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Reconstruction, composition and homology of conodont skeletons – a response to Agematsu *et al*. 2018

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Agematsu *et al*. (2018) comment on our recent paper about testing hypotheses of element loss and apparatus stability in the apparatus composition of complex conodonts (Zhang *et al.* 2017). They take issue not with our approach, but with our specific hypothesis concerning the skeletal apparatus of *Hindeodus parvus*. We proposed that, in marked contrast to the remarkable anatomical conservatism exhibited by ozarkodinid conodonts, which seem not to vary their 15 element 'dental formula' over a period in excess of 250 million years, *H. parvus* had only 13 elements, lacking 2 elements from the posterior P domain of the apparatus.

Our paper presents an hypothesis of homology for the skeletal elements of *H. parvus* that Agematsu *et al*. (2018) argue is incorrrect, based on three lines of reasoning:

1. Previous hypotheses concerning which of the elements found in collections of disarticulated skeletal material belong together as components of the multielement taxon *Hindeodus*;

2. Evidence of stability in the inferred homology of those elements, implied by how previous authors have applied conodont anatomical notation;

3. The new material and interpretations of Agematsu *et al*. (2017).

We take issue with the first two parts of their argument. They discuss apparatus reconstruction and composition as if these things were the same as hypotheses of homology, but there are important distinctions, and we take this opportunity to clarify the differences between reconstructing the multielement composition of a conodont taxon, inferring hypotheses of homology for elements within such a reconstructed taxon, and the evidence required to provide a definitive test of such hypotheses.

Reconstruction and proxies for homology

Conodonts are generally found as individual, morphologically discrete microfossils known as elements, sometimes many thousands in a single sample. For the first few decades of their study, each distinct type of element was treated as if it constituted a taxon. Elements with similar shapes were combined into genera, and a form taxonomy developed that looked superficially like the application of a biological system. From the 1930's, however, evidence began to accumulate that conodont microfossils were in fact components of a skeleton that contained a number of different types of elements. Elements that had been, on the basis of their shape, assigned to different species and genera in fact occurred together within the same skeleton. This clearly had major implications for the single-element approach to naming and defining taxa, but if took several decades of work, starting in earnest in the 1960's to develop a biologically meaningful taxonomy (for discussion see, for example, Sweet 1981; Sweet 1988).

This slow revolution required two distinct things, which are essentially the two arguments put forward by Agematsu *et al*. (2018): first, evidence and methods by which to recognize and put together the elements in collections of isolated skeletal parts that came from the same taxon, and second, the development of hypotheses of homology. Although multielement reconstruction is possible without hypotheses of homology, the ability to recognize, compare and apply consistent terminology to homologous parts of the skeletons of different taxa is a fundamental prerequisite of developing a biologically meaningful taxonomy. Without hypotheses of homology, comparative anatomy is impossible, and discussion of phylogenetic and evolutionary patterns is meaningless.

In many ways it is desirable, and more intellectually robust, to keep separate the process of reconstructing conodont taxa and the process of proposing hypotheses of homology, but the distinction became blurred. Increasing numbers of reconstructed conodont species revealed that many taxa contain the same basic types of elements, conforming to a small number of broad morphological categories, described either using descriptive terms such as pectiniform, ramiform, bipennate, and angulate, or terms derived from the pre-multielement form taxa to which they would have been assigned, such as ozarkodiniform and spathognathidontiform (Table 1 of Agematsu *et al*. (2018) provides examples of both). It also became clear that these element types were recognizable in fossils preserving articulated skeletal remains. Perhaps inevitably, because the number of taxa preserved as articulated skeletons was small compared to the number of taxa being reconstructed, these

two sets of evidence were mixed to provide a morphological search-image of what to look

for when reconstructing conodont taxa, with the consequence that as ideas of homology

developed, they were closely linked to the morphological criteria for recognizing the

elements one would expect to find in a conodont taxon (e.g. Sweet and Schönlaub 1975;

Sweet 1981, 1988).

Topological homology in conodonts and its application to *Hindeodus parvus*

As more fossils preserving articulated conodont remains were discovered, and more effort

was expended in interpreting them (e.g. Norby 1976; Aldridge *et al.* 1987; Purnell 1993;

Purnell and Donoghue 1997), the confusion created by not separating the meaning and

definition of homology from the proxy criteria used to infer it started to create issues of

communication, and the need (anticipated by Sweet 1981) for a more strictly defined

concept of topological homology and means of differentiating this from less secure

morphologically inferred hypotheses, became clear (Purnell 1993; Purnell *et al.* 2000). The

widely used anatomical notation of Purnell *et al*. (2000) proposed an operational concept of

homology as an hypothesis of similarity *based on topological relations* and which contains

potential phylogenetic information (see Rieppel 1994; Purnell *et al.* 2000 for discussion).

Topology refers to the numbers of, and the relative spatial relationships between,

recognizable anatomical units (i.e. conodont elements in a skeletal apparatus). Purnell *et al*.

(2000) were explicit that 'similarity' did not mean morphological similarity of elements. This

is the anatomical notation and underpinning homology concept employed by Agematsu *et

al*. (2014, 2017, 2018) and by Zhang *et al*. (2017). And because this system is based on

topology, the evidence for numbers of elements and the relative spatial relationships

between them in articulated skeletons provides the ultimate test of hypotheses of

homology that have been inferred on the basis of element morphology and proposed

evolutionary relationships.

It also follows from this that these inferred hypotheses cannot test or falsify the evidence of

homology provided by articulated skeletons, and this is what we take issue with in

Agematsu *et al*. (2018). In this context, it does not matter how many authors over multiple

decades have consistently adhered to a concept of *Hindeodus* in which elements of a

particular morphology are considered to be the 'same' element, and Agematsu *et al*. (2018)

are wrong to state that this "strongly suggests that the angulate elements identified in the bedding plane assemblages of *Hindeodus parvus* by Agematsu *et al*. (2014) are P_2 elements". It does not matter because before the discovery of articulated skeletons (Agematsu *et al.* 2014), all hypotheses of homology in *Hindeodus* were inferred on the basis of morphology and are falsifiable by the direct evidence of topology contained in the articulated skeletons. The principal difference between Agematsu *et al*. (2017, 2018) and Zhang *et al*. (2017) concerns the presence of a P_2 element, but the arguments of Agematsu *et al*. (2018) that draw on previous reconstructions of the multielement taxon *Hindeodus* and stability in the inferred homology of those elements (their Table 1, Fig. 1) are simply not relevant because they do not provide a test of the hypothesis.

Table 1 (Agematsu *et al.* 2018) confuses the issue on multiple levels. Because the table is organised into columns labelled with the anatomical notation of Purnell *et al*. (2000) Agematsu *et al*. (2018) imply that the authors of the reconstructions listed in rows each expressed an hypothesis of homology consistent with the topological concepts of Purnell *et al*. (2000), but this is incorrect. In many cases, the authors applied morphologically based descriptive terms to their reconstructions, not terms designed to imply homology between taxa; the apparent stability in these reconstructions simply reflects the fact that different authors were consistently able to find the 'same' element with angulate/ozarkodiniform/ozarkodinan morphology (see Sweet 1981 for discussion). Inferring that within *Hindeodus* these elements were homologous with one another, because of their close morphological similarity, is a reasonable hypothesis, and in many cases the authors' intentions probably extended no further than this. It is a different hypothesis to suggest that these elements were homologous with all other elements identified as occupants of P_2 positions in all other taxa. Yet this is what Table 1 implies, without recognizing the distinction between the relatively strong evidence that morphology can provide for homology *within* a genus compared to its weaker power and lesser reliability as evidence of homology *between* taxa above species level. As we not above, prior to the discovery of articulated skeletons of *Hindeodus*, hypotheses of homology between elements of *Hindeodus* and those of other taxa were *inferred* on the basis of morphological criteria, and this applies to all the reconstructions in Table 1 except Agematsu *et al*. (2014), and Zhang *et al*. (2017). Irrespective of how reliable these morphological criteria seem, they

carry less weight than topological evidence: the direct evidence can test and overturn hypotheses inferred from morphology, but inferred hypotheses cannot overturn the evidence of topology.

The apparatus of *H. parvus*, and the implications for stability and constraint

The important differences between the interpretations of Agematsu *et al*. (2014), Zhang *et al*. (2017) and Agematsu *et al*. (2017) are differences in hypotheses of homology (Figure 1). As Agematsu *et al*. (2017) note, the articulated skeletal material described by Agematsu *et al*. 2014 was insufficient to determine whether the S_1 locations of the apparatus were occupied. Their specimens provided clear evidence for only 13 elements (rather than the typical 15), and in finding evidence in new fused material for a complete S array, Zhang *et al*. (2017) proposed that it was the P_2 locations, and not S_1, that were unoccupied. The new material and interpretations of Agematsu *et al*. (2017) provide a definitive test of these alternative hypotheses of element homology for *H. parvus*. They clearly support the hypothesis of Zhang *et al*. (2017) for a full suite of S_1-S_4 elements, but also find evidence for an additional pair of elements which, in the best preserved of the specimens figured by Agematsu *et al*. (2014, 2017; i.e. those exhibiting the least disruption of original element juxtaposition), are located near to the S array. The most parsimonious interpretation is that put forward by Agematsu *et al*. (2017): these are P_2 elements (the alternative would require duplication of an S element pair, and loss of the P_2 elements). However, the apparent location of P_2 elements, closer to the S array than they are in other ozarkodinid taxa known from articulated skeletons, raises some interesting questions.

The evidence presented by Agematsu *et al*. (2017) is not conclusive (well preserved specimens exhibiting lateral collapse orientations would provide a more stringent test), but it suggests that in *Hindeodus parvus*, the P_2 elements are more closely associated with the S array than in other conodont taxa for which we have direct evidence of the 3D architecture of the skeleton. This implies a shift in function to one more associated with prey prehension or perhaps moving food from the rostral S-M array toward the P_1 elements for processing. Interestingly, the P_2 elements are morphologically somewhat different from more typical examples of ozarkodinid P_2 elements. They have relatively larger cusps, with the flexure and denticulation of the process (e.g. Agematsu *et al*. 2018, figure 1B) to a degree reminiscent of elements that occupy S positions (albeit shorter). The location of the P_2 elements in *H.*

parvus, and their morphology, supports our functional hypothesis (Zhang *et al*. 2017) for a shift in *H. parvus* towards foods that can be ingested with less slicing or crushing. The evidence is less clear, but the specimens of Agematsu *et al*. (2014, 2017) also suggest that the caudal processes of the M elements were perhaps more parallel to the S array that in other ozarkodinid taxa. Although the new evidence highlights subtle differences between *H. parvus* and other ozarkodinid taxa, the broader point we make (Zhang *et al.* 2017) remains true: the 15 element 'dental formula' of ozarkodinid conodonts remained stable for more than 250 million years, and this signal of remarkable functional and/or developmental constraint is worth further investigation.

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Fig. 1. The different hypotheses of topological element homology proposed by Agematsu *et al*. (2014), Zhang *et al.* (2017) and Agematsu *et al*. (2017): diagrammatic representations of how these authors interpreted the articulated skeletal material preserved on bedding planes, not plans of apparatus structure (rostral is towards top of page). Element morphology is simplified. Both Agematsu *et al.* (2014) and Zhang *et al.* (2017) proposed hypotheses of homology for a 13 element apparatus, but they differed in the interpretation of the elements located on what is, as drawn here, the medial side of the S array. Agematsu *et al*. (2017) found evidence for 15 elements; this is typical for ozarkodinids, but the apparent location of the P_2 elements is unusual.
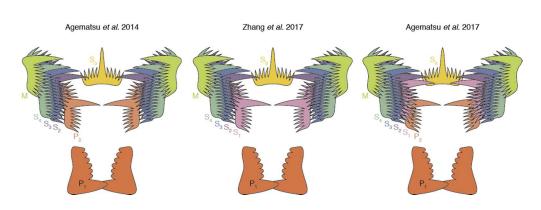
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