induction—specifically enumerative induction, inferring from part to whole— on the presumption of the uniformity of nature (PU). Thus, the Principle of Induction (PI) presupposes PU, *i.e.,* it logically necessitates it: PI → PU. The later, in turn, presupposes parsimony *sensu lato* (Pa) given that assuming the uniformity of nature is explanatorily simpler than assuming its heterogeneity, *i.e.,* PU → Pa. By the *transitivity* of strict implication (*i.e.,* if $(\alpha \rightarrow \beta)$ and $(\beta \rightarrow \gamma)$, then $(\alpha \rightarrow \gamma)$), it follows that PI → Pa. Sober extracts from Hume's legacy the project of a "rational reconstruction of induction", which aims to justify the use of the Principle of Parsimony (PAR) as a link between observations and explanatory hypotheses in science. In the case of phylogenetic hypotheses, Sober crucially notes that these are not enumerative inductions (induction *sensu stricto*) but rather another type of inductive inference *sensu lato* (*i.e.*, non-deductive): phylogenetic hypotheses are abductive *sensu* Peirce. Sober (1988: 50) thus proposes: "Parsimony in abduction says that one hypothesis is *ceteris paribus* preferable to another when it postulates fewer entities or processes." —which is just a slightly less precise version of PAR based on Pa as defined here.

The Principle of Common Cause —attributed to Reichenbach (1956) and Salmon (1975, 1978, 1984)— (see also Sober 1988: 71, 2008: 230, 2015: 120; Fitzhugh 2006a: 70), according to Sober's reconstruction (2008: 231, 234, 235), states that (PCC):

PCC: *If* X *and* Y *are correlated, then* X *is the cause of* Y*,* Y *is the cause of* X*, or both share a common cause.*

Sober emphasizes that this principle is either too strong or incomplete. Overall, maximizing parsimony *sensu lato* (Pa) requires inferring causality from correlation, *i.e.,* PAR is a subcase of PCC, logically entailing it: PAR → PCC. In phylogenetic systematics, PCC does not stipulate that one correlated aspect is the cause of the other; instead, it suggests that both possibly share a common cause. For example, a correlation between genetic and morphological characters does not, by PCC, imply that one explains the other (*e.g.,* genetics explains morphology), but rather that both may be explained by common ancestry. Unrestricted application of TDM is the phylogenetic contextualization of PCC.

Requirement of total evidence (RTE) and TDM (mod RTE). The first implicit constraint in the application of PCC is what Sober (1988: 142, 2008: 136, 139, 2015: 120) calls Carnap's *Total Evidence Principle* (1950). Fitzhugh (2006a: 26, 27, 2006c: 310, 311) takes up and revises this Carnapian principle, reformulating it as the *Requirement of Total Evidence* (RTE), which here can be stated as follows:

RTE: *All available relevant evidence must be considered in conjunction when producing an explanatory hypothesis.*

Some evidence is considered relevant if its inclusion or exclusion as a premise has an effect in the truth or falsity of the conclusion; RTE is trivially satisfied in deductive inference, being contentious only in non-deductive inference, including abduction (Fitzhugh 2006a: 21, 26, 2006c: 309–313). As stated here: i) RTE refers to the initial evidence for the abductive production of a hypothesis, not to the resulting evidence —if available at all— during its deductive and inductive testing; ii) RTE is contingent only to the available relevant evidence, not to the unknown entirety of it. According to Fitzhugh (2006c: 337–339), there's been a lasting confusion about PAR being a 'justification' for RTE, insofar as RTE must be satisfied to ensure maximum parsimony. Instead, he explains, RTE is operational when gathering premises, *i.e.*, prior to the abductive inference, whether the resulting hypothesis is maximally parsimonious to the extent a causal law in use covers the causal questions posited in the premises or it is not. Considering PAR as a subcase of PCC, and the unrestricted application of TDM as PCC's phylogenetic contextualization, PCC and RTE are seemingly in conflict: one is maximized at the expense of the other and vice versa.

If PCC is strictly adhered to, *i.e.,* only hypotheses of homogeny are produced, some available relevant character data typically remain unexplained, contrary to RTE. If RTE is strictly adhered to, *i.e.,* all available relevant character data are considered, some require *ad hoc* explanations of homoplasy in need of different causal theories and even separate abductions, against PCC. Following Fitzhugh (2006a: 69–71), in this paper we advocate strict adherence to RTE, by including all available relevant data as premises in the same abduction, then applying PCC through TDM to the largest subset of data that can be explained by it. Indeed, only strict adherence to RTE guarantees fulfillment of the *ceteris paribus* clause (empirical adequacy) of PAR in every application of TDM. Consequently, a maximal application of TDM subordinated to RTE, or *TDM module RTE* —TDM (mod RTE)— sufficiently describes the implementation of PAR in phylogenetic systematics, *i.e.,* TDM (mod RTE) → PAR.

TDM (mod RTE): *Maximal application of* TDM *subject to* RTE.

RTE and PAR are epistemological principles that operate within the abduction process to obtain 'the best' possible explanation; in this context, the one that maximizes the coverage of TDM (PAR) over all available relevant data (RTE). However, this is neither a defining feature nor a prerequisite for abductive inference. What does seem to be required to satisfy the abductive schema (*Rule* and *Result*, therefore *Case*), is to apply the *Rule* (TDM) to at least one *Resul*t (synapmorphy) in obtaining one *Case* (monophyly). PAR operates through Hennig's 'auxiliary principle', by considering TDM the default causal rule in explaining synapomorphies *sensu lato*. But the production of phylogenetic hypotheses as conclusions of abductive inferences does not require maximization of TDM coverage; in fact, it is quite probable that diverse homologues are, in fact, due to homoplasies, and forcing a homogenic explanation —via

TDM and monophyly— would be an error. As Patterson (1988: 79; see also Williams & Ebach 2014: 170) noted: “Parsimony is a necessary property of methods of analysis, not of nature.” In this paper, we approach PAR as an epistemological principle rather than an ontological one.

The previous analysis describes more accurately and precisely the implementation of PAR in phylogenetic systematics. But it still does not justify it. As Sober insists, an independent justification is required for the use of PAR in science in general and in phylogenetic systematics in particular.

Independent and severe tests of phylogenetic hypotheses. Throughout “The myth of characters as tests of phylogenetic hypotheses,” Fitzhugh (2006a: 32, 92–95) discredits the inherited and commonly held notion of phylogenetic ‘robustness,’ understood as phylogenies that remain unchanged with the addition of new characters, deeming it unfounded. The accumulation of new character information does not provide ‘inductive support’ to a prior phylogenetic hypothesis with which it is ‘congruent’. Instead, in strict adherence to RTE, it requires the abduction of a new phylogenetic hypothesis as a possible explanation for this broader set of character data.

The ‘myth of characters as tests’ thesis directly hinders the design of independent and severe tests *sensu* Popper (1957, 1968, 1971; Fitzhugh 2006a: 80, 84, 85). Independence refers to the necessity of seeking results that are deducible from the hypothesis, if it is true, but which belong to a different class than the facts that led to the abduction of the hypothesis; otherwise, it constitutes circular reasoning with no contrastive value. The main problem is that what is commonly considered contrastive evidence cannot meet the Popperian requirement of independence. As a simple example, suppose that a phylogeny (hypothesis) is generated to explain the wing characters of a butterfly. To test the monophyly hypotheses of that phylogeny, other wing characters not used to generate the initial phylogeny cannot be employed, since they are not independent from those used to generate it. Likewise, characters from the head or thorax, or molecular characters, cannot be used either, because none of these are independent from the original wing characters. In this way, no amount of character data can test phylogenetic hypotheses, parsimonious or otherwise, but only generate them.

Maximum likelihood and bayesianism. The basic idea proposed by Sober (1988: 102–106, 109, 111; 1989, 1994: 129, 139, 152; 2000: 184; 2008: 33; 2015) is that parsimony must be subordinated to maximum likelihood: the preference for more parsimonious explanatory hypotheses (*i.e.,* maximally homogenetic) is justified only when they are also more likely compared to alternative hypotheses; namely, when the observed correlations are less probable as products of independent causes (*i.e.,* due to homoplasy). Refinements of his probabilistic approaches, developed over decades of addressing the issue, arise from the complications in calculating, filtering, and comparing likelihood factors among phylogenetic hypotheses. Furthermore, the likelihood of a hypothesis must be weighed together with other relevant factors, *e.g.,* prior probabilities or ‘nuisance’ parameters. For this reason, Sober has developed and defended versions of Bayes’ Theorem as one of the best available —but not definitive— strategies for comparative evaluation of alternative hypotheses. The following subsections address the overarching ideas behind Sober’s proposal, followed by Fitzhugh’s arguments against them.

Phylogenetic maximum likelihood. The likelihood (l) of a hypothesis (H), given certain evidence (E), is the probability (p) that the evidence (E) occurs given the hypothesis (H):

$l(\mathrm{H} \mid \mathrm{E}) = p(\mathrm{E} \mid \mathrm{H})$

The likelihood of H *given* E *is the probability of* E *given* H.

i.e., the likelihood $l(\mathrm{H} \mid \mathrm{E})$ is the inverse of the conditional probability $p(\mathrm{H} \mid \mathrm{E})$; generally, $p(\mathrm{E} \mid \mathrm{H}) \neq p(\mathrm{H} \mid \mathrm{E})$. When calculating $p(\mathrm{H} \mid \mathrm{E})$, parameters (input) are known and the goal is to predict outcomes (output), *i.e.,* it is predictive. When calculating the likelihood $l(\mathrm{H} \mid \mathrm{E}) = p(\mathrm{E} \mid \mathrm{H})$, outcomes (output) are known and the goal is to find their parameters (input), *i.e.,* it is explanatory. According to Fitzhugh’s Peircean model (2006a: 53, 65), phylogenetic hypotheses, as abductive arguments, have the following basic structure:

Rule:	**Causal theory**	TDM
Result:	**Homologues**	Data matrix
Case:	**Homogeny / Homoplasy**	Cladogram

As such, parsimony is reduced to the question of the degree of coverage of a causal theory, taken as a *Rule*, in explaining a set of observed phenomena, taken as *Results*, through a hypothesis, taken as *Case*. Since likelihood is the probability of a *Result* (Data matrix) given the *Case* (Cladogram), it does not involve TDM as a *Rule* or explicit causal theory but rather probabilistic criteria for fitting possible cladograms to the data matrix. This latter point is crucial to understand how the subsumption of PAR to maximum likelihood constitutes a proposal for independent justification, not a circular argument. Sober’s strategy relies on the ability to assign likelihood values to cladograms without resorting to TDM, to justify the choice of a parsimonious hypothesis, provided it is also the most likely one.

According to Fitzhugh (2006a: 72, 76, 77), phylogenetic parsimony refers to maximizing the coverage of the causal theory in explaining the data taken as a whole, *i.e.,* TDM (mod RTE) as defined here. Fitzhugh’s main point is that if TDM, as a *Rule*, is applied maximally by being parsimonious, it is because the relation between hypothesis (H) and evidence (E) is assumed to be causal, *i.e.,* $\mathrm{H} \rightarrow \mathrm{E}$. But if this happens, then the probability that E occurs given H is certain, which maximizes its likelihood: $l(\mathrm{H|E}) = p(\mathrm{E|H}) = 1$. Thus: "parsimony and likelihood go hand in hand — a hypothesis that is most parsimonious will also be of greatest likelihood. The only form of optimization that is possible in phylogenetic inference is that of parsimony" (Fitzhugh 2006a: 78). Albeit Fitzhugh's argument seems valid, it wouldn't be sound if we, as Sober, seek an independent justification for the application of TDM, versus taking it as a *Rule*, axiom or 'auxiliary principle' and applying it based only on an indispensability argument like Hennig's.

Phylogenetic Bayesianism. An important corollary of the Principle of Simple Conditionalization, *Bayes' Theorem* is a formula that allows for dynamic adaptive measurement of probability. Bayesianism incorporates relevant contingent information as initial probabilities or *priors*, to calculate the posterior probability of a hypothesis when adding new data. In principle, it seems reasonable and promising to apply the theorem for the generation or testing of phylogenetic hypotheses. Based on Fitzhugh (2006a: 96), the application of Bayes' Theorem in phylogenetic systematics, in its most schematic and general form, would be through the following formula:

$$p(\mathrm{H} \mid \mathrm{E}) = \frac{p\,(\mathrm{E} \mid \mathrm{H}) \bullet p(\mathrm{H})}{p(\mathrm{E})}$$

E = evidence (data matrix)
H = hypothesis (cladogram)
$p(\mathrm{E} \mid \mathrm{H})$ = likelihood
$p(\mathrm{H})$ = *prior* probability of H
$p(\mathrm{E})$ = probability of E (*total probability*)

Versions of this formula are implemented in computational programs —*e.g.,* MrBayes— where cladograms H are constructed from random attempts or according to imposed evolutionary models, searching for the one that maximizes the likelihood $p(\mathrm{E}□\mathrm{H})$ given a data matrix E. Fitzhugh's (2006a: 97, 100, 101) critique against this implementation is based on three main points: i) probabilistic and statistical methods, including maximum likelihood and Bayesianism, are inductive inferences *sensu stricto*, making them logically irrelevant in the abductive production of phylogenetic hypotheses; ii) consequently, there is a lack of justification —or even sense— in the assignment of probabilities $p(\mathrm{H})$ and $p(\mathrm{E})$ for the production of phylogenetic hypotheses; iii) when attempting to implement Bayes' theorem in the testing of phylogenetic hypotheses, more character data is typically used as 'new contrasting evidence', overlooking its inability to fulfill that role. From this, Fitzhugh concludes, against Sober, the inadequacy of Bayes' theorem in the generation or testing of phylogenetic hypotheses, understood as explanatory abductions *sensu* Peirce.

Despite Fitzhugh's critique, parsimonious and Bayesian trees consistently remain highly compatible or even indistinguishable. So, the question arises: what is the reason for such agreement? It could be assumed that one reason for the congruence is the truthfulness of the hypothesis. However, even though both methods aim to explain the same observations, *e.g.*, homologous characters, the parsimonious criterion of hypothesis selection requires TDM as a causal theory, while the probabilistic criterion applies as theory an —often *ad hoc* (Suárez-Díaz & Anaya-Muñoz: 469)— evolutionary model. So, unless the Bayesian tree is somehow restated in terms of TDM, it does not constitute a phylogenetic hypothesis *sensu stricto*, rendering the congruence or not between Bayesian and Parsimony trees irrelevant.

Evidence of monophyly beyond similarity. Thus far, PAR *sensu* TDM (mod RTE) does not appear to have a convincing independent epistemological justification, not only *a priori* but also *a posteriori,* through empirical evidence in its favor. Different lines of evidence are required, beyond the similarity of homologous characters, both to test phylogenetic hypotheses rigorously and to justify the monophyletic explanation of synapomorphies in their production.

Gradualism, triple(s) parallelism(s), and character polarization. Sober (2008: 314–332) has explored and discussed alternative pathways to homologous character similarity as potential evidence of monophyly; namely, convergent hypotheses, the fossil record, and biogeography.

The first pathway, concerning convergent hypotheses, can be dismissed for two reasons:

i) This practice falls under the scope of the critique of the 'myth of characters as tests' and against 'taxonomic congruence' of 'partitioned' analysis, *e.g.,* in the production of consensus trees and supertrees. As argued by Fitzhugh (2006a: 68, 2006c: 340–342), no phylogenetic hypothesis can serve as evidence to 'support' or reject another: "Since these hypotheses are independent of one another, per the fact that they serve to causally account for distinct sets of effects."

ii) According to Sober (2008: 315), the question about choosing between parsimonious hypotheses differs from the question about preferring parsimonious hypotheses *simpliciter*, *i.e.,* justifying PAR.

The second pathway, the fossil record, is based on the idea that if we assume evolutionary change occurs gradually enough, and species X and Y share a common ancestor, then intermediate forms or 'intergrades' must have existed between them and can be searched for in the fossil record. Sober (2008: 319, 320, 323, 324) calls this the 'assumption of gradualism' and defends it through a quasi-Humean naturalized rethoric: "What more stunning evidence could there be that the extant species X and Y stem from a common ancestor? The human eye finds it irresistible to connect the dots" (Sober 2008: 24).

The assumption of gradualism extends to biogeography as a third evidential pathway: the fact that species X and Y live in the same region provides evidence for their common ancestry. More generally, if X and Y live in separate regions, the existence of phenotypic intergrades inhabiting an intermediate region is evidence for their common origin, *i.e.,* gradual geographic distribution is to space what fossils are to time. Sober (2008: 324, 326, 327), aware of the parallelism proposed by Darwin (1859), calls this the *Darwinian principle* of *space-time*, which he reformulates in terms of a phylogenetic relationship, irreducibly ternary, as follows (ST):

ST: *If* X, Y, *and* Z *are living or fossil organisms, and the true genealogical grouping is* (XY)Z, *then it is likely that* ***X*** *and* Y *will be geographically and temporally closer to each other than either is to* Z.

This principle of correlation between (tacit) form, space, and time is not exclusive to Darwin or an evolutionary framework, *e.g*., it is akin to Aggassiz's (1857) three-fold *parallelism*, which differs from the later sense of 'parallelism' as a kind of homoplasy (independent 'parallel' development of an identical character state from the same ancestral state). According to historical-philosophical studies on the subject (Gould 1977; Winsor 1979; Bryant 1995; Wilkins 2009; Richards 2010; Rieppel 2016), a brief chronology of theories about *parallelisms* as strong observational correlations, leading to Hennig's notion of *reciprocal illumination*, can be summarized as follows:

i) *Meckel-Serres Law* (Meckel 1821, Serres 1860; see also Gould 1977: 37, 46). Embryonic stages of complex organisms correspond to mature adults of less complex organisms. It is based on the medieval idea inherited from the *scala naturae* or 'Great Chain of Being', which sequentially orders all things from the simplest to the most complex (Lovejoy 1936; see also Wilkins 2009: 51). It forms a linear hierarchy (*i.e.,* a partial, trichotomic ordering relationship; see Amor-Montaño 2011: 21). It is a morphological and morphogenetic parallelism.

ii) *Agassiz's Three-fold Parallelism* (1857): The correlation between morphological distribution, morphogenetic development, and the fossil record of organisms reveals the creative plan of God and grounds taxonomy in objectivity and naturalness. The embryonic stages of complex living organisms correspond to the mature stages of simpler extinct organisms. It is based on Cuvier's theory (1829; see also Agassiz 1857: 26–28, 30, 141, 159, 160, 169) of four *embranchements* (branches) within the animal kingdom, typified by the structural distinction and topological irreducibility between their body plans. It forms several linear hierarchies between organisms of each type or embranchment. It is a morphological, morphogenetic, and paleontological parallelism.

iii) *Darwin's Space-Time Principle* (1859): Organisms that are closer in genealogical origin tend to be more similar in morphology and embryonic development stages, as well as being closer in the fossil record (time) and geographic distribution (space). It is based on: i) Principle of Divergence (*i.e.,* the most divergent members or varieties of each group are preserved, as they face less competition in the natural economy of the region they inhabit, unlike intermediate forms, which go extinct); ii) Theory of Natural Selection of varieties as the main —though not exclusive— speciation mechanism, with an important factor of geographic isolation contributing to reproductive isolation. It forms a branching hierarchy or 'Tree of Life': a partial order among nested groups, more or less inclusive of one another based on their degree of common ancestry. It is a morphological, morphogenetic, paleontological, biogeographical, and phylogenetic parallelism.

iv) *Haeckel's Biogenetic Law* (1866): Ontogeny is a brief 'recapitulation' of phylogeny, *i.e.,* embryonic stages of living organisms correspond to embryonic stages of their extinct ancestor, whose mature adults might be found in the fossil record. It is based on: i) Principles of heterochrony (*i.e.,* different developmental rhythms) and heterotopy (*i.e.,* different morphological spatial positions) operating during embryonic development; ii) von Baer's (1828) differentiation theory (Rieppel 2016: 47, 51), *i.e.,* embryonic stages of less complex organisms correspond to those of more complex organisms, which then differentiate during the rest of their development, so less general characters develop from more general ones; iii) Darwin's principle of divergence and natural selection; iv) Principle of progression *sensu lato*, *i.e.,* natural selection leads to a morphological 'progression' from the simplest to the most complex; v) Agassiz's triple parallelism, but taken as *consilient* evidence of descent with modification. It forms linear ancestor-descendant hierarchies, as branches within the general hierarchy of the 'Tree of Life' (partial order). It is a morphological, morphogenetic, paleontological, and phylogenetic parallelism.

v) *Hennig's Reciprocal Illumination* (1966; see also Mooi & Gill 2016): Various morphological, ecological, physiological, geographical, and developmental (*i.e.,* ontogenetic) similarities, taken as parts, 'reflect' and serve to 'disclose' or 'check' the overall structure of the phylogenetic system, taken as a whole; whose hypotheses of common descent, in turn, throw light back onto finer-grained studies of said parts. It forms a cladogram, *i.e.,* a strictly dichotomically-branching 'Tree of life' (special partial order). It is a morphological, morphogenetic, biogeographical, ecological and —holistically— phylogenetic parallelism.

Bryant (1995) presents and discusses the existence of a metaparallelism between the 'triple parallelisms' (form, space, and time) of Agassiz, Haeckel, and the three admissible methods of character polarization in phylogenetic systematics according to de Queiroz (1985):

i) External group method (M-Ex): The morphology of the external group provides relative plesiomorphic characters.

ii) Ontogenetic method (M-Ont): The broadest distribution of characters, in comparative ontogenetic studies, provides relative plesiomorphic characters. It should not be confused with the *ontogenetic criterion of character precedence*, or ontogenetic 'recapitulation' (Hennig 1966: 95, 96), where characters that appear earlier in ontogeny are considered relatively plesiomorphic.

iii) Paleontological method (M-Pal): The morphology of fossils found lower in the stratigraphic record provides relative plesiomorphic characters.

M-Ont is simply an extension of M-Ex for immature semaphoronts. The successful application of M-Pal presupposes a strict linear order (*i.e.,* no reversals) and the absence of phylogenetic heterochrony, which heterobathmy often proves not to be the case. Hennig (1966: 95–101; see also Schmitt 2014: 47–62) proposed additional criteria to the three previous ones in the polarization of characters, such as the chorological criterion (*i.e.,* the geographically farthest species, or one with a different ecological niche, provides the relative apomorphic characters) and special criteria for correlation with already polarized characters.

The most important point to highlight here is that, although a theoretical framework is necessary and its choice changes the possible explanations of parallelisms (Bryant 1995: 197, 201, 214), these remain intertheoretically as observational data correlating form, space, and time. From an evolutionary perspective, it can be observed that the assumption of gradualism, or the existence of intergrades, is indispensable in applying these criteria and in searching for parallels between them. In Darwin's seminal work (1859), the assumption of gradualism performs two conceptual tasks:

i) *Conceptual transformation of sequences into hypothetical trends:* Sufficient observational evidence of gradualism is required, whether in characters (form), the fossil record (time), or geographical distribution (space), so their ordered display in a series can be interpreted as phases of a process (Darwin 1859: 57). In particular, sufficient gradualism within an ordered sequence of forms suggests the hypothesis of a generative process or trend amongst them. This idea is crucial for the conceptual shift from characters to polarizable states of one same character (transformational homologues).

ii) *Ensuring the operability of the Principle of Divergence in speciation:* It is necessary to ensure the existence of sufficient intraspecific morphological gradualism to guarantee the production of new species as divergent and selected limits within that variation, whose intermediates become extinct. The principle of divergence, then, operates through two mechanisms in natural selection: positive, in the preservation of varieties better adapted to divergent conditions; negative, in the elimination of varieties that are less divergent, among which competition in the natural economy is larger (Darwin 1859: 358–360).

The intertheoretical persistence of triple parallelisms —form, space, and time— framed by the assumption of gradualism, along with their key applications within a processual explanatory framework (*i.e.,* inference of common cause among parallelisms and inference of character states), warrants serious consideration as an independent justification for the application of PAR *sensu* TDM (mod RTE), in the monophyletic explanation of synapomorphies *sensu lato*.

Goethe's 'Genetic Method' and Character Polarization. The idea that observing a gradual sequence leads to the inference of a process, even when restricted to the context of transformations between living forms, is not an unprecedented proposal of Darwin or his evolutionary conception. Johann W. von Goethe is less known for his scientific work than for his literary and artistic contributions; however, as a natural philosopher, he was a penetrating theorist and rigorous experimental researcher, who proposed a phenomenological theory of color that surpassed Newton's in several aspects (Goethe 1840; see also Bortoft 1996). Crucially, he was the foundational reference for both German idealistic morphology and early phylogenetic theory; according to Rieppel (2016: xvii, 22): "Haeckel was a fervent devotee of the German culture icon Johann Wolfgang von Goethe (1749–1832), whom he considered to be a predecessor of Darwin [...] Haeckel introduced [his *Generelle Morphologie*] with a quote from Goethe that placated German Idealism [and] Goethe continues to accompany the reader throughout the text."

Goethe introduced the term 'morphology' as the foundation of science in general, and as a theory of form (*Gestalt*), formation (*Bildung*), and transformation (*Unbildung*) of organic bodies particularly (Steigerwald 2002: 295). According to Miller (1988; see also Goethe 2009: 105–112), *ca.* 1790 Goethe applied in his studies on the 'metamorphosis' (*Metamorphose*) of plants what he called the 'genetic method' (Miller 1988: 75; *Genetische Behandlung* in Bednarczyk 2012: 28), or in its more descriptive version, the "method of the unfolding of development" (*entwickelnde entfaltende Methode* in Bednarczyk 2012: 33). This 'genetic' method consists of seeking the origin or 'genesis' and transformative laws of something, through careful observation of its varieties arranged in sequential ordered manner, *e.g.,* variation in leaves and other parts in search of the 'elemental plant' (*Urpflanze*) that allows for inferring the laws of possible transformations between plant forms.

The genetic method does not constitute a study of organismic development or *Ontogenie sensu* Haeckel (1866), *i.e.,* individual *Morphogenie* (also *ontogeny sensu* Hennig

1965, 1966); rather, it is morphogeny *sensu lato*, *i.e.,* a study of comparative morphology among concrete organisms, aimed at obtaining their laws of generation and transformation. Idealist morphology interpreted Goethe's 'elementary phenomena' (*Urphänomene*) as archetypes *sensu* Owen (1848). Haeckelian Phylogeny (collective *Morphogenie*) interpreted the archetype as an ancestral form; Hennigian phylogenetics associates morphogenetic processes with common ancestry, by linking the production of apomorphies with hypothetical speciation events through TDM. The study of morphological sequences, along with their conceptual transformation into morphogenetic trends, precedes their phylogenetic interpretation, both historically and inferentially, which requires them in advance. Thus, ordering and polarization of characters —through a morphogenetic theory or another auxiliary method— are prior and necessary conditions for inferring phylogenetic relationships *sensu* Hennig (1965, 1966).

Serial arrangement of characters is necessary but not sufficient for their polarization: on many occasions, the same transformative process can be coherently conceived in both directions. Regarding reversals, Mooi & Gill (2016: 276–277) explain that: "Hennig did not consider reversals to be synapomorphies, but instead, [...] they were neutral [...] Information about relationships comes instead from characters that could be considered synapomorphic *a priori*." The polarization criteria suggested by Hennig and others can be understood as analogical arguments *sensu* Hesse (1966: 58–72): non-polarized sequences are compared with another class of objects that is already polarized or polarizable, so that their parallelisms allow the inference of a common order to the whole, explainable by TDM. Thus, important factors for good polarization, as part of the genetic method in general, are: i) analogical effectiveness through parallel correlation, by rephrasing the polarization problem in contexts where it is less problematic and inheriting its solutions; ii) the ability to explain parallelisms through a common cause, by subsuming groups of regularities under a more general rule, *i.e.,* performing a *consilience* of inductions.

Principle of Inductive Consilience (PIC). Consilience of Inductions (CI) refers to the subsumption of ideas under a more general one (Whewell 1984; Richards 2010: 124–131), *e.g.,* the idea of universal gravitation unifies planetary motion, free falling in the sublunar world, and the phenomenon of tides. By analogy with logical jargon concerning first, second or higher-order logics, it can be proposed that consilience of inductions *sensu lato* (CI) constitutes a higher-order induction.

CI: *Higher-order induction applied to lower-order inductions.*

CI is achieved through 'colligation of facts' and 'explication of conceptions'. The former refers to first-order induction, which links observational facts about things through ideas. Second-order induction occurs in the later, which coincides with 'explication' *sensu* Carnap (1950), *i.e.,* producing a clearer concept that can serve as a definition within a scientific theory. Whewell proposed CI as a test for the 'truth' of a scientific theory, *i.e*., an epistemic virtue that justifies preferring it on alethic value.

The work of Whewell (1840), which preceded Darwin's (1859) by nearly 20 years, had a decisive influence on him and subsequent authors dealing with common descent and character polarization. During a resurgence of idealist morphology, Tschulok (1910; see also Rieppel 2016: 89–92) initially adopted a typological idea of unity in variety (*unité dans la verité*) as a classificatory foundation. However, he changed his position considering the overwhelming evidence for common descent through CI. This shift occurred when it was conceived as the only 'comprehensible' explanation for: i) the observable morphological gradualism in typological classification; and ii) the triple parallelism among ontogeny, the fossil record, and biogeography. In this context, 'comprehension' refers to the consilience among these classes of phenomena, initially unrelated but linked and explained together by common descent. As a result of these reconsiderations, Tschulok proposed what later became known as the 'principle of generality' in character polarization, *i.e.,* the most broadly distributed form, in comparative morphology studies, provides the relatively plesiomorphic characters (Rieppel 2016: 89–92).

From the above, the epistemological value of CI emerges as an independent criterion for preferring unificationist scientific hypotheses or theories, as they provide a single explanation —and surprising predictions— for classes of initially disparate phenomena. The resulting unified hypothesis or theory must have at least the same degree of empirical adequacy as the respective theories or hypotheses of its linked classes of phenomena; moreover, it must preserve and explain intertheoretical parallels among phenomena from these classes. Therefore, the successful application of CI must include a *ceteris paribus* clause of overall empirical adequacy. This can be termed the *Principle of Inductive Consilience* (PIC):

PIC: *ceteris paribus, the most consilient theory or hypothesis is preferred.*

Thus, PIC is introduced as an intertheoretical criterion to justify the preference for scientific hypotheses or theories based on a maximal application of PCC, insofar as they can explicate parallelisms through a common cause. In this way, fulfilling PIC constitutes sufficient justification for applying the principle of parsimony, PAR *sensu* Pa; in logical terms: PIC → PAR. In fact, within the context of phylogenetic systematics, PIC is a more demanding requirement than the application of TDM (mod RTE). Applying TDM (mod RTE) requires only data from a single-character system. Applying PIC, however, demands the production of a more comprehensive parsimonious phylogenetic hypothesis, that jointly explains data from multiple character systems and other relevant evidence (*e.g.,* fossil record or biogeography). Thus, fulfilling PIC in the context of phylogenetic systematics is sufficient to fulfill TDM (mod RTE) (which, in turn, is necessary for it); in logical terms: PIC → TDM (mod RTE).

In this way, an independent and sufficient —not necessary!— epistemological criterion for the application of TDM (mod RTE) is obtained, *i.e.*, fulfilling PIC justifies both logically and epistemologically the application of the principle of parsimony (PAR) in phylogenetic systematics. In the following section, an even stronger version of PIC is proposed.

***Principle of Triple Consilience with Intergrades* (3PCI).** Throughout the preceding sections, the following points were outlined:

i) The historical and contemporary existence of intertheoretical parallelism between form, space, and time, which have been part of the justification for naturalness, objectivity or truth in pre- and post-evolutionary systematics.

ii) The importance of these parallels and their evolutionary interpretation in the application and discussion of character polarization strategies in phylogenetic systematics.

iii) The importance of the assumption of gradualism, or the existence of sufficient intergrades, in the inference of explanatory processes and polarization criteria.

iv) The central importance of consilience as an epistemic virtue, guiding the preferential choice of theories and hypotheses that maximize coverage of common-cause explanations.

v) The sufficiency of consilience as a justification for phylogenetic parsimony.

Based on this analysis, the concept of *Triple Consilience with Intergrades* (3CI) and the *Principle of Triple Consilience with Intergrades* (3PCI) are proposed as epistemic virtues in the selection of scientific hypotheses and theories in general, as well as in the production of phylogenetic hypotheses and character polarization particularly (whenever the phylogenetic hypothesis or polarization is derived from gradual correlations in form, time and space):

3CI: *If* X *and* Y *are such that:*

i) They exhibit a high degree of correlation in form, space, and time.

ii) There are intergrades Z *such that* X < Z < Y *in those three aspects.*

Then it is highly probable that the correlated aspects of X *and* Y *are due to a common cause.*

3PCI: *ceteris paribus, the theory or hypothesis most consilient sensu* 3CI *is preferred.*

In the antecedent of 3CI, (i) is the condition of triple parallelism and (ii) is the condition of gradualism; the consequent is the abductive inference of a common cause through consilience. The wording is ontologically agnostic *ex profeso*, aside from the requirement that X and Y be individual entities or processes *sensu* Ghiselin (1969, 1997). For this, they must possess concreteness (*i.e.,* finitude and spatiotemporal localization), internal continuity (*i.e.,* integration and cohesion between their inner parts), and the capacity to participate in causal processes.

Based on these results, the conclusion on the controversy explored is that 3PCI seems the most demanding affordable epistemological criterion for the maximal application of PCC, thus an independent and sufficient justification for the application of the principle of parsimony (PAR) in phylogenetic systematics, *i.e.,* 3PCI → TDM (mod RTE). In a later work, Fitzhugh (2012: 55) criticizes appealing to Whewellian consilience to justify using topological congruence between 'disjunct' cladograms (*i.e.,* inferred from partitioned character data) as test evidence for an overall phylogeny. The usage of consilience advocated in this section falls out of the scope of that critique, since 3PCI is not proposed as a strategy to inductively test a phylogenetic hypothesis at all, but to independently justify its abductive inference as a parsimonious explanation.

As presented, 3PCI serves as an independent justification for Hennig's auxiliary principle, which indeed is "just a restatement of [...] the parsimony principle" (Wiley & Lieberman 2011: 118), albeit restricted to apomorphous characters (Mooi & Gill 2016: 264). Also, 3PCI is operational in half of Hennig's reciprocal illumination method, about considering consilient disparate empirical data as a good reason to infer monophyly. According to Rieppel (2016: 29, 30), in the context of the evolutionary turn in idealistic morphology: "homology is supposed to indicate phylogenetic relationship and not the other way around. What Gegenbaur really wanted to say is that homology and ancestry stand in a relation of reciprocal illumination, subject again to the consilience of evidence." Consilience *sensu* 3PCI agrees with this; however, it is decoupled from testing purposes entirely, about taking consilient empirical data as positive contrastive evidence for a given hypothesis. Thus, 3PCI also falls out of reciprocal illumination's charge of circularity in the context of hypothesis testing.

Extended parsimony model (PAR+): summary and logical relations. As a result of these explications, the definition of the *Extended Parsimony Model* (PAR+) is proposed, understood as the set of explicated definitions, principles and their mutual logical relations (Fig. 2):

PAR+: *Parsimony through gradualism, triple parallelism and consilience.*

In the following section, an example of the application of PAR+ will be shown, highlighting the importance of morphogeny in overall consilience and bridging morphology with phylogeny.

CASE STUDY: EXOCHORIONIC MORPHOGENY APPLIED TO PHYLOGENETIC SYSTEMATICS OF PIERIDAE

Exochorion as a character system in Papilionoidea.

Extended Parsimony Model (PAR+)

Parsimony through Gradualism, Triple Parallelism, and Consilience

ceteris paribus: *"all else being equal"*
(empirical adequacy clause)

- **TDM** ***Theory of Descent with Modification***
  If character α existed among members of an ancestral species h, which was an effect of an earlier speciation event, and this character was subsequently replaced during tokogeny by character β among members of h, and h later underwent speciation, then members of the descendant species would exhibit character β.
- **Pa** ***Parsimony sensu lato***
  The most parsimonious theory or hypothesis is the one that minimizes the number of entities or processes required to fulfill its explanatory function.
- **PAR** ***Principle of Parsimony***
  ceteris paribus, the more parsimonious theory or hypothesis is preferred.
- **PaC** ***Cladistic Parsimony***
  The most parsimonious phylogenetic hypothesis is the one that minimizes the number of evolutionary changes required to explain the observed characters altogether.
- **PaC1** ***Cladistic Parsimony* 1**
  The most parsimonious phylogenetic hypothesis is the one that minimizes the number of homoplasies required to explain the observed characters altogether.
- **PAC1'** ***Cladistic Parsimony* 1'**
  The most parsimonious phylogenetic hypothesis is the one that maximizes the number of homogenies required to explain the observed characters altogether.
- **PaC2** ***Cladistic Parsimony 2***
  Only synapomorphies, not symplesiomorphies, are evidence of phylogenetic relationships between groups (i.e., of monophyly).
- **PU** ***Principle of Uniformity of Nature***
  Nature is uniform, i.e., homogeneous in space and time.
- **PI** ***Principle of Induction sensu lato***
  What has not yet been observed will be like what has already been observed of the same kind.
- **PCC** ***Principle of Common Cause***
  If X *and* Y *are correlated, then* X *is the cause of* Y, Y *is the cause of* X, *or both share a common cause.*
- **RTE** ***Requirement of Total Evidence***
  All available relevant evidence must be considered in conjunction when producing an explanatory hypothesis.
- **TDM (mod RTE)** ***TDM module RTE***
  Maximal application of TDM *subject to* RTE.
- **CI** ***Consilience of Inductions sensu lato***
  Higher-order induction applied to lower-order inductions.
- **PIC** ***Principle of Inductive Consilience***
  ceteris paribus, the most consilient theory or hypothesis is preferred.
- **3CI** ***Triple Consilience with Intergrades***
  If X *and* Y *are such that:*
  i) They exhibit a high degree of correlation in form, space, and time.
  ii) There are intergrades Z *such that* X< Z < Y *in those three aspects.*
  Then it is highly probable that the correlated aspects of X *and* Y *are due to a common cause.*
- **3PCI** ***Principle of Triple Consilience with Intergrades***
  ceteris paribus, the theory or hypothesis most consilient sensu 3CI *is preferred*

LOGICAL RELATIONS

PI → PU → Pa
PaC → Pa
PaC1' ↔ PaC1 ↔ PaC → PaC2
3PCI → PIC → TDM (mod RTE) → PAR → PCC

Figure 2. Extended Parsimony Model (PAR+) summary and logical relations.

Butterfly eggs consist of five basic components: chorion, serosa layer, vitelline membrane, cytoplasm, and nucleus (Hernández-Mejía *et al*. 2013). The surface of the egg, referred to as 'shell' or 'chorion' in insects, can be considered a composite structure formed by molecularly complex layers and sublayers (Rezende *et al*. 2016). These layers and their configurations provide protection during larval development, although some also perform other functions, *e.g.*, gas exchange ('plastron' *sensu* Hinton 1981). The chorion is divided into 'endochorion' and 'exochorion'; both contain amino acids in a tripartite secondary structure composed of more than 100 distinct polypeptides (Telfer 2009), precursors of a complex extracellular matrix composed of over 400 proteins in Lepidoptera (Giannopoulos *et al.* 2013). Endochorion and exochorion differ in that the latter includes carbohydrates intertwined within (Richards & Davies 1977, Trougakos & Margaritis 2008). The arrangements of proteins and carbohydrates in the exochorion form reticular microstructures of great variation, but with sufficient regularity at species and supra-specific levels.

Since the late 19th Century, the exochorion has been seriously considered as a character system (Flores-Gallardo *et al*. 2023); however, only in recent years has its utility in phylogenetic systematics of Lepidoptera been reassessed. Llorente-Bousquets (1980, 1984) presented a comprehensive taxonomy of Mexican Dismorphiinae, examining wing characters, male genitalia, geographical distribution, and oocytic traits. The author and colleagues continued studying exochorionic characters in subsequent years, progressively refining staining and imaging techniques, as well as conceptualization and terminology proposals (Llorente-Bousquets & Castro-Gerardino 2007; Hernández-Mejía *et al.* 2013, 2014a,b, 2015; Nieves-Uribe *et al.* 2015, 2016a,b,c,d, 2017a,b, 2018a,b, 2019a,b, 2020a,b, 2021a,b, 2022; Llorente-Bousquets *et al.* 2018, 2019; Campos-González *et al.* 2020; Rivera-Galicia *et al.* 2020; Flores-Gallardo *et al*. 2021, 2022, 2023).

Exochorionic research is part of the holomorphological studies (*sensu* Hennig 1965, 1966) in phylogenetic systematics of Lepidoptera. The caterpillar, chrysalis, or adult butterfly (imago) can serve as semaphoronts, as can the egg. However, the ideas of Llorente-Bousquets and colleagues regarding the semaphoront under study have changed over time. Currently, the authors consider exochorionic characters to be part of the female imago, viewing the chorion as a complementary trait of her reproductive system, *i.e.,* not as part of the embryo it encloses but as a transitional character of the mature state or imago. This character is produced and regulated exclusively by female genes, not by those of the male or the embryo (Telfer 2009, Rezende *et al.* 2016). Nevertheless, this conceptualization of the chorion has yet to become standard practice in insect morphological systematics, where it is typically regarded as part of the egg and thus part of the study of immature stages (Flores-Gallardo *et al.* 2021).

Example of application of PAR+: Klots hypothesis (hK). Alexander B. Klots (1931–1933) provided a comprehensive pre-Hennigian study of the Pieridae family, based on detailed morphological descriptions of multiple characters present in both males and females (*e.g.,* wing shape, venation, and coloration; length and shape of antennae and palps). Klots complemented his study with descriptions and illustrations of male genitalia from species of various genera within the family. Through a comparative study of wing characters, Klots (1931–1933: 150, 214, 215) proposed the existence of two subgroups within the genus *Leptophobia*; however, as he did not find evidence of this division in genital characters, he did not consider them subgenera (Figs. 3, 4). In the following discussion, Klots hypothesis *sensu lato* (hK) refers to the existence of such subgenera as monophyletic subgroups:

hK: *Existence of two monophyletic subgroups in the genus Leptophobia, consistent with the division proposed by Klots (1931–1933).*

Hernández-Mejía *et al.* (2015: 363) revisited hK, introducing flight microhabitat as an additional criterion for subdivision within the genus, which can also be explained by hK. Klots hypothesis *sensu stricto* (hKss), based on wing morphology, constitutes a parallelism between two types of forms: short (V_1) vs. long (V_2) discocellular venation, and glossy (T_1) vs. matte (T_2) ventral texture. The proposal of Hernández-Mejía *et al*. (2015) adds an ethological, ecological, and ultimately spatial criterion based on the relationship between organisms and their environment: flight microhabitat in open areas (H_1) vs in the understory (H_2). Thus, the authors showed a parallelism between two aspects of form and one spatial aspect, explainable together by hK. This allows hypothesizing the division of *Leptophobia* into two monophyletic subgroups based on wing venation and texture, alongside flight microhabitats ($VTH_1 \mid VTH_2$).

That result brought hK closer to fulfilling the highly demanding requirements of 3PCI, for abducting a monophyletic hypothesis as a parsimonious explanation for these parallelisms. However, the main result defended by Hernández-Mejía *et al*. (2015: 363) was the proposal of a third morphological criterion, also explainable by hK, based on two subsystems of exochorionic characters in Pieridae: types of axes, short vs. long, and types of periapical projections, bulbs vs. bulges (Fig. 5). The distinction between axes is strict: long axes connect to the apex and shorts do not, as they are interrupted by ribs between the adjacent long axes. The main distinction between bulbs and bulges at the top of long axes, is that the former rise above and 'outward' the apex, while the later do not.

Exochorionic characters allowed dividing *Leptophobia* into two subgroups: species with short axes and bulbs (E_1) vs. without short axes and with bulges (E_2). This additional parallelism allows reformulating hK's abduction in terms of four evidential pathways, comprising three aspects of form and one spatial aspect, all consiliently explained by the monophyly of each subgroup ($VTHE_1 \mid VTHE_2$) (Fig. 6). If 'X' denotes a body of evidence explainable by hK, call 'Klots hypothesis module X' —hK (mod X)— to its corresponding version in the application of TDM (mod RTE):

hK (mod X) = Klots hypothesis (module X)

e.g., **hK (mod VTHE)** = Klots hypothesis (module $VTHE_1 \mid VTHE_2$)

In terms of 3CI and given the larger number of independent evidence routes considered in the abduction of hK (mod VTHE), this hypothesis is a better candidate for receiving a common cause explanation than the original Klots hypothesis, *i.e.,* hK (mod VT).

***Contributions of exochorionic characters to* hK (mod VTHE).** Klots did not consider subgenera of *Leptophobia* the subgroups delimited by wing characters, as he did not find consistent evidence for that division among male genital characters, considered of greater relevance. The inclusion of exochorionic characters can be seen as an amendment in this regard, if the exochorion is considered a system of characters, not of the semaphoront 'egg', but of the semaphoront 'female imago with mature eggs in her ovarioles'. This is an integral part of the proposal by

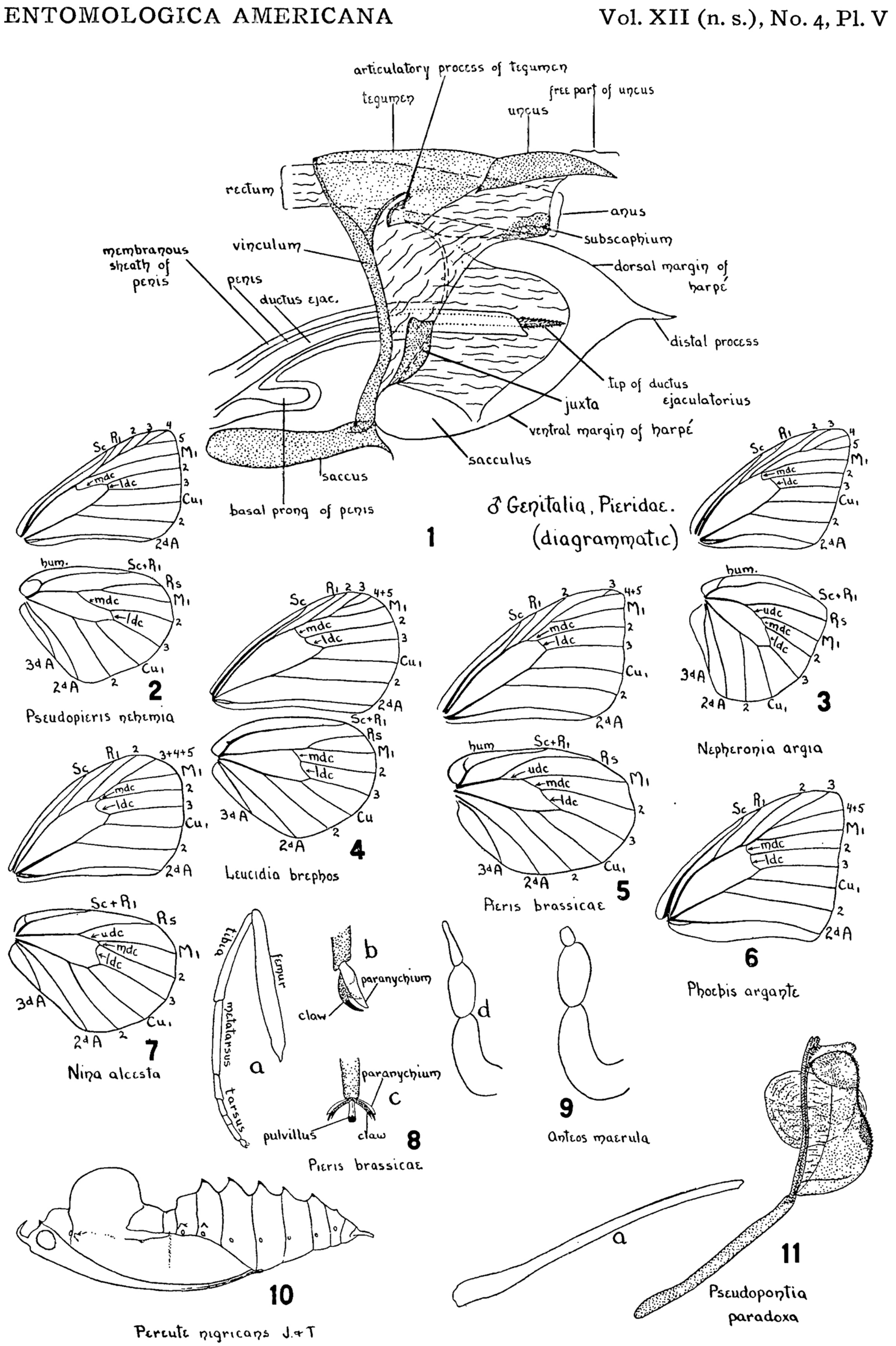


Figure 3. Diagrams of select morphological characters in species of the Pieridae family. These include generalized male genital morphology; types of wing shape and venation patterns; legs, palps, and examples of pupa and male genital capsule with its aedeagus. Taken from Klots (1931–1933: Plate V).

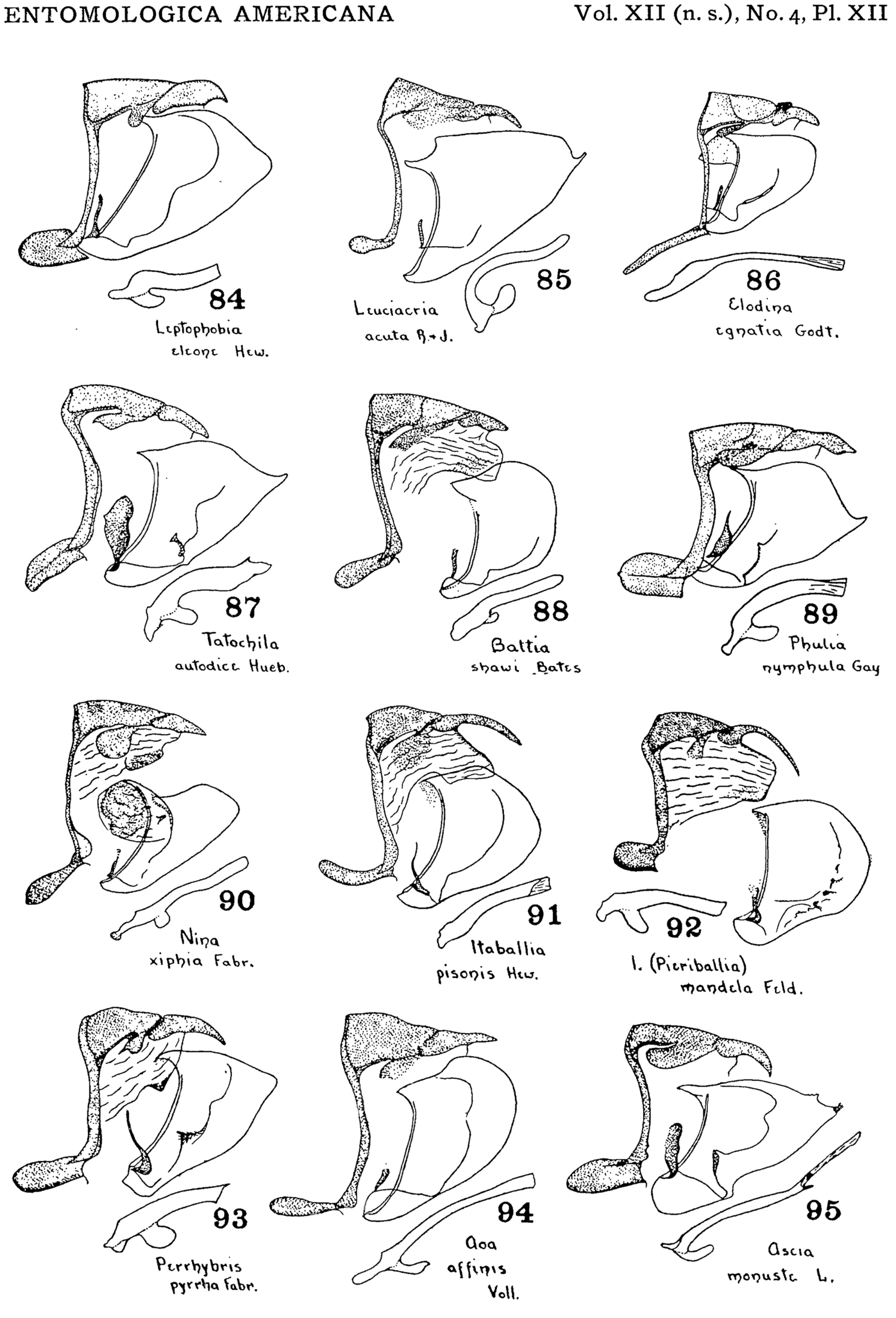


Figure 4. Diagrams of genital capsules and aedeagi of species belonging to various genera of the Pieridae family. The author proposed the existence of a subdivision of the genus *Leptophobia* based on wing characters; however, he could not corroborate it with genital characters, and therefore did not assign the resulting groups the rank of subgenera. Taken from Klots (1931–1933: Plate XII).

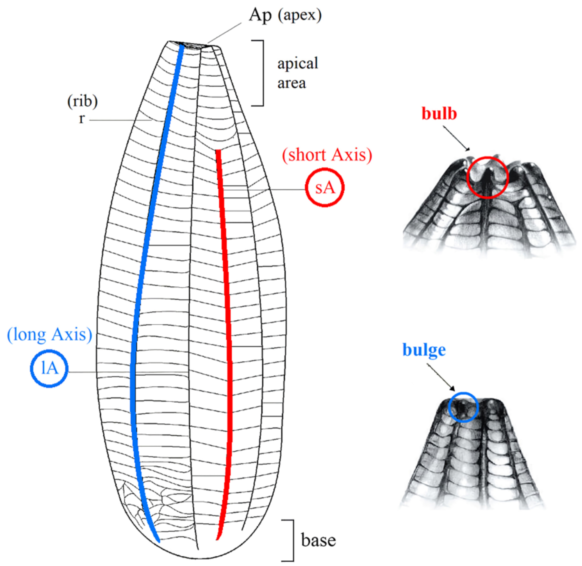


Figure 5. General diagrams of Pieridae eggs, with correlated characters (red and blue) used by the authors in the discussion of the Klots hypothesis. In *Leptophobia*, eggs with long axes ending in bulbs also have short axes, while eggs with only long axes ending in bulges do not. Modified from Hernández-Mejía *et al*. (2015: Figure 2).

Llorente-Bousquets and colleagues, within the framework of which the work by Hernández-Mejía *et al*. (2015) was conducted. Thus, insofar as (derived) female genital traits, exochorionic characters constitute a type of evidence closer to what Klots sought in the discussion and defense of hK.

An additional contribution emerges from the fact that the first formal-spatial parallelism, between wing characters and flight microhabitats, can be explained without recourse to a hypothesis of monophyly. This occurs because the presence of light and glossy wings in species that fly in open areas, versus the presence of dark and matte wings in species that fly in the understory (TH$_1$ | TH$_2$), can be explained in a 'functional' sense as per Díez & Moulines (1997: 261–264), which coincides with 'teleonomic' explanation *sensu* Mayr (1982: 11, 48, 88) and teleological explanation by 'final cause' according to Aristotle's etiology in *Physics* II ([*c.a.* 350 B.C.E] 1995a: 3 194b16–195a10), *Metaphysics* V 2 ([*c.a.* 350 B.C.E] 1994: 1013a26–34), and *Posterior Analytics* ([*c.a.* 350 B.C.E] 1995b: 98a1–8, b6–16) (see also Richards 2010: 26). In historical hindsight, characters explainable by any teleological-functional theory have constituted weak evidence for monophyly, since the same adaptive mechanisms can emerge independently under similar ecological pressures —*e.g.*, carcinization among decapods (Borradaile 1916, Keiler *et al*. 2017).

The functional explanation of the referred parallelism (TH$_1$ | TH$_2$) would be given by the same adaptive mechanism: butterflies' mimicry of their surroundings, driven by the need to go unnoticed by predators. Thus, wing textures and flight microhabitats could be considered aspects of the same (ecological) phenomenon, rather than two phenomena (morphological and ethological) linked and explained by consilience through a hypothesis of monophyly. On the other hand, the subdivision into two groups by exochorionic characters (E$_1$ | E$_2$) is not explained by mimicry; therefore, its correlation with the previous aspects (THE$_1$ | THE$_2$) and with wing venation types (VTHE$_1$ | VTHE$_2$) forms a clearer parallelism, which constitutes a stronger empirical basis in the abduction of monophyly for each group through hK (mod VTHE).

***Degree of adequacy of* hK (mod VTHE) *to* 3PCI.** Justifying the application of 3PCI in the abduction of an explanatory hypothesis by consilience involves showing the highest possible degree of adequacy with the antecedent of 3CI, *i.e.,* meeting the conditions of triple parallelism in form, space, and time, as well as the existence of intergrades in those three aspects. As shown, hK (mod VTHE) is based on four parallelisms: one spatial and three of form. For the sake of economy in the argument, exochorionic morphology was considered as a single additional aspect; however, the types of axes (short or long) and periapical projections (bulbs or bulges) can be considered separately, since they do not necessarily appear together among other Pieridae. This results in a total of five parallelisms: four of form and one of space.

In principle, hK (mod VTHE) does not include parallelisms in time or explicit gradualism of any aspect, *e.g.,* it does not consider intergrades between glossy (V$_1$) and matte (V$_2$) wings. The flight habits of some species in riparian vegetation (Hernández-Mejía *et al*. 2015: 363) could be considered an intergrade between flight habits in open sites (H$_1$) and in the understory (H$_2$). However, the most relevant intergrades were found among exochorionic characters, according to a later work by Nieves-Uribe *et al*. (2021b). Whereas distinction between long and short axes is strict, distinction between bulbs and bulges turned out to be gradual when reconceptualized, through a geometric model (Fig. 7), as stages in a continuous morphogenetic process of periapical differentiation in Pieridae.

Thus, *sensu stricto*, hK (mod VTHE) does not meet all the criteria required by the antecedent of 3CI to logically justify the inference of a consilient monophyletic hypothesis. However, 3PCI is a gradual criterion as it stipulates preference for the 'most consilient' theory or hypothesis according to 3CI. It is obvious that hK (mod VTHE) is more adequately aligned with 3CI than hK (mod VT); therefore, it is a better candidate for parsimonious explanation by monophyletic common cause according to 3PCI.

Goethe's 'Genetic Method' in exochorionic morphogeny. The overarching goal of Morphogeny is that, as Darwin (1859: 52) stated: "differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage." —Or as Goethe ([*ca.* 1790] 2009, Miller 1988: 75) said about his 'Genetic method': "If

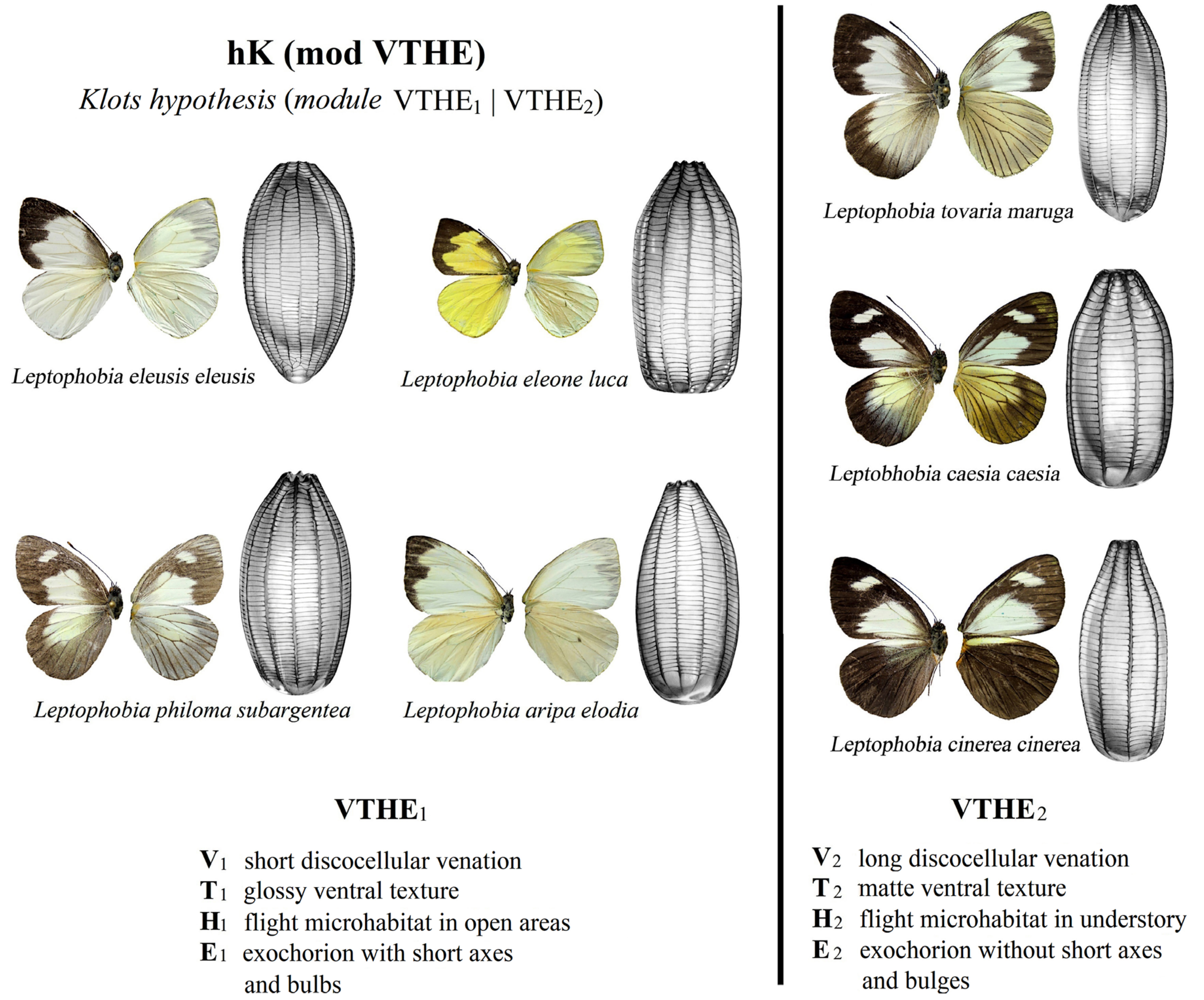
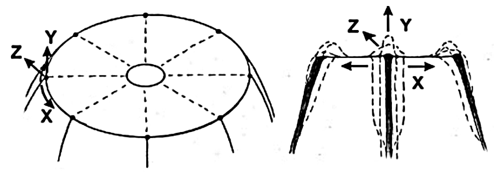


Figure 6. Representation of Klots hypothesis module VTHE —hK (mod VTHE)— obtained by consilience through parallelisms between three aspects of form and one spatial aspect: wing venation and texture, flight microhabitats and exochorionic characters (VTHE1 | VTHE2). Modified from Hernández-Mejía *et al*. (2015: Figures 1, 3, 4).

I look at the created object, inquire into its creation, and follow this process back as far as I can, I will find a series of steps […] but nature leaves no gaps, and thus, in the end, I will have to see this progression of uninterrupted activity as a whole.” One of Llorente-Bousquets and colleagues’ methodological contributions in exochorionic research, lies in visualizing —*i.e.,* making visible— morphological sequences and possible morphogenetic trends among subsystems of characters, using their *sui generis* pictorial representation techniques (Flores-Gallardo *et al*. 2021, 2022, 2023, Flores-Gallardo 2024). The visualization of bulges and bulbs as phases of transformative morphogenetic processes, allowed for their reconceptualization as polarizable states of the same character, in this case, periapical projections within Pieridae.

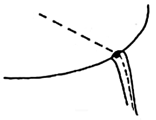
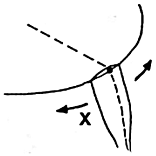
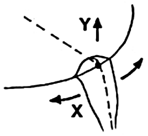
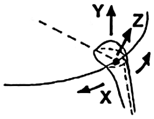
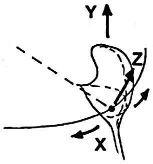
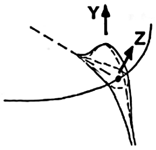
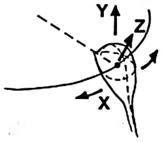
Morphogenetic distinction between types of axes and projections became relevant because: i) the presence of short axes was considered apomorphic with respect to the exclusive presence of long axes; ii) understood as the result of a larger projective trend along the Y and Z axes within the geometric model, bulbs were also considered apomorphic with respect to bulges. In *Leptophobia*, eggs with long axes ending in bulbs also have short axes, while eggs with only long axes ending in bulges do not. This does not always occur within the heterobathmic mosaic of exochorionic characters in Pieridae, so the correlation between axis types and periapical differentiation can be considered an additional parallelism among forms.

VTHE *as productive —not contrastive— evidence for* hK. It is crucial to understand that, even if their cladograms have the same topology, each version of hK constitutes, *de facto*, a different phylogenetic hypothesis. As shown by Fitzhugh (2006a: 62–63), no number of additional characters serves as contrastive evidence for the severe test of a phylogenetic hypothesis obtained through other means,



Three spatial directions or components

X = parallel to the equatorial plane and to the perimicopylar surface
Y = parallel to the longitudinal axis and orthogonal to the equatorial plane
Z = oblique projection with respect to X and Y, out of the chorion

Structure	Illustration	Augmentation per spatial component	Inequality key	Examples
None (unmodified)		X minimal / null Y minimal / null Z minimal / null	**X≃Y≃Z≃0**	Dismorphiinae, Coliadinae
Thickening		X moderate Y minimal / null Z minimal / null	**X > 0 Y ≃ 0 Z ≃ 0**	*Leptophobia* Butler, 1870
Bulge		X moderate Y low Z minimal / null	**X >> Y > 0 Z ≃ 0**	*Anthocharis* Boisduval, Rambur, Duméril & Graslin, 1833, *Euchloe* Hübner, 1819
Projections			**X, Y, Z ≠ 0**	
Small		X moderate Y low Z very low	**X > Y > Z > 0**	*Hesperocharis* Felder, 1862
Tubercular*		X low Y high Z moderate	**Y > Z > X > 0**	*Itaballia* Kaye, 1904, *Pieriballia*, *Perrhybris* Hübner, 1819
Laminar*		X very low Y moderate Z moderate	**Y, Z > 0 X ≃ 0**	*Ascia* Scopoli, 1777, *Ganyra* Billberg, 1820, *Glutophrissa* Butler, 1887
Bulbous (Bulb)		X moderate, similar to Y Y moderate, similar to X Low z	**X ≃ Y ≃ Z > 0**	Aporiina

* := presence of reminiscent ribs

Figure 7. Table showing a general geometric model of periapical differentiation in Pieridae. Projections were analyzed in three spatial components (X, Y, and Z) to facilitate their study, typification and recognition of possible morphogenetic trends. Understood as the result of a larger projective trend along the Y and Z axes, bulbs (red) were considered apomorphic with respect to bulges (blue). Modified from Nieves-Uribe *et al.* (2021b: 308).

since each one answers to a different set of causal questions represented as columns in their respective data matrices. Thus, hK (mod VTHE) does not 'support,' 'corroborate' or 'strengthen (the robustness of)' hK (mod VT) at all; rather, it simply replaces it.

Considering the provided framing of a hypothesis 'testing' as its *empirical demodalization* (in section: **Logic of phylogenetic hypotheses production and testing**), the possible results of an independent and severe test *sensu* Popper (1957, 1971) are verification, refutation, or revision of the hypothesis. By adding characters or other relevant empirical data, a previous phylogenetic hypothesis is not verified or refuted, thereby not demodalized nor tested, but revised and replaced by another more encompassing one. This 'replacementist' conception of phylogenetic research aligns with Fitzhugh's statement (2012: 52): "At best one can say that *(a-us (b-us (c-us, d-us)))* has been *replaced* by *(a-us (c-us (b-us, d-us)))* for the fact that the explanations of new observations 0101 and 0101 have relevance to the explanations of old observations 0011 and 0111."

The argument proposed here is not about testing hK (mod VT) through hK (mod VTHE), taken as contrastive evidence, but a justification for replacing hK (mod VT) with hK (mod VTHE) as the latter constitutes a more consilient hypothesis in terms of 3CI. It is neither an argument about hK (mod VTHE) being more parsimonious than hK (mod VT): they are either equally parsimonious with respect to their respective data sets, or simply incomparable. Klots did not consider VT sufficient evidence to propose the monophyly of the two subgroups; however, his division does not require the addition of *ad hoc* hypotheses, *i.e.,* it is maximally parsimonious in explaining the existence of two subgroups according to VT, by a single common (morphological) cause. For its part, hK (mod VTHE) also constitutes an explanatory hypothesis by a common (monophyletic) cause based on all the relevant evidence, without additional homoplastic hypotheses, and thus could be said to be as parsimonious with respect to VTHE as hK (mod VT) is with respect to VT. However, it cannot be said that hK (mod VTHE) is more parsimonious *simpliciter* than hK (mod VT), since they refer to different sets of observations, rendering them incomparable as explanations. On the other hand, hK (mod VTHE) is more parsimonious than the alternative of an ecological hypothesis, which considers the same full set VTHE of evidence, but deals with TH through an *ad hoc* functional explanation of adaptive mimicry.

***Conclusions on* hK (mod VTHE).** 3PCI constitutes an independent epistemological criterion for evaluating and justifying the (abductive) production of parsimonious hypotheses based on their degree of consilience, not for their (deductive and inductive) testing or even direct comparison when adding new evidence. There is no testing whatsoever in adding any kind of characters to a previous hypothesis, only the production of a new more encompassing —hopefully better— one. The analysis provided neither shows that hK (mod VTHE) is more 'robust' or parsimonious than hK (mod VT), as they are not even rival explanations of the same total body of evidence. Rather, it shows that hK (mod VTHE) is better justified as an application of PAR through TDM (mod RTE), on the independent basis of being more consilient *sensu* 3CI, *i.e.,* it exemplifies the proposed independent justification for applying the Principle of Parsimony, based on a stronger version of the Principle of Consilience.

CONCLUSIONS

In this paper, a logical-epistemological analysis of the Principle of Parsimony (PAR) was presented and advocated, based on a stronger version of inductive consilience, to reassess monophyly as the theoretical foundation of phylogenetic systematics; the results were exemplified through a case study of exochorionic morphogeny in Pieridae (Lepidoptera: Papilionoidea). The core epistemology and abductive logic of phylogenetic systematics *sensu* Hennig were outlined, following Fitzhugh's analysis. Sober's philosophical research on PAR and its usage in phlylogenetic systematics was revised and reframed as 'Extended Parsimony Model' (PAR+), resulting in the 'Principle of Triple Consilience with Intergrades' (3PCI). As case study, PAR+ was used to review the contributions of the exochorionic morphogeny to the discussion of the 'Klots hypothesis' (Hernández-Mejía *et al*. 2015). It was shown that exochorionic characters allowed for a better version of hK, insofar as more consilient *sensu* 3PCI, with morphogeny —based on Goethe's 'genetic Method'— serving as 'bridge' theory between morphology and phylogeny.

At a metalevel, this paper was developed based on the following general assumption: The conceptualization and utility of a set of traits as a character system can be analyzed and reviewed according to its adequacy to the concepts and principles of morphology *sensu* Goethe ([*ca*. 1790] 2009), morphogeny *sensu* Haeckel (1866) —*i.e.,* ontogeny or phylogeny—, and phylogenetic systematics *sensu* Hennig (1965, 1966); whose intersection is a 'bridge' concept of morphogeny *sensu lato*, *i.e.,* laws of transformation among organic forms.

This paper began by affirming homology, explicated as homogeny or homoplasy, as the central concept in phylogenetic systematics. With references that include Fitzhugh (2006b) and Rieppel & Kearney (2002), Cracraft (2022) holds that the inherited concept of 'homology' (*i.e.,* homogeny) no longer plays a useful role in comparative biology, given that hypotheses of species' common ancestry (*i.e.,* monophyly) cannot ever be tested by observation of characters' patterns. Instead, he proposed considering synapomorphies as units of phenetic change, which in fact turns phylogenetic analysis into researching "the history of characters (*i.e.,* the phenotype *sensu lato*)" (Cracraft 2022: 4). This proposal aligns partially with the concept of morphogeny *sensu lato* proposed here, under the influence of Goethe's genetic method; *i.e.,* laws of transformation between organic forms, or studies of comparative morphology to obtain laws of generation and transformation of instantiated forms. It also recalls Laubichler's (2014: 70, 77) Wagnerian account of homologues as: "units of phenotypic evolution [in which] mechanistic explanation of the homology of morphological characters has to involve the systemic properties of developmental processes of both morphogenesis and morphostasis".

We consider morphogeny *sensu lato* a worthy avenue of scientific research by itself. We also agree with Fitzhugh (2006a, 2012) and Cracraft (2022) that phylogenetic hypotheses are untestable by any amount of character data, which only serves to produce them. However, aligned with Havstad *et al.*' (2015) 'semaphorontic view' of homology, we disagree with Cracraft's rejection of the concept, as well as with his reduction of morphogeny to an ultimately phenetic approach. Instead, we advocate: i) conceiving morphogeny as a link between homologues and their possible homogenetic or homoplastic explanations, *i.e.,* as 'bridge' theory between morphology and phylogeny; ii) monophyly's explanatory power of disparate empirical data, including synapomorphies, under a stronger version of inductive consilience, *i.e.,* TDM (mod RTE) based on 3PCI.

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