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The Ambiguous Use of the Prefix 'Pan' in Arthropod Systematics

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Research Article

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ABSTRACT

'Pancrustacea' and 'Panarthropoda' are commonly used terms in arthropod systematics. Yet, both terms suffer from a severe shortcoming: they are not equivalent to any possible pan-monophylum concept applied to (any form of) 'Crustacea' or 'Arthropoda'. Therefore, both terms lack precision and can refer to quite different monophyletic groups. With this they do not provide the precision of alternative names for similar groupings, which also allow to express certain specific relationships, such as Crustacea sensu lato, Tetraconata or Arthropoda sensu lato. We emphasise the importance of unambiguous group names in order to provide a precise scientific communication.

INTRODUCTION

In the systematics of organisms, maybe more than in other scientific fields, names tend to be unstable on the long run. As new hypotheses of relationships between groups arise, also new names are assigned to newly supposed monophyletic groups (clades, taxa). Such new names often make reference to older, well-established names. These references are in many cases forged by applying prefixes to the old, established name. One of those prefixes that has been used in these instances is 'Pan', the Ancient Greek word for “all”. This prefix has especially been used for coining names of groups which include fossils (then sometimes also called 'total group'). In the following, two well-known examples of the use of the prefix 'Pan' in arthropods will be discussed.

The term 'Pancrustacea' has been introduced by Zrzavý & Štys[1] for a monophyletic group comprising crustaceans and hexapods. The term 'Panarthropoda' was introduced by Nielsen[2] for a monophyletic group comprising the sclerotised arthropods, Onychophora, and Tardigrada. These two terms have since been used by several authors subsequently[3-9]. Also the name Arthropoda has frequently been understood as including Onychophora[10,11]. Furthermore, Štys & Zrzavý[12] suggested to use it as such and apply the name Euarthropoda for the in-group comprising Crustacea, Hexapoda, Myriapoda, Chelicerata, and Trilobita.

Yet, among the many available names for arthropod groups these terms appear quite unfortunate because of the ambiguities of the use of the prefix 'Pan': The prefix 'Pan' can also be used to describe a specific relation of a monophyletic group with this prefix to a monophyletic group without it, i.e., the Pan-group includes the group without the Pan-prefix. For showing the resulting ambiguities, we are discussing the application of the pan-monophylum concept(s) to different scenarios based on different assumed relationships of arthropod sub-groups. With this, we aim at demonstrating that both terms, 'Pancrustacea' and 'Panarthropoda', could refer to several different groupings of which none is identical to the originally proposed group.

One pan-monophylum concept was introduced by Lauterbach[13]. In this concept it was intended to apply 'Pan-' as a provisional name for a monophyletic group often termed crown group[14] for a discussion of deviation from the crown-group concept; see also Budd & Jensen[15] plus its entire evolutionary lineage of fossil representatives (often termed stem-group, or also stem-lineage)

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down to the node on which a group branches off that has extant representatives. In the notation of Lauterbach, this provisional name was written as 'Pan-Xxxx', i.e. hyphenated, and not intended to be an official taxonomic name. The proposers of the PhyloCode (current version 4c) adopted for their concept the principal application of the prefix 'Pan' in the way it was introduced by Lauterbach[13]; however, they changed its notation to 'Panxxxx', i.e. without a hyphen, and accepted it as a valid taxonomic name. Hence, the main difference between the two concepts is the notation.

Why is the Use Of 'Pancrustacea' ambiguous?

'Crustacea' is currently not considered to be monophyletic (the "paraphyly of Crustacea" problem[3,5,16] which makes it difficult to apply the pan-monophylum concept(s) in this case. Two monophyletic groups could be used as a reference point for 'Pancrustacea': Eucrustacea as characterised by Walossek[17], or Crustacea sensu lato as characterised by Stein et al.[18]. Both names are linked to specific sets of autapomorphies instead of being linked to a specific taxonomic composition and should, therefore, remain valid (even if, for example, Hexapoda, or even Tracheata could be finally shown to be a stable in group of one of these monophyletic groups).

In the following, we discuss examples how a pan-monophylum concept could be applied to crustaceans.

Example 1) Hexapoda as sister group to (Eu)Crustacea: Zrzavý & Štys[1] assumed that hexapods represent the sister group to 'Crustacea' (probably referring to Eucrustacea as they did not discuss the fossil forms, which provide the features that characterise Crustacea sensu lato; **Figure 1A**). If we would now apply the pan-monophylum concept(s) as proposed, it would not include Hexapoda, as Hexapoda has extant representatives. Hexapoda would in this case represent the sister group to Pan-Crustacea (or Pancrustacea).

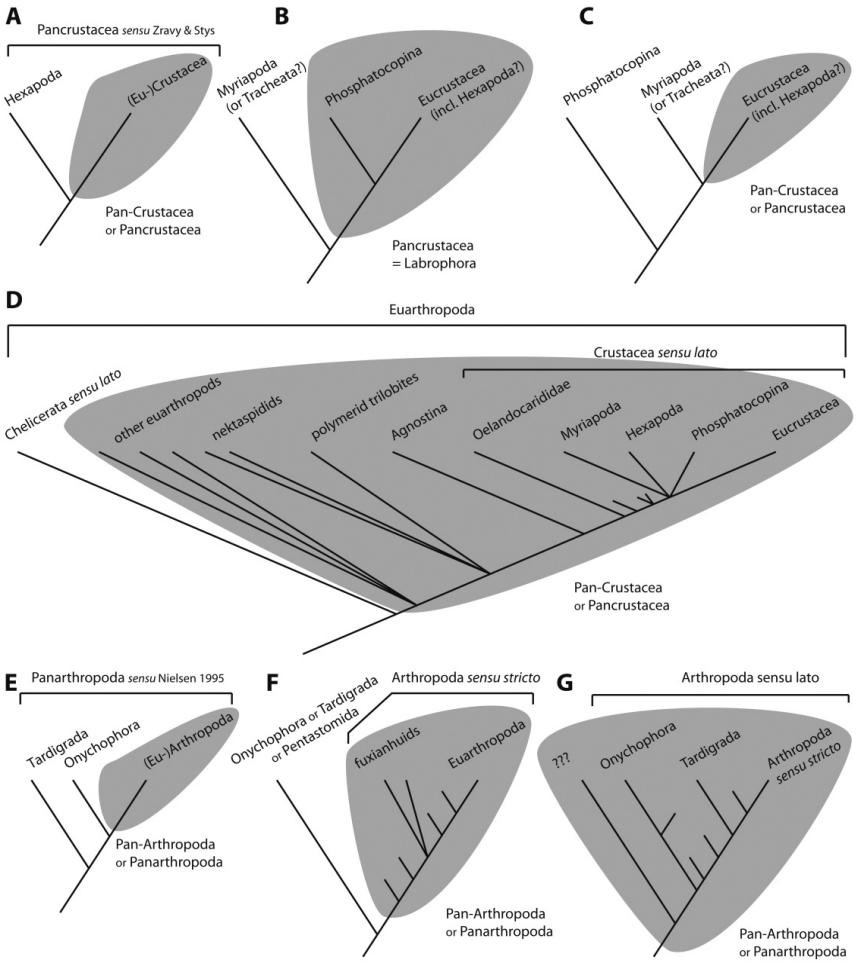

Figure 1: Different constructions of pan-monophyla based on different phylogenies.

Hence the application of the pan-monophylum concept(s) leads to a different meaning than that proposed by Zrzavý & Štys [1]. The term Pancrustacea is therefore ambiguous if used in this way. If one wants to stress this specific supposed sister-group relationship between (Eu-) Crustacea and Hexapoda, the non-ambiguous term Tetraconata is available [19].

Example 2) Hexapoda as a crustacean in group: Different authors have used Pancrustacea as a substitute for (Eu-)Crustacea, but with an emphasis on Hexapoda being a deeper ingroup of it. In this way, the term Pancrustacea is in fact equivalent with Eucrustacea **(Figure 1C)**. Eucrustacea has been characterised based on autapomorphies [17]. Hence, adding a group somewhere inside does not change the validity of this group. As for Reptilia it has now been stressed for many years that Crustacea is not

valid, but a paraphylum. Yet, Reptilia has been re-established as simply including birds and is now a valid monophyletic group [20]. Similarly, if Hexapoda is indeed an ingroup of Eucrustacea, this would simply mean that hexapods are eucrustaceans. Concluding: Pancrustacea in this use differs to that of other applications, has no relation to any pan-monophylum concept, as it does not make a reference to fossils and is simply equivalent to Eucrustacea.

Example 3) 'Crustacea'=Eucrustacea: We could also “construct” Pan-Crustacea/Pancrustacea based on Eucrustacea in a different way. We generally face the problem that the exact relationships of Eucrustacea are partly unclear. The exclusively fossil Phosphatocopina is closely related to Eucrustacea, based on numerous shared characters of the feeding apparatus (differentiated hypostome-labrum complex, sternum with paragnaths, different details such as setation [21]. Yet, most of these, if not all characters appear to be present also in Myriapoda and Hexapoda, or at least these groups can be deviated from an ancestor with such morphology [22-24]. Hence, we cannot reliably resolve Hexapoda, Myriapoda, Phosphatocopina and Eucrustacea. Still, we can think of the different possibilities.

For example, if Hexapoda would be definitely identified as a stable ingroup of Eucrustacea, 'Pancrustacea' could be applied, referring to Eucrustacea plus Phosphatocopina but excluding the next branch with extant representatives which could be Myriapoda. In this case, 'Pancrustacea' would comprise Eucrustacea (with Hexapoda as an ingroup) plus Phosphatocopina. Hence 'Pancrustacea' would be synonymous to Labrophora (**Figure 1B**; as characterised by Siveter et al. ; although it would be probably more stable if the name Labrophora would be linked to only one of these autapomorphies) [25-27].

Yet, it is possible that Myriapoda is more closely related to Eucrustacea (with Hexapoda as an ingroup) than Phosphatocopina to Eucrustacea. In this case, the pan-monophylum concept could not be applied as there would be no known fossil branching off the evolutionary lineage towards Eucrustacea after the branch of Myriapoda. The same scenarios can also be applied if Hexapoda and Myriapoda form a monophyletic Tracheata.

Therefore, this application of pan-monophylum concept(s) means something different than implied by Zrzavý & Štys [1], hence would be ambiguous. And an alternative name is instead available.

Example 4) 'Crustacea'=Crustacea sensu lato: Eucrustacea, Phosphatocopina, Hexapoda and Myriapoda are very likely all ingroups of Crustacea sensu lato [23,24]. Crustacea sensu lato includes also a number of fossil representatives which have been addressed as stem-crustaceans [18,28] or stem-mandibulates [28], better as early derivatives of the evolutionary lineage towards Eucrustacea [18,21,29,30].

There is no application of the pan-monophylum concept that can be used as an equivalent for Crustacea sensu lato. This is due to the fact that the sister group of Crustacea sensu lato, Agnostina, has no extant representatives and therefore would have to be included into any pan-monophylum also including the early representatives of Crustacea sensu lato (together with many further groups, see below). Yet we could still use Crustacea sensu lato for “constructing” Pan-Crustacea/Pancrustacea.

If we now apply the pan-monophylum concept based on Crustacea sensu lato (or on a monophyletic group Eucrustacea that includes Hexapoda and Myriapoda [31], 'Pancrustacea' would be a very large group including also Agnostina, probably trilobites, possibly also nectaspidids and many other fossil euarthropods **(Figure 1D)** [32] as the next group with extant representatives is Chelicerata sensu lato [33,34]. Thus, 'Pancrustacea' in this case would equalize that part of Euarthropoda that does not comprise chelicerates[35].

To summarize: Pan-Crustacea or Pancrustacea can mean quite different groups than Pancrustacea sensu Zrzavý & Štys [1] Hence, the term is ambiguous and does not allow a distinct communication about hypotheses of relationships among researchers. For the different possible meanings other less ambiguous names are available.

Why is the use of 'Panarthropoda' ambiguous?

With the term 'Panarthropoda' we face similar problems as with 'Pancrustacea'. Currently, as for 'Crustacea' there is no generally well-recognised monophyletic group named 'Arthropoda' (exceptions see below). Thus, we have to discuss several cases independently.

Example 1) Panarthropoda=Arthropoda+Onychophora+Tardigrada: Nielsen [2] introduced the term Panarthropoda to include Arthropoda (apparently in the sense of Euarthropoda, see below), Onychophora, and Tardigrada **(Figure 1E)**. As Onychophora and Tardigrada are groups with numerous extant representatives, this use has to differ from any construction of a pan-monophylum. If applied to Arthropoda (as Nielsen applied the term), Pan-Arthropoda/Panarthropoda would exclude Onychophora and Tardigrada. Hence, the term is ambiguous in this case.

Example 2) Arthropoda=Euarthropoda or Arthropoda sensu stricto: 'Arthropoda' could be equalised, following a neontological view, to Euarthropoda. The most stable use of Euarthropoda is probably the one introduced by Walossek [17] as it is again an autapomorphy-based characterisation, founded on 1) a head including five segments, the ocular and four appendage-bearing ones, and 2) the formation of a basipod on the appendages of the second post-ocular segment and further posterior ones (although also here it would be more stable to choose one of the two, i.e., to choose a kind of “holotype” character that is unchangeably connected to the name, like a holotype is unchangeably connected to the name of a species, would indeed make

sense; see above). Based on this use of Euarthropoda, 'Panarthropoda' could, for example, include all fossil representatives down before Pentastomida, Tardigrada or Onychophora [25] branch off the evolutionary lineage towards Euarthropoda. This use of 'Panarthropoda' could equalise more or less the monophyletic group Arthropoda sensu stricto, also an autapomorphy-based group including all sclerotised arthropods **(Figure 1F)** [36]. Yet, this application of 'Panarthropoda' to Euarthropoda most likely additionally includes the one or other lobopodian [37].

The grouping Arthropoda sensu stricto could also be addressed as Arthropoda as it is supposed by Hou & Bergström [38], or as 'upper euarthropod stemgroup' of Budd, yet especially the last term is at least as ambiguous as Panarthropoda [39].

If we apply a pan-monophylum concept to Arthropoda sensu stricto, Onychophora and/or Tardigrada would not be included as these have extant representatives. To be more precise, it makes in fact no difference whether Euarthropoda or Arthropoda sensu stricto is used for this approach, as all extant representatives of Arthropoda sensu stricto are ingroups of Euarthropoda.

Two group names are available for a monophyletic group, which includes sclerotised arthropods plus Onychophora and Tardigrada (and other groups, e.g., lobopodians): Arthropoda sensu lato [36] or Aiolopoda [38].

Example 3) Arthropoda=Arthropoda sensu lato: If the monophyletic group Arthropoda sensu lato is used as a basis for forming a pan-monophylum 'Panarthropoda', we face the problem that we currently do not have a fossil candidate branching off the evolutionary lineage towards Euarthropoda before Onychophora (or Tardigrada, depending which is interpreted as the earliest branch; **Figure 1G**). It is, of course, likely that the one or other long-legged lobopodian could indeed occupy such a position. Yet, currently Panarthropoda/Pan-Arthropoda in this sense would be equal to Arthropoda sensu lato, i.e., there is no gain in this application.

As before for Pancrustacea, Panarthropoda could refer to numerous different groups, none of which is identical with the original one used by Nielsen [2]. Hence again the term is highly ambiguous.

CONCLUSION

In summary, the application of the prefix 'pan' to crustaceans and arthropods has been rather unfortunate. The original use was different from any previously suggested pan-monophylum concept, and even a strict use of such a concept is hindered by systematic uncertainties.

We do not suppose a strict catalogue of how to name monophyletic groups or banish certain names. The important point here is that the names 'Panarthropoda' and 'Pancrustacea' can be understood in (sometimes very) different ways. Such an ambiguity hampers a precise communication among researchers.

As shown above, for all cases for which the two 'Pan-' names have been applied, alternative names are available, often even several ones to emphasise the different compositions or characters. Also additional names are available for addressing specific nodes in between the “normal” monophylum and the pan-monophylum. This allows a very precise communication for addressing very specific evolutionary events or referring to explicit events in character evolution. We therefore suggest to use one of these names instead of the terms 'Pancrustacea' and 'Panarthropoda'. If one intends to use these latter two names, one needs to take action to prevent any possible misunderstanding and should also state why such a highly ambiguous term is used instead of a more precise one. Such a procedure would be one step forward to reach a terminology that is scientific in the sense of being unambiguous, or at least being less ambiguous.

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