



Peter Ax's views on homology – a comparison with Remane and Hennig

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Abstract

Peter Ax's major theoretical contribution, the book 'Das Phylogenetische System' (The phylogenetic system) (1984; English 1987) is compared with Remane's 'Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und Phylogenetik' (The foundations of the natural system, of comparative anatomy and of phylogenetics) published in 1952, and Hennig's (1950) 'Grundzüge einer Theorie der phylogenetischen Systematik' (Introduction to the theory of phylogenetic systematics). While Hennig and Ax's goal was to plead the case for a 'phylogenetic system', Remane's objective was to describe how to establish a 'natural system'. For Remane, homology is the core of the 'natural system'. His 'systematic type' is based on the distribution of homologous correspondences, and his 'homology criteria' are still in use today. In Hennig's book (1950), homology is only mentioned peripherally. Later (1953), he would emphasize the importance of distinguishing synapomorphies from symplesiomorphies, which both constitute homologies. Ax very much followed Willi Hennig's view, and certainly helped to clarify how phylogenetic systematics should be applied. He referred to Remane's 'homology criteria' too, but rejected the term 'criterion' on the grounds that what Remane described were just 'pointers' on how to look for similarity or correspondences. In doing so, however, he may have failed to have acknowledged sufficiently that identifying 'correspondence/ sameness' is indeed an independent empirical method.

Keywords homology criteria | synapomorphy | typology | convergence | Ockham's razor

Peter Ax, Adolf Remane, Willi Hennig

Most zoologists and systematists will remember Peter Ax (1927–2013) for the role he played in phylogenetic systematics. Participants in the Phylogenetic Symposium from the 1960s to the early 1990s (Ax stopped participating the Symposium after his retirement in 1992, with the exception of the one held in Göttingen in 2005; Fig. 1) will recall Ax's lively and stringent contributions to the discussion. His major theoretical contribution is a 350-page book published in 1984 (English in 1987) whose concise title 'Das Phylogenetische System' characterizes his personality very well (see Xylander, this volume).

My task is to compare Ax's book, and particularly his views on homology, with books on the same topic and with comparable intentions written by authors of the previous generation: Remane's 'Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik' (The foundations of the natural system, of comparative anatomy and of phylogenetics) published in 1952, and Hennig's 'Grundzüge einer Theorie der Phylogenetischen Systematik' (Introduction to the theory of phylogenetic systematics) published in 1950 (see also Richter 2013).

The books by Hennig and Remane are based on the same (mainly German) scientific tradition and were written at almost the same time. It is known that Hennig's book was written in 1945 when he was a prisoner of war

(Schmitt 2013: 56), and Remane's book was also at least partly written long before it was published. His chapter on evolutionary theories was written seven years earlier (i.e. around 1945), and the latest citation in his book is from 1949. It is probable that Remane was not aware of Hennig's book. Neither was ever translated into English. Hennig's very influential 'Phylogenetic Systematics', published in 1966, which laid the foundation for phylogenetics/cladistics worldwide, is a translation of a fundamentally revised version of the 1950 book, which Hennig finished around 1962. The German version was only published in 1982.

Adolf Remane (1898–1976), certainly for decades one of the most influential zoologists in Germany, was the PhD supervisor (1950) and scientific advisor of Ax until 1961, when Ax obtained a full professorship in Göttingen. Willi Hennig (1913–1976) is generally seen as the founder of phylogenetic systematics (e.g., Schmitt 2013). It is not clear when Hennig and Ax met for the first time. Hennig only rarely attended the annual (Northern German) Phylogenetic Symposia. Westheide (2014) remembers several visits by Hennig to Göttingen during the 1970s, where he discussed the theory of phylogenetic systematics with Ax. Ax (1984: 47) mentions that personal discussions with Hennig resulted in the introduction of the concept of 'adelphotaxon'.

In this article I will focus on the importance to Ax and his predecessors of the concept of homology in identifying phylogenetic relationships. The article is not intended to give a full account of this topic, which is one of the most discussed in systematics, but aims to contribute to the history of phylogenetics by comparing the three key books mentioned. The differences between them become visible almost immediately. Alone the titles

of the books speak volumes. While Remane's focuses on the 'natural system', both Hennig and Ax place the 'phylogenetic system' at the heart of their contributions. While it can easily be said that homology forms the core of Remane's entire book, Hennig (1950) only mentions the term homology when he compares 'true homologies' with the concept of homoiology (p. 176). Ax's account of homology is fairly detailed (20 pages), but doesn't start until page 166, by which point he has already discussed methods of reconstructing phylogenetic relationships.

Natural system or phylogenetic system

In his 1952 book, Remane accepts the importance of pre-phylogenetic morphology but rejects the metaphysical (Platonic) interpretation of the type and suggests the term 'pure morphology' to replace 'idealistic morphology.' He also rejects the idea (p. 11) that the natural system should be based on phylogenetic insights, arguing that it precedes and is therefore independent of phylogenetics. Phylogenetics, on the other hand, has no research method of its own but usurps findings from systematics and morphology and interprets them in an evolutionary way. 'Phylogenetic trees are primarily nothing other than a historical interpretation of the natural system.'¹ And two pages later: 'Phylogeny does not dictate the structure of the natural system, the natural system forms the basis of phylogeny.'² A few years later (1955: 171–172), this was rephrased as: 'Phylogeny does not dictate homology, homology dictates phylogeny.'³ It appears obvious that Remane used the term 'phylogeny' here to mean phylogenetic hypothesis (Schmitt 1989), which actually corresponds very well to the way the English term 'phylogeny' is used today. Nevertheless, for Remane, the natural system and identification of homologies had priority over phylogenetic hypotheses. Furthermore, following the tradition of idealistic morphology, the term type (typus) played an important role in his argumentation: 'the independence of homologous type characters from analogous structural and functional correspondences is the most important principle of morphology.'⁴ Later in the book, Remane (p. 163) describes the main



Figure 1. Peter Ax at the Phylogenetic Symposium in Göttingen 2005. Behind Ax Profs. Kraus and Götting. Photo: Rainer Willmann

¹ „Stammbäume sind zunächst nichts weiter als historische Interpretationen des Natürlichen Systems.“

² „Nicht die Phylogenie entscheidet über den Aufbau des natürlichen Systems, sondern dieses bildet die Grundlage für die Phylogenie.“

³ „Nicht die Phylogenie entscheidet über die Homologie, sondern die Homologie über die Phylogenie.“

⁴ „... gerade die Unabhängigkeit der homologen Typusmerkmale von den analogen Struktur- und Funktionsübereinstimmungen [ist] wichtigster Grundsatz der Morphologie.“

method of phylogenetics as ‘identifying homologous correspondences, on whose distribution the natural system and, at the same time the systematic type and the pure stem form [in the sense of ancestor] are – simply and clearly – based.’⁵ Remane’s ‘systematic type’ (which he contrasts with other kinds of types; see also Rieppel 2013) corresponds closely to a real ancestor. He describes how the systematic type can be reconstructed and then transformed (Umformung) into the ancestor. Here, Remane is rooted firmly in the tradition of empirical idealistic (pure) morphology, postulated, for example, by Adolf Naef (1883 – 1949) (see also Rieppel 2012, 2013).

Naef (1919: 5) described Haeckel’s phylogenetics as ‘naïve’ and criticized the older, pre-Darwinian, idealistic morphology in the same way for its failure to provide an explicit methodology. Naef’s goal was a natural system and his main methodology was the reconstruction of the type (as in the case of Remane). ‘Johannes Müller just takes the type as a given; we look for it’⁶ (p. 27). ‘I have come to realise that the natural system is nothing other than an expression of the typical correspondences actually identified or presumed to exist’⁷ (p. 19). For Naef (1919: 35) it was clear that the ‘typical correspondence (or form-relatedness) of organic species is the result of phylogenetic relatedness (or “Stammesverwandtschaft”’, and that the morphological characters of the ideal type correspond with those of a real stem form (ancestor).⁸

Neither Naef nor Remane were essentialists, and any attempt to equate idealistic morphology, typology and essentialism would be entirely misplaced. Platonic types were considered to be constant and timeless, and sharply delineated from other types, but in no sense are they the kind of types favored by Naef or Remane. Mayr (1999: 24) saw Remane’s book as promoting the ‘typological (idealistic-morphological) tradition, following Goethe’, mainly because of its lack of ‘population thinking’ (a complaint Mayr did not limit to Remane’s work). However, typology is conceptually neutral with respect to hypotheses of evolutionary mechanisms and there is no contradiction between ‘population thinking’ and ‘typological thinking’, as convincingly shown by Levit & Meister (2006). Remane was, without doubt, a true ‘phylogeneticist’ (Schmitt 1989, Zachos & Hosfeld 2006).

⁵ „Sie besteht aus der Feststellung der homologen Ähnlichkeiten. Aus ihrer Verteilung ergibt sich das natürliche System und gleichzeitig in einfacher und klarer Weise der systematische Typus oder die reine Stammform.“

⁶ „Joh. Müller setzt den Typus einfach voraus; wir suchen ihn!“

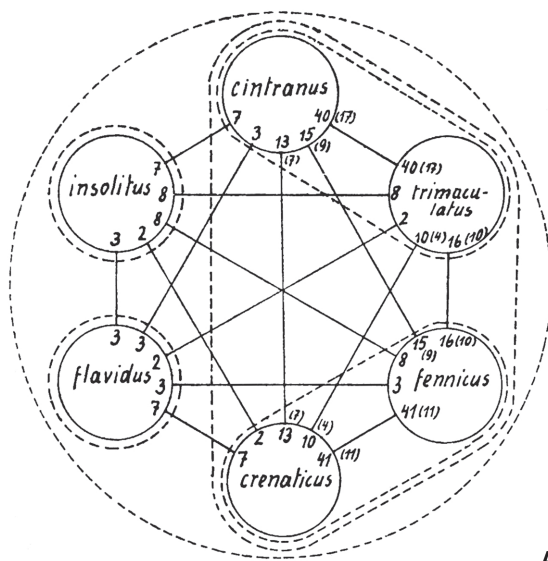
⁷ „Ja, ich stelle fest, dass das natürliche System nichts anderes ist als der Ausdruck für die erkannten oder angenommenen typischen Ähnlichkeiten.“

⁸ „Die typische Ähnlichkeit (oder Formverwandtschaft) organischer Arten sei die Folge ihrer “phylogenetischen Verwandtschaft” (oder “Stammesverwandtschaft”) und die morphologischen Charaktere des idealen Typus stimmen mit denen einer realen Stammform überein.“

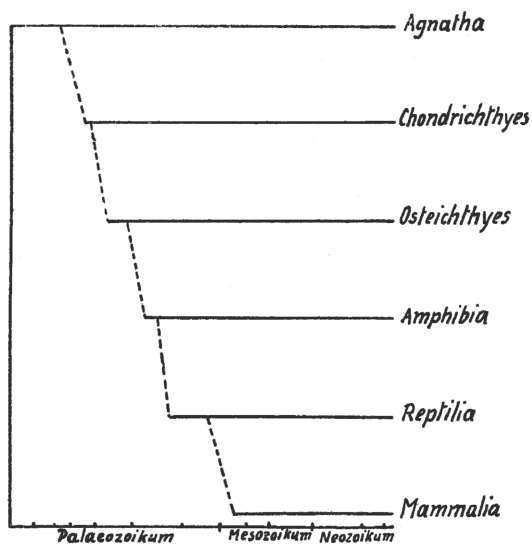
Hennig (1950) is well known for arguing that a phylogenetic system should be preferred over all other kinds of potential biological system, and that only phylogenetic relatedness should be considered in the establishment of such a system. He also gives a clear definition of what ‘phylogenetic relatedness’ actually means (Richter & Meier 1994, Schmitt 2013). In particular, he argues against all kinds of systems which are based solely on general similarity (Gestaltähnlichkeit), though as we have seen this would not really apply to Naef or Remane. Hennig (p. 108–110) compares three figures (fig. 24a–c; here Fig. 2A–C) representing different approaches to typological/phylogenetic relatedness. Whereas Fig. 2A is clearly based on similarity only, Figures 2B and 2C represent some kind of phylogenetic relationship. Interestingly, only Figure 2C shows phylogenetic relationships as sister group relationships, and for Hennig, this is the only true way of representing a phylogenetic system. Figure 2B is considered to be somehow typological. Twenty years later, Günther (1971) suggested several synonyms for the word pair natural vs. phylogenetic system (reflecting Figs 2B and 2C), including typological vs. phylogenetic system, patristic-phylogenetic vs. cladistic-genealogical system and paraphyletic vs. consequent-phylogenetic system. This implies that Ernst Mayr’s (e.g. 1990) evolutionary classification is actually a typological system.

Hennig also rejects on several grounds the idea that phylogenetic systematics is historical and logically founded in non-phylogenetic systems (i.e. in idealistic morphology) (see also Rieppel 2012, who compares Naef’s and Hennig’s thoughts). Hennig writes (p. 26) that the argument that idealistic morphology must precede a phylogenetic system for logical reasons would only be true if morphological correspondences were the only basis on which phylogenetic relationships were recognizable.⁹ He admits that in many cases, phylogenetic systematics starts with morphological correspondence and in this way does indeed go back to idealistic morphology, but argues that phylogenetic systematics is not restricted to a new interpretation of morphological findings and actually embodies the ‘principle of reciprocal illumination’ (see Schmitt 2013: 163–164 for general comments), which also needs to include zoogeography, ecology and genetics. However, if we consider that phylogenetic systematics/cladistics was, for decades, effectively nothing other than using morphological correspondences to reconstruct phylogenetic relationships (see for example Ax’s approach), this argument might be seen in a new light (see also Rieppel 2012). Later on, Hennig (p. 147–149) deals

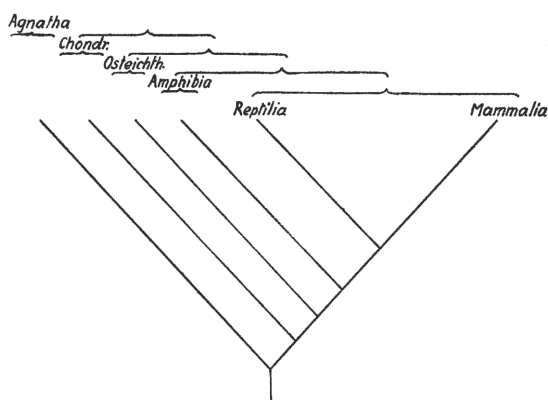
⁹ „Sie wäre das nur, wenn der phylogenetischen Systematik zur Aufdeckung der Abstammungsbeziehungen keine anderen Mittel zur Verfügung stünden als die Analyse der morphologischen Ähnlichkeitsbeziehungen.“



A



B



C

Figure 2. Representations of different approaches to typological/phylogenetic relatedness (A–C). From Hennig (1950) fig. 24 a–c.

with Naef's take on of idealistic morphology and clearly shows that Naef's approach is a mixture of typological and phylogenetic systematics. This leads Hennig (p. 149) to suggest that phylogenetic systematics should adopt many of the results of idealistic morphology, particularly the kind advocated by Naef (Naef'scher Prägung) 'with regard to the morphological primacy of certain character types.'¹⁰

Ax (1984: 39) is very clear in his preference for the term phylogenetic system: 'The object of our particular science is to uncover the products of phylogenesis and to arrange them on the basis of the chronology of speciation. Logically, we call this science phylogenetic systematics and its aim the establishment of a phylogenetic system.'¹¹ And later (p. 41): 'It is only consistent to refrain from using the enigmatic term 'natural system'.¹²

Homology and Methodology

As already mentioned, the chapter on homology in Ax's book appears as a kind of addendum without homology being allotted any particular importance for the reconstruction of phylogenetic relationships. He writes (p. 166): 'The definitions of the terms symplesiomorphy, synapomorphy and convergence cover – in a clear and complete way – all possible kinds of evolutionary correspondence between different evolutionary species. The meaning of the term homology and that of its supposed counterpart analogy are insufficient for the goals of phylogenetic systematics.'¹³ He provides a definition of homology which only refers to characters shared between evolutionary species (this was later extended to all kinds of supra-individual taxa, Ax 1988), ignoring other aspects of homology such as serial homology (see e.g. Schmitt 1995). Homologous characters go back to the exact same character and are either unchanged or transformed (p. 167). Because his definition includes

¹⁰ „...hinsichtlich des morphologischen Primats bestimmter Merkmalstypen.“

¹¹ „Der Forschungsgegenstand unserer Wissenschaft ist die Aufdeckung der Produkte der Phylogenese sowie ihre Ordnung entsprechend der zeitlichen Abfolge von Speziationen. Logischerweise nennen wir sie eine phylogenetische Systematik und das Ziel ihrer Bestrebungen ein phylogenetisches System.“

¹² „...ist es nur konsequent, auch von dem buntschillernden Begriff „Natürliches System“ Abstand zu nehmen.“

¹³ „Mit den Definitionen der Wörter Symplesiomorphie, Synapomorphie und Konvergenz verfügen wir über einen Begriffsapparat, der die prinzipiell möglichen Formen evolutiver Übereinstimmungen zwischen verschiedenen evolutionären Arten einwandfrei und vollständig erfasst. Die Bedeutungsinhalte des Wortes Homologie und seines vermeintlichen Wortpartners Analogie sind dagegen für die Ziele der phylogenetischen Systematik unzureichend.“

no reference to similarity or correspondence, Ax argues that no term which expresses similarity, e.g. analogy, can be regarded as the antonym of homology. For Ax, the antonym of homology is simply non-homology. Ax also refers to Remane's 'homology criteria' but rejects the term 'criterion' on the basis that what Remane proposes are simply 'pointers' (Anregungen) on how to look for similarity or correspondences.

The term 'homology criterion', however, does not stem from Remane but from the earlier author Bertalanffy (1936). For Bertalanffy (p. 164), 'typological homology', i.e. the identification of a correspondence in position, is the 'most important criterion for phylogenetic homologization'. The phylogenetic homology concept did not replace the typological concept for Bertalanffy, who actually discusses the importance of the typological concept. 'Homology in a typological sense, i.e. based on a correspondence in position, is open to direct testing; if we define homology on the basis of shared ancestry following Haeckel, we push the criterion of homology back into an unknowable past.'¹⁴ It was also Bertalanffy who characterized phylogenetic relationships as an 'explanation' of typological homology. What can be regarded as a typological homology concept can clearly be seen in Naef's work (1919). Naef (p. 10, 11) compared 'typical similarity' (typische Ähnlichkeit) with geometrical figures. Two rectangles possess corresponding, i.e. homologous, parts. Homology means 'morphological equivalent', which presupposes the typical similarity of the whole.¹⁵ Naef (p. 70) concluded that 'the identification of homology is based on comparable spatial and temporal correlation (...) between the parts of the compared whole.'¹⁶ Here, identification of homology is clearly independent from the historical explanation for such homology.

When we now turn to Remane, we must first remember that for him, homology was the obvious core of the natural system. His main method of phylogenetics, the identification of homologous correspondences, has already been cited above. It should be noted that Remane always refers to correspondences, although he admits that homologous correspondences might exist 'regardless of their apparent similarity or dissimilarity'¹⁷ (p. 30).

¹⁴ „Die Homologie im alten typologischen Sinn, auf Grund der Übereinstimmung der Lage, ist direkter Nachprüfung zugänglich; definieren wir aber mit Haeckel als homologe Organe, die durch gemeinsame Abstammung erhalten sind, so verlegen wir das Kriterium der Homologie in eine unkontrollierbare Vergangenheit.“

¹⁵ „Es entsteht damit der Begriff der „Homologie“ oder „morphologischen Gleichwertigkeit“, der, wie man sieht, die typische Ähnlichkeit des Ganzen voraussetzt, ohne die ein solcher Vergleich überhaupt wegfällt.“

¹⁶ „Die Feststellung der Homologie gründet sich auf den Nachweis gleicher räumlicher (und zeitlicher) Korrelation (...) zwischen den Teilen der verglichenen Ganzen.“

¹⁷ „...ungeachtet ihrer äußeren Ähnlichkeit oder Unähnlichkeit.“

Before Remane discusses in detail his three main and three auxiliary criteria, he criticizes the previous use of 'homology definitions' because their sheer disparity might indicate that different homology concepts exist (p. 32).¹⁸ For Remane (p. 33) it is very clear that this is not the case: what differ are, at most, subcriteria (Teilkriterien) of a uniform and impartible concept of homology.¹⁹ Clearly, Remane uses the term 'criterion' not to mean a necessary condition, but more loosely. Only after a detailed discussion of his six criteria does Remane (p. 67–68) discuss phylogeny as part of the homology definition. For Remane, however, common descent is not part of the 'definition' but the 'explanation' for homology. In 1955 (p. 172), this term was replaced by 'explication'. Interestingly, Remane (p. 65–66) accepts that decisions on homology might be driven by probability, with some homologies being more likely than others, which shows that in his view too, not every detailed correspondence (sameness) is necessarily a true homology. Hennig (1953) criticized Remane for not distinguishing clearly between definition and criteria, and Mayr (1984: 187) objected that 'Remane used the criteria which serve as the proof of homology as part of the definition of homology.'²⁰ Indeed, Remane used the terms criteria and definition almost interchangeably and used explanation/explication for what Hennig and Mayr would call definition. Remane might well be criticized for a lack of precision in his terminology, but this does not mean that his general concept is flawed.

Remane (1952: 163) also suggests what can be considered a methodology for establishing a natural system. The systematic type (i.e. the stem form) can be reconstructed on the basis of the distribution of homologies, and the 'order of types in the branching of the phylogenetic tree shows us an essential aspect of phylogenesis.'²¹

To explain what the 'distribution of homologies' really means, the term 'homology circles' (Homologiekreise) is introduced (p. 106). *Sciurus*, for example, is part of the homology circle of rodents (steht im Homologiekreis der Nagetiere), the rodents together with other mammal orders are part of the homology circle of mammals, and mammals together with reptiles and birds part of the homology circle of amniotes, etc. In his summary

¹⁸ „Diese Vielfältigkeit der Definitionen, die z.T. gar nichts Gemeinsames aufwiesen, ließen schließlich den Verdacht aufkommen, es gäbe mehrere ihrem Wesen nach verschiedene Homologiebegriffe.“

¹⁹ „Was in verschiedene „Homologiebegriffe“ zerspalten wurde, sind in Wirklichkeit nur Teilkriterien des einen einheitlichen und unteilbaren Homologiebegriffs.“

²⁰ „...dass Remane die als Beweis für Homologie dienenden Kriterien zur Definition von Homologie erhob.“

²¹ „Die Typenfolge wiederum im Geäst des Stammbaums übermittelt uns einen wesentlichen Teil der Stammesgeschichte.“

(p. 379), he very clearly states that ‘when two or more species share homologous structures the structure already existed in their common ancestor.’²² Remane (p. 106) argues that if this kind of encaptic system (this is not the term he uses, however) of homologies were always valid, the resulting grouping would be an exact and correct system. However, this is not the case. Monotremes, for example, exhibit both mammalian and reptile characters. Here, he introduces the term ‘homology bridges’ (Homologiebrücken) to describe the phenomenon where certain homologies overlap ‘typical groups’ (most homologies are restricted to typical groups). Remane (p. 106) even suggests a law (Gesetzmäßigkeit) by which ‘if two natural groups are connected by a homology bridge with a third group, they themselves are not connected by homology bridges.’²³ When discussing homology bridges, Remane does not distinguish between primitive and derived characters, though Dohle (1965) clearly showed that when symplesiomorphies are used, the homology circles enclose completely different taxa. It is difficult to imagine how this methodology (even without the problems Remane himself discusses later) can lead to anything like a natural/phylogenetic system without additional instructions.

It is interesting to note that Hennig (1950: 176–177) used the term homology only to distinguish it from homologies, which have a ‘curious intermediate position between true homologies and convergences.’²⁴ If his avoidance of the term homology had been intended as a real critique of the concept, Hennig would surely have emphasized the fact. In his critical remarks on insect phylogeny (Hennig 1953), Hennig refers to Remane (1952) and uses the term homology without hesitation, insisting, however, that Remane’s homology criteria are clearly subordinated to the phylogenetic definition of homology (p. 11). This work is the first in which Hennig (1953: 16) writes about the relationship of the term homology to the terms he himself introduced: ‘Homologies are not only the true synapomorphies but also the symplesiomorphies. The concepts of synapomorphy and homology, therefore, do not coincide. Of course, the homology criteria form the starting point of any systematic work which uses morphological methods. Only correspondences in homologous characters can be compared. But not all homologies are important for systematics: symplesiomorphies are not.’²⁵

²² „Wenn zwei oder mehrere Arten homologe Strukturen aufweisen, so ist die homologe Struktur bereits bei dem gemeinsamen Ahnen vorhanden.“

²³ „Sind zwei natürliche Gruppen des Systems durch eine Homologiebrücke mit einer dritten verbunden, so sind sie untereinander nicht durch weitere Homologiebrücken verbunden.“

²⁴ „...eine merkwürdige Zwischenstellung zwischen echten Homologien und Konvergenzen.“

²⁵ „Homologien sind ja nicht nur die echten Synapomorphien,

In his revised book, Hennig (1966: 93) provides a very specific definition of homology. ‘Different characters that are to be regarded as transformation series of the same original character are generally called homologous.’ Here, the concept of homology becomes incorporated into Hennig’s ideographic character concept, where characters are transformation series (see Grant & Kluge 2004). The fact that Hennig actually emphasized that ‘transformation’ refers to the real historical process and not to any formal process, as in idealistic morphology, makes the definition even more interesting for us.

In his discussion of Remane’s criteria, Hennig (p. 94) states: ‘But with respect to defining the concept “homology”, all three of his “principal criteria” are only accessory criteria that we have to use because the real principal criterion – the belonging of the characters to a phylogenetic transformation series – cannot be directly determined.’ It is interesting to note that Hennig here is also guilty of mixing up definition and criterion, at least when he uses the term ‘real principal criterion.’ Comparing Remane’s three main criteria, Hennig suggests that the first – ‘criterion of sameness of position’ – must take priority, for without it the other criteria are unusable.

When Hennig (1966: 95) discusses ‘character phylogeny’ it again becomes clear that for him, the starting point for the reconstruction of phylogenetic relationships is indeed the identification of homology. ‘If it can be shown that a character is homologous in a series of species, the question arises: in which direction is this transformation to be read.’ In other words, which character state is apomorphic, which plesiomorphic. Hennig (p. 94–95) also noted that ‘the concepts of symplesiomorphy and synapomorphy go somewhat beyond what are ordinarily called ‘homologous characters’ because ‘a “character” may also be the absence of an organ but generally we speak only of the homology of organs.’ Ax (p. 181) discusses this point under the heading of ‘negative characters’ (Negativmerkmale). For him it is ‘simply impossible to hypothesize whether something which does not exist is homologous or non-homologous.’²⁶

Ax rejects in a footnote Hennig’s posthumously published idea (1984: 38–39) of extending the term ‘homologous character’ to the absence of structures when a particular position on the body is considered (e.g. the wings or lack of wings in insects), because for

sondern auch die Symplesiomorphien. Die Begriffe Synapomorphie und Homologie decken sich also nicht. Natürlich stehen die Kriterien der Homologie am Anfange der systematischen Arbeit, soweit sie morphologische Methoden benutzt. Verglichen werden können überhaupt nur Übereinstimmungen in homologen Merkmalen. Aber nicht alle Homologien sind für die Lösung einer systematischen Frage von Bedeutung: die Symplesiomorphien sind es nicht.“

²⁶ „... man kann schlechterdings nichts als homolog oder auch als nicht-homolog hypothetisieren, was gar nicht existiert.“

certain characters (e.g., amnion, allantois, serosa), no corresponding position exists.

It is clear that Ax (1984, 1988) adopted most of Hennig's (1966) ideas. However, the chronological principle of identifying homologous characters first before making a decision on the direction of transformation is apparently missing in Ax's approach (but see also Hennig 1969). Ax (1984: 66–67; 151) suggests first deciding between plesiomorphy and apomorphy, and then between synapomorphy and convergence. He does not recognize any specific 'empirical measure' (Maßstab) to help with the latter decision, but refers to the principle of parsimony (Ockham's razor). This is odd, because the decision between plesiomorphy and apomorphy requires a previous decision to have been taken that both states belong to the same transformation series (i.e. are homologous characters/character states if we follow Hennig). Ax clearly avoids using the term homology here. When discussing homology explicitly, he writes (p. 170): 'This does not mean that homologies can only be identified by deduction based on previously accepted phylogenetic hypotheses. The logic of the decision-by-probability between homology and non-homology corresponds exactly to the logic of the decision-making procedure between synapomorphy and convergence.'²⁷ This point could also be argued the other way round, starting with the decision between homology and non-homology. Ax continues: 'if characters are very similar or identical in their spatial and/or temporal structure, the principle of parsimony requires an *a priori* assumption of homology, unless this conflict with the distribution of characters in the organisms being compared.'²⁸ Contrary to what Ax claims, the identification of similar or identical spatial or temporal structures (interestingly, Ax uses Naef's phrase) does indeed require its own 'empirical measure', which in turn corresponds with Remane's first and second homology criteria.

It is not the intention of this contribution to discuss the current view on homology and phylogenetics. In Germany in particular there is still a tradition which emphasizes an empirical *a priori* criterion for identifying homologies which is often referred to as the 'complexity criterion' (Dohle 1976, 1989, Scholtz 2005; see also Riedl 1975). The cladistics community, on the other

hand, argue that homology identification is a two-step approach, resulting in what often has been called primary and secondary homology (de Pinna 1991). For some decades the identification of secondary homology by character congruence was considered more important (Farris 1983). Although Ax never used a computer to analyze phylogenetic relationships, his writings appear to tend towards the second approach. Although these two approaches are not really contradictory (de Pinna 1991 quotes Remane on the identification of primary homologies; see also Richter 2005), their emphasis is clearly different. Patterson's (1982) equation of homology and synapomorphy is still defended by some (Brower & de Pinna 2012), but rejected by others (Nixon & Carpenter 2012, Farris 2014) - the latter position representing Hennig's view, as we have seen. Ax (1984: 183) is explicit in his rejection of Patterson's view, emphasizing that synapomorphy refers to a very specific hierarchical level and that this needs to be stated unambiguously. Ax in this respect is more precise than Hennig in his use of the term synapomorphy to refer exclusively to sister group relationships. The problem of applying the concept of homology to the absence of organs remains. One final aspect of Ax's view on the relationship between homology and synapomorphy should be mentioned. Ax (1984: 184) cites Bock's 'conditional phrasing', e.g. 'the wings of birds and the wings of bats are homologous *as the forelimbs of tetrapods*' (Bock 1973: 387) and not, in Bock's opinion, as wings. For Ax this conditional phrase is just a circuitous way of expressing the hierarchical level on which a homology is relevant to systematics as a synapomorphy. Wagner (2014) recently phrased this slightly differently, incorporating Hennig's character concept: 'In fact bird wings and bat wings are homologous, but what is not synapomorphic is their character state as a wing'. While all these approaches refer to the contribution of the homology concept to phylogenetics, it has long been considered that homology also needs to have some kind of mechanistic cause (Riedl 1975, 1978). However, this goes beyond the focus of the present contribution (see Wagner 2014).

Peter Ax strictly rejected the evolutionary but still typological approach (a term which in my view should have no negative connotation) advocated by Adolf Remane. He was a keen follower of Willi Hennig's view, and certainly helped to clarify the way in which phylogenetic systematics should be applied. When Ax degraded Remane's criteria to mere 'pointers', he may have failed to acknowledge sufficiently that identifying 'correspondence/ identity' is indeed an independent empirical method. Peter Ax will be remembered as a great advocate of phylogenetic systematics, particularly in Germany. Even if I do not agree with all of his writings,

²⁷ „Das allerdings bedeutet keineswegs, dass Homologien nur deduktiv anhand vorab akzeptierter Verwandtschaftshypothesen „festgestellt“ werden können. Die logische Situation der Wahrscheinlichkeitsentscheidung zwischen Homologie und Nicht-Homologie entspricht vielmehr exakt dem Procedere bei der Entscheidung zwischen Synapomorphie und Konvergenz.“

²⁸ „Bei einer sehr ähnlichen oder identischen Raum- und/oder Zeitstruktur verlangt das Prinzip der sparsamsten Erklärung von uns, Merkmal für Merkmal solange der Hypothese einer homologen Beziehung zu verfechten, solange sie mit der Merkmalsverteilung bei den verglichenen Organismen nicht in Konflikt gerät.“

it remains a pleasure to read him and I remember that I felt the same when I listened to him. He was a champion of the maxim that clear thoughts require clear language.

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