



## CLADISTIC TESTS OF MONOPHYLY AND RELATIONSHIPS OF BIOSTRATIGRAPHICALLY SIGNIFICANT CONODONTS USING MULTIELEMENT SKELETAL DATA – *LOCHRIEA HOMOPUNCTATUS* AND THE GENUS *LOCHRIEA*

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**Abstract:** Since the 1960s, huge progress has been made in reconstructing the multielement skeletons of conodont species and developing a biologically defensible taxonomy. Nevertheless, a widespread prejudice remains that certain parts of the conodont skeleton, particularly the P<sub>1</sub> elements, are more informative than others with regard to taxonomy and evolutionary relationships. Here, we test these views. A new partial multielement reconstruction of the skeleton of the biostratigraphically significant conodont originally described as *Gnathodus commutatus homopunctatus* allows us to conduct a cladistic test of the alternative hypotheses of phylogenetic placement of this species. Our analysis also provides the first test of the hypothesis that *Lochriea* – species of which are markers for global correlation – is monophyletic and tests hypotheses concerning the origins of the genus. Our results demonstrate that *homopunctatus* is a species of *Lochriea* and that the genus is monophyletic. The widely held view that *Lochriea* arose from a species of *Bispathodus* is not supported. Our results show that it is difficult to predict *a priori* which parts of the conodont skeleton carry phyloge-

netic signal, and provide strong support for the hypothesis that similarity in the morphology of conodont P<sub>1</sub> elements alone is not a reliable guide to relationships and taxonomic groupings of conodont species. This is because P<sub>1</sub> elements with similar morphologies are convergently acquired in multiple conodont clades, because reliance on the characters of only one of the six or seven morphologically distinct elements of the conodont skeleton ignores phylogenetically significant data and because P<sub>1</sub> elements can lack characters that might seem to be diagnostic of a genus. Conodonts are no different to other organisms: ignoring data that have the potential to be phylogenetically informative is unlikely to produce the most reliable hypotheses of evolutionary relationships. We suggest that other biostratigraphically significant hypotheses of relationship between conodont taxa that are based on P<sub>1</sub> elements alone should be subject to cladistic testing.

**Key words:** conodont, multielement, biostratigraphy, phylogeny, cladistic, taxonomy.

CONODONTS, like all organisms, are never preserved as anatomically complete fossils. With few exceptions (Aldridge *et al.* 1993; Gabbott *et al.* 1995; von Bitter *et al.* 2007), the soft tissues of the body have disappeared without trace, and the skeletal remains, like those of other animals with multicomponent skeletons, are found in varying states of completeness. Many taxa are known from articulated skeletons (Purnell and Donoghue 1997) but, for a variety of taphonomic reasons, the vast majority are found only as disarticulated elements (Purnell and Donoghue 2005). Since the 1960s, conodont workers have risen to the challenges of reconstructing the multielement

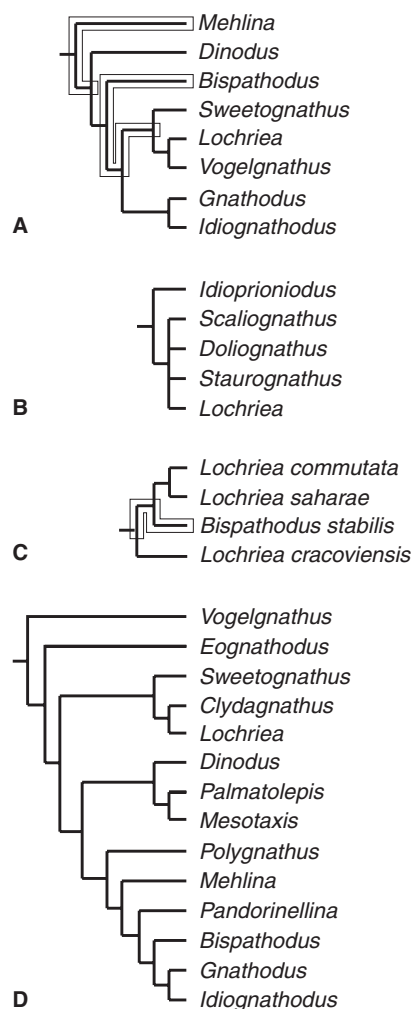
composition of conodont taxa and developing a biologically defensible taxonomy (see Sweet and Donoghue 2001 for an overview). They have mostly moved away from the form taxonomy that characterized earlier studies, where genera and higher taxa were erected to accommodate morphologically similar element types. Under this scheme, the different elements that in life belonged to an individual conodont might have been assigned to five or six different genera.

Despite the huge strides made, there is still a widespread view among conodont workers that some parts of the conodont skeleton are more informative than others

with regard to taxonomy and evolutionary relationships. In terms of species-level taxonomy this may be defensible in some cases because, in many species, it is the P<sub>1</sub> element that is the most morphologically complex and character rich element of the skeleton. However, this is not always true (some P<sub>1</sub> elements are morphologically simple), and over-reliance on the P<sub>1</sub> element (or any other single component of the skeleton) as a guide to the relationships between species, genera and more inclusive clades of conodonts makes the risky and dubious assumption that the selected part of the skeleton has not been affected by homoplasy. In this study, we take common and familiar conodont taxa – the genus *Lochriea*, and the species originally erected as *Gnathodus commutatus homopunctatus* – and demonstrate using cladistic approaches to analysis and testing of phylogenetic hypotheses that P<sub>1</sub> elements alone are not a reliable guide to evolutionary relationships and generic-level taxonomy.

*Lochriea* is a biostratigraphically important conodont taxon. First appearances of *Lochriea* species and transitions within evolutionary lineages of *Lochriea* are markers for global correlation (e.g. Somerville 2008 for discussion), and the first appearance of *L. zieglerei* in the lineage *L. nodosa*-*L. zieglerei* is currently under investigation as a marker for the GSSP identifying the Viséan–Serpukhovian boundary (Menning *et al.* 2006). Yet hypotheses concerning the origins of the genus and its monophyly remain untested, with several alternatives in the literature (Fig. 1). Many authors have suggested that *Lochriea* evolved from *Bispathodus stabilis* (Meischner 1970; Higgins 1975; Park 1983), although Nemyrovska *et al.* (2006; Fig. 3) imply that *Lochriea* is polyphyletic with the type species, *L. commutata* evolving from *Bispathodus stabilis* via *L. saharae*, while another early species *L. cracoviensis*, evolved direct from *B. stabilis*. Sweet (1988) interpreted *Lochriea* as a close relative of and possibly congeneric with *Vogelgnathodus* and suggested that, perhaps together with *Sweetognathus*, these taxa formed a group of conodonts derived from *Bispathodus* (following Belka 1985). Dzik's (1991) classification suggested that the origin of *Lochriea* was within bactrognathidae, along with taxa such as *Scaliognathus*, *Doliognathus*, *Staurogathus*, possible descendants of *Idioproniodus*. The results of the cladistic analysis of Donoghue *et al.* (2008; based on complete skeletal data, available only for *L. commutata*), partially supported Sweet's (1988) view (*Lochriea* forming a clade with (*Sweetognathus* + *Clydagnathus*), but not as a close relative of *Vogelgnathus*). This result is incompatible with Dzik's (1991) hypothesis.

Similar difficulties centre on the conodont originally described as *Gnathodus commutatus homopunctatus* Ziegler 1960. This is also a biostratigraphically important taxon, taken as a globally correlated marker for the base of the Viséan (Lower Mississippian; Menning *et al.* 2006), but the agreement over the biostratigraphic significance



**FIG. 1.** Previously proposed relationships for *Lochriea*, expressed as cladistic hypotheses. A, Sweet (1988). B, Dzik (1991). C, Nemyrovska *et al.* (2006). D, Donoghue *et al.* (2008). Where *Bispathodus* was interpreted as ancestral to multiple descendant taxa, a white boxing shows it as paraphyletic, spanning several nodes on the tree. The study of Donoghue *et al.* (2008) contains detailed discussion of how the cladograms shown in A and B were derived from the original ancestor–descendant hypotheses of Sweet (1988) and Dzik (1991).

of this conodont contrasts markedly with confusion over its taxonomy and phylogeny. Originally erected as a subspecies of what is now *Lochriea commutata* (Ziegler), it has since been referred to *Gnathodus* (Somerville and Somerville 1999; Menning *et al.* 2006), *Paragnathodus* (Tian and Coen 2005) and *Protognathodus* (Dzik 1997). A number of recent papers refer the species to *Pseudognathodus* (Groves *et al.* 2003; Nemyrovska 2005; Nemyrovska *et al.* 2006; Kullmann *et al.* 2008; Pazukhin *et al.* 2010), but there is little sign of taxonomic consensus except that it is not a species of *Lochriea* (note however that Norby (1976, p. 143) speculated that *L. homopunctatus* ‘may well

belong to *Lochriea*' but also cautioned that such an assignment required evidence from non-P<sub>1</sub> elements). The lack of agreement over the taxonomy of this species presents us with the difficulty of how we should refer to it here. To facilitate discussion, we use the name *Lochriea homopunctatus* throughout this paper. This has the advantage of avoiding different names being applied to the same species in different parts of the paper, but it does rather pre-empt our conclusions.

Our purpose with this paper is to exemplify some of the difficulties caused by over-reliance on P<sub>1</sub> elements in conodont taxonomy and to clear up some of the taxonomic and phylogenetic difficulties outlined above. To do this, we present a new, partial reconstruction of the skeleton of *Lochriea homopunctatus* and a phylogenetic analysis designed to test the following:

1. Alternative hypotheses of phylogenetic placement of *L. homopunctatus*
2. Monophyly of *Lochriea*
3. Hypotheses of *Lochriea* origins and the affinities of the genus.

## PREVIOUS WORK

Previous attempts to address the issues outlined above have failed to reach satisfactory conclusions for a number of reasons. Firstly, in the absence of knowledge of the rest of the skeleton, all previous attempts to determine the relationships of *Lochriea homopunctatus* have been forced to rely on evidence from P<sub>1</sub> elements only. This approach to the taxonomy and systematics of conodonts has long been known to be unreliable, and evidence is now very strong that the relative scarcity of P<sub>2</sub>, M and S elements of many taxa reflects a taphonomic bias in the conodont fossil record, and does not indicate that some taxa had apparatuses containing only one type of element (Purnell and Donoghue 2005). Yet rejection of the hypothesis that *L. homopunctatus* is a species of *Lochriea* is based entirely on features of the P<sub>1</sub> element: the absence of polygonal microtextures on the tips of the denticles of the carina, the shape of the basal cavity and the shape of the blade in 'lateral' view (subrectangular in *Lochriea*).

The assignments by previous workers of *L. homopunctatus* to *Paragnathodus* and *Pseudognathodus* beg important questions regarding the validity of these genera. In fact, neither are available as generic names. *Paragnathodus* was formally defined by Higgins (1975), but its status as a junior synonym of *Lochriea* is now well established (Stone 1991; Skompski et al. 1995). *Pseudognathodus* was defined by Park (1983) in a PhD thesis and does not satisfy the requirements of publication specified by the International Commission on Zoological Nomenclature (1999; chapter 3). The name is thus a *nomen nudum*.

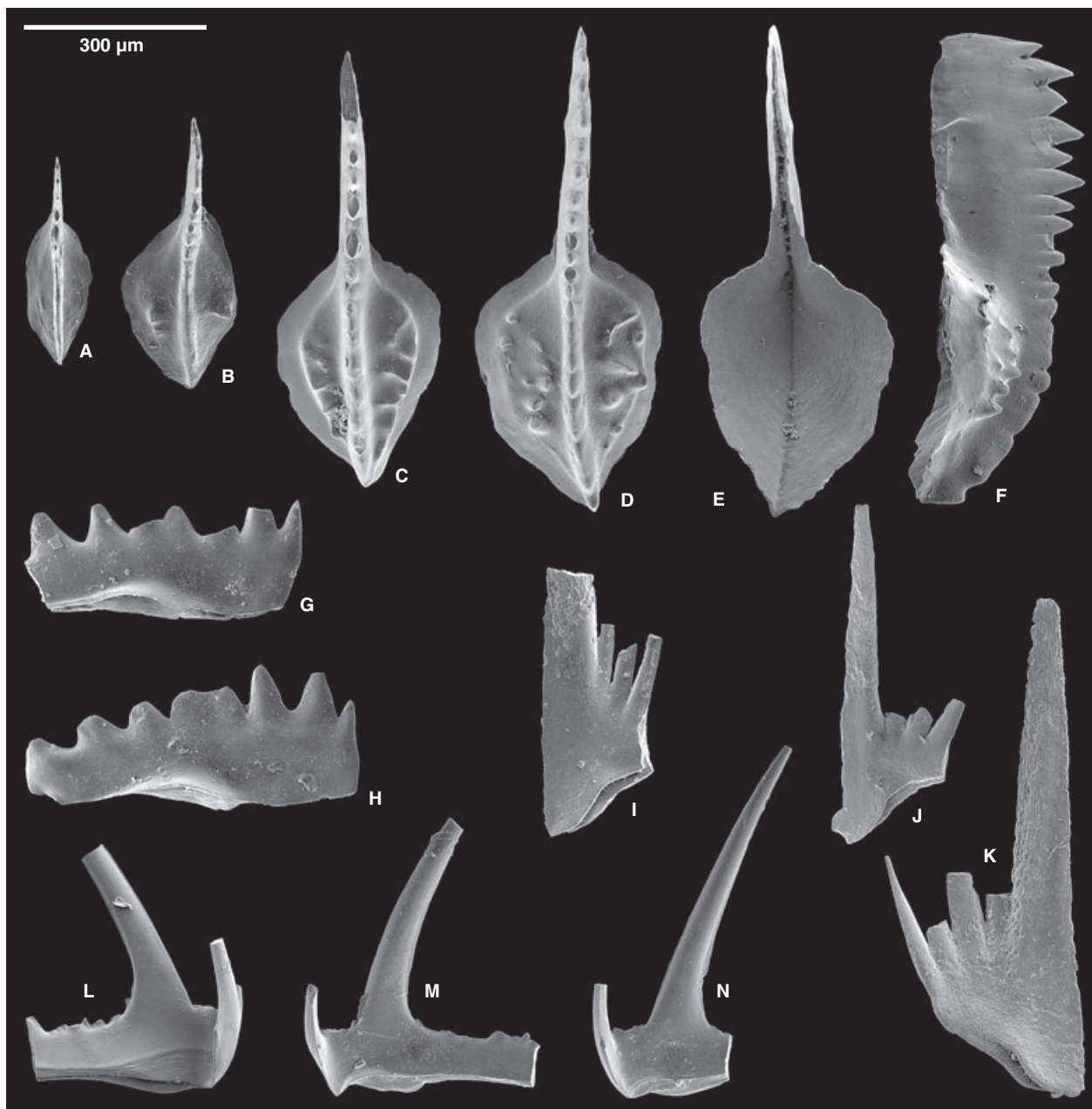
Most previous hypotheses of the origins of *Lochriea* and relationships between *Lochriea* species have placed too much reliance on similarities between P<sub>1</sub> elements. Nemyrovskaya et al. (2006, p. 366), for example, acknowledged the contradiction in the data, but explicitly down-weighted the evidence of the non-P<sub>1</sub> elements in reaching their conclusions: 'The availability of forms with intermediate features between the Pa (= P<sub>1</sub>) elements of *Bi. stabilis* and *L. cracoviensis* and between those of *Bi. stabilis* and *L. saharae* seems to support the suggestion of the derivation of *Lochriea* from *Bi. stabilis* (text-fig. 3), in spite of the other elements (Pb, M and S) of *Lochriea* differing from those of *Bispathodus*.'

Given the importance of *L. homopunctatus* and *Lochriea* species as global biostratigraphic markers, robust testing of monophyly of the genus and phylogenetic relationships and resolution of taxonomic difficulties are overdue.

## MATERIAL AND METHODS

Our reconstruction of the apparatus of *L. homopunctatus* is based on material collected from the Rain Gill Limestone Member of the Hodder Mudstone Formation, of Mid Mississippian age (Arundian Stage) from Lancashire, UK (Riley 1990; UK grid reference SD 6945 4833). This argillaceous limestone includes several parallel laminated beds and horizons of coarse shelly debris; it is interpreted as a turbidite bed deposited in a deepwater hemipelagic setting (Riley 1990). Five samples were found to contain P<sub>1</sub> elements of *L. homopunctatus* along with morphologically distinctive P<sub>2</sub>, M and S elements that could not be assigned to any of the 11 other co-occurring species. The most parsimonious interpretation of these elements (Fig. 2) is that they are part of the skeleton of *L. homopunctatus*. The taxa, together with abundances of the elements recovered from the studied samples, including the P<sub>2</sub>, M and S elements of *Lochriea homopunctatus*, are shown in Table 1.

We have adopted a cladistic approach to testing hypotheses of affinity and relationships of *Lochriea* species. Although widely applied to other vertebrate groups, this approach has been used only rarely to test relationships between conodont species (Donoghue 2001a, b; Zhang and Barnes 2004; Wickström and Donoghue 2005; Donoghue et al. 2008; Jiang et al. 2001). Donoghue's (2001a) analysis, like this paper, used cladistic methods to compare hypotheses of relationships based on single elements with those based on reconstructed apparatuses. We refer readers to the study of Wickström and Donoghue (2005) in particular for discussion of the problems inherent in non-cladistic approaches to conodont phylogenetics. The framework for our analysis is provided by the recent work of Donoghue et al. (2008). Their analysis was designed to test hypotheses



**FIG. 2.** *Lochriea homopunctatus* (Ziegler, 1962). A–C, P<sub>1</sub> elements, oral views, specimens BGS MPK 14219, 14220, 14221. D–F, P<sub>1</sub> element, oral, aboral and ‘lateral’ views, specimen MPK 14222. G–H, P<sub>2</sub> elements, ‘lateral’ views, specimens MPK 14223, 14224. I–K, P<sub>3</sub> elements, ‘posterior’ views, specimens MPK 14225, 14226, 14227. L–N, S<sub>3/4</sub> elements, ‘lateral’ views, specimens MPK 14228, 14229, 14230. All elements from sample MPA 20680.

of relationship between the higher taxa of conodonts with apparatuses composed of morphologically complex elements. Because the scope of our analysis is more limited, we have restricted our taxon sampling to include the range of conodonts within which previous hypotheses have placed the genus *Lochriea* and *L. homopunctatus*. Additionally, a number of more basal but closely related taxa (Donoghue *et al.* 2008) were selected as outgroup taxa for the

purposes of tree rooting (*Wurmiella excavata*, *Ozarkodina confluens*, *Ozarkodina hassi* and *Kockelella ranuliformis*; multiple outgroup taxa are preferable to a single taxon). In total, our taxon sampling equates closely to the superfamily Polygnathacea (*sensu* Donoghue *et al.* 2008), but we have included only the taxa of their ‘tranche 2’ data set because this provides the best compromise between breadth of taxon coverage and quality of data (Table 2).



**TABLE 1.** Abundance of conodont elements in all analysed samples from the Rain Gill Limestone that contain elements of *Lochriea homopunctatus* (samples have BGS numbers).

Sample no	20680	20683	20684	20685	20686
<i>Mestognathus beckmani</i>					
P <sub>1</sub>	5	2	1	1	3
P <sub>2</sub>	1				
M	2				
<i>Cavusgnathus unicornis</i>					
P <sub>1</sub>			2		
<i>Patrognathus capricornis</i>					
P <sub>1</sub>		2			
<i>Vogelgnathus campbelli</i>					
P <sub>1</sub>	23				
S	2				
<i>Vogelgnathus gladiolus</i>					
P <sub>1</sub>	1				
M	1				
<i>Polygnathus bischoffi</i>					
P <sub>1</sub>	15	4			
<i>Lochriea homopunctatus</i>					
P <sub>1</sub>	11	19	6	3	12
P <sub>2</sub>	2				
M	3		1		2
S	5				
<i>Gnathodus texanus</i>					
P <sub>1</sub>	23	13	6	2	13
P <sub>2</sub>	17			1	
M	2				
S	5				
<i>Hindeodus cristulus</i>					
P <sub>1</sub>	2			1	
P <sub>2</sub>				1	
M	5				
S	1				
<i>Syncladognathus</i> sp.					
Pa	4				
S	9		1		
<i>Idioproniodus healdi</i>					
	11	4	2	7	1
<i>Kladognathus</i> sp.					
S	2				1
Indet	3				
Indet. S fragments	47		4	4	17
Indet. elements	4	1		1	
Indet. P <sub>2</sub> elements	1	1		1	2
Indet. fragments	65	7	8	4	16
Total	272	53	31	26	67

In addition, the following taxa are included: *L. homopunctatus*, *Lochriea saharae*, *Bispathodus stabilis* and *Protognathodus kockeli*. *Bispathodus stabilis* and *L. saharae* are included to test the interpretation of Nemyrovska *et al.* (2006) that *Bispathodus stabilis* was the ancestor of *Lochriea saharae*, which in turn was the ancestor of

*L. commutata*. Ideally, we would also have liked to test hypotheses of relationship of other species of *Lochriea*, but only their P<sub>1</sub> elements are known with certainty because samples containing P<sub>1</sub> elements of only one species of *Lochriea* accompanied by the non-P<sub>1</sub> elements are not common. For the purposes of our analysis, it is important that we do not make assumptions about the P<sub>2</sub>, M and S elements. For this reason, even though Nemyrovska *et al.* (2006) stated that the P<sub>2</sub>, M and S elements of *L. commutata*, *L. saharae* and *L. cracoviensis* were morphological indistinguishable, the co-occurrence of these elements and taxa in their samples make this hypothesis difficult to test, and we do not include *L. cracoviensis* in our analysis. *Lochriea saharae* is included because Nemyrovska *et al.* (2006) illustrate an M element (pl. 2, fig. 8) from a sample (3191) that contains P<sub>1</sub> elements of only one *Lochriea* species: *L. saharae*. We interpret this M element that of *L. saharae*, and our coding reflects this. For *Bispathodus stabilis*, we follow the reconstruction of Over (1992, fig. 6; positional homologies: P<sub>1</sub> = Pa, P<sub>2</sub> = Pb, M = M, S<sub>0</sub> = Sa, S<sub>1</sub> = Sb<sub>2</sub>, S<sub>2</sub> = Sb<sub>1</sub>, S<sub>3</sub> = Sc<sub>2</sub>, S<sub>4</sub> = Sc<sub>1</sub>).

*Protognathodus kockeli* is included to test Dzik's (1997, p. 130) hypothesis that the affinities of *L. homopunctatus* lie with *Protognathodus*. Although he acknowledged that his faunas did not allow him to recognize anything except the P<sub>1</sub> elements of *L. homopunctatus*, Dzik concluded that 'the primitive morphology of the sp (=P<sub>1</sub>) elements suggests that it is rather a direct successor of early Tournaisian *Protognathodus*.' We follow Dzik's (1997, fig. 8) reconstruction of *P. kockeli*; to our knowledge, this is the only species of *Protognathodus* for which a reconstruction is available (positional homologies: P<sub>1</sub> = sp, P<sub>2</sub> = oz, M = ne, S<sub>0</sub> = tr, S<sub>1</sub> = lo, S<sub>2</sub> = pl, S<sub>3/4</sub> = hi). Along similar lines, Nemyrovska *et al.* (2006, p. 366) speculated 'about the origin of *Lochriea* from *Protognathodus*' but noted that 'there is no evidence on their common multi-element construction'. They did not include *L. homopunctatus* in the genus and, as noted above, favoured a hypothesis deriving *Lochriea* from *B. stabilis*.

The characters upon which our analysis is based are the same as those used by Donoghue *et al.* (2008; with a few minor corrections to coding – Table 2, see Donoghue *et al.* 2008 for character descriptions). These characters were designed to test broader hypotheses of relationships between morphologically complex conodonts, and consequently, their use in our analysis has both advantages and disadvantages. A number of characters are phylogenetically uninformative because our taxon sampling is limited to taxa for which they score either all zeros or all ones. These will have no impact on our results. The criticism could also be made that the characters are not optimal for testing the specific hypotheses of relationship in which we are interested, but given the fairly broad range of taxa within Polygnathacea with which *Lochriea* and *L. commu-*

TABLE 2. Data matrix.

	1	2	3	4	5	6	7	8	9
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>B. stabilis</i>	11100100?1	10?0000100	011000?000	0011011000	1111101000	0110011000	0001101010	1?01010101	11100?0?11
<i>B. aculeatus</i>	1110010101	10?0000100	011000?000	0011011000	1111101000	0110011000	0001101010	1101010101	1110010111
<i>Chydagnathus</i>	1100010101	10?0000100	011000?000	0111011000	11110?0101	1110011000	0001001010	1101110?01	10?010010
<i>Dinodus</i>	1110110101	1100000?11	0110011000	01110110??	???101000	0110011000	0001100010	0100110?01	11010???0?
<i>P. cockeli</i>	1110010101	10?0000?00	011000?000	0011011000	1111101000	0110011000	00011010??	1101010101	11100?1?10
<i>Gnathodus</i>	1110010101	10?0000100	011000?000	0011011000	1111101000	0110011000	0001101010	1101110101	1101011110
<i>Hindeodus</i>	11100100?1	10?0000100	011000?000	0011011000	11110?0101	1110011000	0001101010	1?01010?01	11010?0?00
<i>Idiogonathodus</i>	1100010101	10?0000000	011000?000	0011011000	1111101000	0110011000	00?1101010	1101110101	1101011111
<i>Kockella</i>	11100100?1	00?0010000	011000?000	1010001000	11010?0101	1110011000	0111101010	0?00010?01	0??0?0?000
<i>L. commutata</i>	1100010101	10?0000000	011000?000	0011011000	11110?0101	1110011000	0011000010	1101110101	10?01010?0
<i>L. homopunctatus</i>	1110010101	10?0000010	011000?000	0111?????	???101000	1110011000	0011000010	1101110?01	10??1?1?0
<i>L. saharae</i>	1100010101	10?00000??	???????	???????	???????	???????	00110000??	110111?01	10??1?0?0
<i>Mehlina</i>	11100100?1	1110000011	011000?000	0111011000	11?10?0101	1110011000	0011101010	1?00010101	11010?0?11
<i>Mesotaxis</i>	1110010111	1100000??	0110011000	0111011000	11010?0101	1110011000	0001100010	11?110001	11100?0?00
<i>N. brevis</i>	11100100?1	00?0111000	011000?000	0011001000	1111111000	0110011000	0001101010	0?10010101	11100?0?11
<i>O. confluens</i>	11100100?1	00?0110100	011000?000	0010001000	11010?0101	1110011000	0001101010	0?10010?01	11010?0?00
<i>O. hassi</i>	11100100?1	00?0111010	011000?000	0010001000	1101???	?110011000	0011101010	0?00010?01	11010?0?00
<i>O. remscheidensis</i>	11100100?1	00?01?0100	011000?000	0011001000	11110?0101	1110011000	0001101010	0?10010?01	11010?0?11
<i>Palmarolepis</i>	1110110110	1100100?11	0110011000	0010101110	11110?0101	1110011000	0011100010	10?0110001	1110010000
<i>Pandorinella</i>	11100100?1	1110000111	011000?000	0111011000	1111101000	0110011000	0011101010	1?01010101	11010?0?11
<i>Polygnathus</i>	1110010101	0110000111	011000?000	0111011000	11110?0101	1110011000	0011101010	1101110101	1101010111
<i>Sweetognathus</i>	1110010101	10?0000110	011000?000	0011011000	1111???	?110011000	00010001010	1101110101	10?0?0?10
<i>Voegelgnathus</i>	11100100?1	10?0000010	011000?000	0011011000	11110?0101	1110011000	0011101010	1?01010001	1101010?11
<i>W. excavata</i>	11100100?1	10?0111010	011000?000	0110001100	11110?0101	1110011000	0011101010	0?00010?01	0??0?0?000

tata have been linked, the scope of the matrix of Donoghue *et al.* (2008) is appropriate (indeed, our analysis is not dissimilar to the partitioned 'ozarkodinid' analysis of Donoghue *et al.* 2008). Furthermore, because we have not added or modified any characters, our cladistic tests are stringent: we cannot be accused of falling into the trap of designing characters with a particular *a priori* hypothesis of relationships in mind. However, the lack of characters designed to specifically test *Lochriea* monophyly or the affinities of *L. homopunctatus*, for example, will tend to reduce the likelihood that nodes uniting these taxa with their nearest relatives will be strongly supported. This will also reduce the probability of finding significant differences ( $p < 0.05$ ) between alternative hypotheses of relationship.

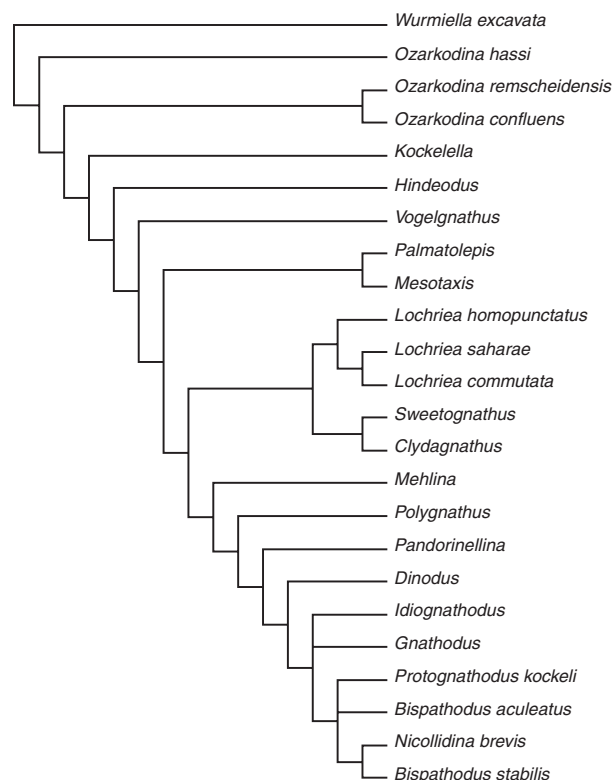
All characters are scored using the same contingent coding strategy adopted by Donoghue *et al.* (2008; Hawkins *et al.* 1997), and our analyses generally used the same methodological protocols. Our matrix was constructed using MacClade (version 4.08); analyses were performed using PAUP version 4 (Swofford 2002) and TNT version 1.1 (Goloboff *et al.* 2008).

To further test the phylogenetic signal in the data set and its support for hypotheses of relationships for *Lochriea* and *L. homopunctatus*, we carried out a double-decay analysis (Wilkinson *et al.* 2000). We also carried out Templeton tests and one-tailed Kishino–Hasegawa tests (an approximation of the Shimodaira–Hasegawa test (Goldman *et al.* 2000)) to determine whether the results of our analysis, in terms of phylogenetic placement of *Lochriea* and *Lochriea homopunctatus*, are significantly better than the previously proposed alternative hypotheses. The constraint trees used in these tests are included as an Appendix.

## RESULTS OF ANALYSIS

Unweighted analysis of the 24 taxa (heuristic search, tbr branch swapping algorithm, random stepwise addition, 100 replicates, 10 trees held) failed to produce a well-resolved tree (strict consensus of 491 MPTs with a tree length of 125 was completely unresolved except for a (*Mesotaxis* + *Palmatolepis*) clade). The same results (in this and subsequent analyses) were obtained whether all outgroup taxa or just *Wurmiella excavata* was designated as the outgroup and whether run using PAUP or TNT.

A *a posteriori* reweighting (weights assigned according to the rescaled consistency index) produced four trees of 50.9 steps. A second round of reweighting resulted in the same 4 trees, but with shorter tree length (33.18 steps). The strict consensus tree is shown in Figure 3; the consistency index (excluding 52 uninformative characters – CIe) is 0.36. The expected CI for 24 taxa



**FIG. 3.** Hypotheses of relationships of *Lochriea* species. Strict consensus of four trees resulting from analysis of reweighted data set (weights assigned according to the rescaled consistency index).

(Sanderson and Donoghue 1989) is 0.49, and the CI random is 0.15. Thus, although the tree contains more homoplasy than expected for a data set of this size, there is a significant phylogenetic signal. The retention index (RI) of the tree is 0.65; the rescaled consistency index (RC) is 0.23.

Importantly, all four MPTs give the same results with respect to our hypotheses of relationships of *L. homopunctatus* and *Lochriea*. It is the positions of *Protognathodus*, *Gnathodus* and *Idiognathodus* that are unstable (*Protognathodus* resolved either as sister to the clade (*B. aculeatus* (*B. stabilis* + *Nicollidina brevis*)) or in a polytomy with *B. aculeatus* and (*B. stabilis* + *N. brevis*); *Gnathodus* and *Idiognathodus* resolved as a clade, with *Idiognathodus* as the sister to the clade (*Gnathodus* (*Protognathodus* (*B. aculeatus* (*B. stabilis* + *N. brevis*))))), or with *Gnathodus* and *Idiognathodus* in a polytomy with the clade (*Protognathodus* (*B. aculeatus* (*B. stabilis* + *N. brevis*))))).

Using double-decay analysis (DDA) to further explore the data, we found that although the strict consensus of the trees resulting from the unweighted analysis was almost completely unresolved, it did contain a significant underlying phylogenetic signal. DDA yielded 22 reduced

component consensus trees, 15 of which had higher total decay (TD) and CIC values than the strict consensus tree resulting from unweighted analysis (CIC 5.43, TD 1). Two of these trees do not include any *Lochriea* species. Of the remaining 13, eight recover clades that provided direct support for our hypotheses that *L. homopunctatus* is a species of *Lochriea* and that *Lochriea* forms a clade with *Clydagnathus*: one tree recovers the three *Lochriea* species as a clade; six trees recover the clade containing the three *Lochriea* species with *Clydagnathus*; and one tree recovers the clade containing the three *Lochriea* species with *Clydagnathus* and *Sweetognathus*. None of the 15 reduced component consensus trees recover clades that are compatible with any of the previously proposed alternative hypotheses of relationship for *Lochriea*: *Lochriea* species are never resolved as being most closely related to *Bispathodus*, *Protognathodus* or *Gnathodus*. Similarly, no trees contain *L. homopunctatus* in a clade that does not also include other species of *Lochriea*.

Results of Templeton and one-tailed Kishino–Hasegawa tests indicate that our hypothesis of phylogenetic placement of *Lochriea* is significantly better than the previously proposed alternative hypotheses. These tests compared the results of our reweighted analysis with constraint trees as follows. The hypothesis of Nemyrovska *et al.* (2006) that *Lochriea* species arose from *Bispathodus stabilis* was tested by comparing our results (but with *L. homopunctatus* excluded because this species was not part of the phylogenetic hypothesis of Nemyrovska *et al.* 2006) with a tree that constrained the *Lochriea* clade to form a clade with *B. stabilis*. This tree is 11 steps longer and can be rejected in favour of our MPT (Templeton test,  $z = -2.84$ ,  $p = 0.004$ ; one-tailed Kishino–Hasegawa,  $t = 2.95$ ,  $p = 0.002$ ). The hypothesis that a monophyletic clade, including *L. homopunctatus*, forms a clade with *Bispathodus* was tested by comparing our results with a tree in which the *Lochriea* clade sits in a polytomy with the two species of *Bispathodus* (the *B. stabilis* + *N. brevis* clade was collapsed into this polytomy). This polytomy also includes *Protognathodus*, and the tree thus allows testing of the hypothesis (speculated upon by Nemyrovska *et al.* 2006) that this genus might form a clade with *Lochriea*. This tree is nine steps longer and can also be rejected in favour of our MPT (Templeton test,  $z = -2.71$ ,  $p = 0.007$ ; one-tailed Kishino–Hasegawa,  $t = 2.81$ ,  $p = 0.003$ ).

We also used Templeton and one-tailed Kishino–Hasegawa tests to further test the alternative hypotheses for the generic affinities of *L. homopunctatus* by comparing our results with trees in which *L. homopunctatus* was constrained to form a clade with *Gnathodus* and with *Protognathodus*. These trees are, respectively, 4 and 5 steps longer than our MPTs, but despite the results of the DDA – which are consistent with the hypothesis that *L. homopunctatus* is a species of *Lochriea* and provide no support for the alter-

native hypotheses – the results fall short of being significant at the  $p = 0.05$  level (*L. homopunctatus* + *Gnathodus* – Templeton test,  $z = -1.26$ ,  $p = 0.21$ ; one-tailed Kishino–Hasegawa,  $t = 1.27$ ,  $p = 0.1$ ; *L. homopunctatus* + *Protognathodus* – Templeton test,  $z = -1.51$ ,  $p = 0.13$ ; one-tailed Kishino–Hasegawa,  $t = 1.52$ ,  $p = 0.07$ ).

Strictly speaking, we are unable to unequivocally reject the null hypothesis that there is no difference between our hypothesis and the alternative *Gnathodus* and *Protognathodus* hypotheses, but the lack of significant difference is a result of incompleteness in our data set, and it does allow us to propose a simple test of our hypothesis. Examining the character distributions in our reweighted analysis (Fig. 3) reveals that the taxa of the derived clade into which the *Gnathodus*/*Protognathodus* hypotheses place *L. homopunctatus* are united in sharing a number of  $S_2$  element characters as synapomorphies. The  $S_2$ ,  $S_1$  and  $S_0$  elements of *L. homopunctatus* are, however, currently unknown. Thus, when we test the alternative hypotheses by placing *L. homopunctatus* into the derived clade, tree length is not altered as much as it would be if  $S_2$  characters were known. Our prediction, and the test of our hypothesis of relationship of this species, is that the remaining  $S$  elements of *L. homopunctatus* will, when found, be like those of other *Lochriea* species and that this will be enough to unequivocally reject the *Gnathodus*/*Protognathodus* hypotheses. Indeed, even if we code just the  $S_2$  elements of *L. homopunctatus* as being like those of *Lochriea commutata* (which does not change the topology of the resulting tree) and repeat the Templeton and one-tailed Kishino–Hasegawa tests, we find that our hypothesis is significantly better than the alternatives (*Gnathodus* hypothesis: tree 10 steps longer, Templeton test,  $z = -2.5$ ,  $p = 0.012$ ; one-tailed Kishino–Hasegawa,  $t = 2.57$ ,  $p = 0.006$ . *Protognathodus* hypothesis: tree 11 steps longer, Templeton test,  $z = -2.67$ ,  $p = 0.008$ ; one-tailed Kishino–Hasegawa,  $t = 2.76$ ,  $p = 0.0035$ ). The ultimate test of the phylogenetic affinities of *L. homopunctatus* awaits discovery of the  $S$  elements, the  $S_2$  in particular, but our analysis supports the hypothesis that *L. homopunctatus* is a species of *Lochriea*.

To summarize our phylogenetic results: contrary to the consensus in the literature, our analysis consistently resolves *Lochriea homopunctatus* in a clade with other *Lochriea* species; our results do not support hypotheses that *L. homopunctatus* is a close relative of *Gnathodus* or *Protognathodus*. *Lochriea* species are consistently found to form a clade together (*L. homopunctatus* (*L. commutata* + *L. saharae*)), supporting the hypothesis that *Lochriea* is monophyletic. *Lochriea* is consistently resolved in a sister group relationship with (*Sweetognathus* + *Clydagnathus*). Our analysis provides no support for the hypothesis that *Lochriea* is a direct descendant of *Bispathodus stabilis* (Meischner and Nemyrovska 1999; Nemyrovska *et al.* 2006) or another species of *Bispathodus* (Sweet 1988), but



it does support the hypothesis that *Lochriea* forms a clade with *Sweetognathus* (Sweet 1988) and *Clydagnathus* (Donoghue *et al.* 2008).

Our analysis consistently resolves *L. homopunctatus* as the most primitive member of the genus, but this result should be interpreted with caution because our analysis includes only three species of *Lochriea* (because of paucity of data regarding non-P<sub>1</sub> of other species). However, for anyone seeking close relatives and potential ancestors of the *Lochriea* clade, our results suggest that *L. homopunctatus* may prove to be more informative than more derived species such as *L. commutata*.

#### *Comparison with previous analyses*

Our results are broadly compatible with those obtained by Donoghue *et al.* (2008), particularly their analysis of the ‘tranche 2’ data set (i.e. similar to the taxon sampling used here). We consistently recovered a clade of *Lochriea* + *Sweetognathus* + *Clydagnathus*, as did they, but with *Lochriea* resolved in a sister group relationship with (*Sweetognathus* + *Clydagnathus*), which differs from the results of Donoghue *et al.* (2008; they consistently resolved a *Lochriea* + *Clydagnathus* clade). Otherwise, the main difference between our tree and those of Donoghue *et al.* (2008) – specifically the ‘tranche 2’ results (figs 5–6), the partitioned analysis of ozarkodinid taxa (fig. 12), and the summary tree (fig. 13) – is in the placement of *Palmatolepis*, *Mesotaxis*, *Dinodus* and *Nicollidina brevis*. For all these taxa, Donoghue *et al.* (2008) concluded that interrelationships were poorly understood. The fact that these taxa occupy different positions in our analysis supports this view: more work is required to confidently resolve their relationships with other ozarkodinids.

The other significant difference in our results concerns the relationships between taxa within the derived subclade which forms the sister group to the clade (*Lochriea* + (*Sweetognathus* + *Clydagnathus*)) (Fig. 3). Although, with the exception of the rogue taxa mentioned above, the composition of this clade is the same as in the analysis of Donoghue *et al.* (2008), it is less well resolved, presumably as a result of inclusion of *Protognathodus*.

#### *Character distributions*

As we note above, *Lochriea* is consistently resolved as forming a clade with (*Sweetognathus* + *Clydagnathus*). The distribution of characters in our strict consensus tree (optimized using MacClade and ACCTRAN and DELTRAN results in PAUP) reveals that these taxa are united by the morphology of their M elements, which are makelate but lack an anterolateral process (characters 65, 82).

Taxa within this clade also have P<sub>1</sub> and P<sub>2</sub> elements with ‘normal’ basal cavities (i.e. they lack recessive basal margin, characters 12 and 20), but this P element characteristic has a more complex distribution: it is plesiomorphic for the set of taxa analysed and is acquired either (1) independently in the (*Mesotaxis* + *Palmatolepis*) clade and in the common ancestor of *Mehlina* and all more derived taxa or (2) in the common ancestor of the clade (*Mesotaxis* + *Palmatolepis*) and all more derived taxa but then secondarily lost in the (*Lochriea* + (*Sweetognathus* + *Clydagnathus*)) clade. Under either scenario, recessive basal margins are lost in the common ancestor of the derived idiognathodontid–bispathodid clade.

Within the (*Lochriea* + (*Sweetognathus* + *Clydagnathus*)) clade, characters of M and P elements are again important, with all *Lochriea* species possessing M elements that lack an adaxial bulge at the base of cusp (character 67), have a basal cavity that is restricted to the cusp (character 63), and P<sub>1</sub> elements that lack a prominent anterior crest (character 18). These three characters exhibit considerable homoplasy in the consensus tree, but they distinguish *Lochriea* species from *Clydagnathus* and *Sweetognathus*.

Within *Lochriea*, *L. homopunctatus* differs from *L. commutata* and *L. saharae* in the presence of posterior carina in P<sub>1</sub> elements in late ontogeny (character 3; that is, the carina does not expand into paired nodes), in having a P<sub>1</sub> element with an asymmetric lanceolate basal cavity that tapers more posteriorly than anteriorly (character 87), and a P<sub>2</sub> element in which the basal cavity extends along the processes (character 19). All of these characters exhibit some homoplasy, but for 3 and 87, this is limited.

## SYSTEMATIC PALAEOLOGY

We follow the suprageneric taxonomy of Donoghue *et al.* (2008). Terms for orientation, process disposition and element location follow the recommendations of Purnell *et al.* (2000).

Phylum CHORDATA Bateson, 1886  
 Class CONODONTA Pander, 1856  
 Division PRIONIODONTIDA Dzik, 1976  
 Order OZARKODINIDA Dzik, 1976  
 Suborder OZARKODININA Dzik, 1976  
 Superfamily POLYGNATHACEA Bassler, 1925

Genus LOCHRIEA Scott, 1942

1942 *Lochriea* Scott, p. 298.

1970 *Paragnathodus* Meischner, p. 1173 (*nomen nudum*).

1975 *Paragnathodus* Higgins, p. 70.

*Type species.* *Lochriea montanaensis* by original designation (a subjective junior synonym of *Spathognathodus commutatus* Branson and Mehl 1941).

*Revised diagnosis.* Typical 15-element ozarkodinid apparatus with sinistral and dextral paired P<sub>1</sub>, P<sub>2</sub>, M and S<sub>1-4</sub>, unpaired S<sub>0</sub>. P<sub>1</sub> elements carminiscaphate with free blade and large, lanceolate or lachrymiform 'posterior' basal cavity, the oral surface of which may be unornamented, bear a few nodes or rows of nodes. P<sub>2</sub> elements angulate. M element makellate, with large cusp, and arched 'posterolateral' process; process height and denticle length decreasing distally. S<sub>0</sub> element alate. S<sub>1-2</sub> elements technically digyrate but bipennate in appearance; S<sub>3-4</sub> elements bipennate. S<sub>1-4</sub> elements have an 'anterior' process that is deflected upwards distally. (Diagnosis modified from Norby 1976).

*Remarks.* Previous arguments against including *L. homopunctatus* in *Lochriea* have focussed on differences between P<sub>1</sub> elements of *L. homopunctatus* and other species of the genus. Indeed, when Bischoff (1957) originally diagnosed the species (under the name *Gnathodus commutatus punctatus*), it was distinguished from *L. commutata* in having lines of nodes directly next to the blade on both the inner and outer sides of the platform. Thus, our phylogenetic evidence that *L. homopunctatus* is a species of *Lochriea* requires us to expand the generic concept to include P<sub>1</sub> elements with rows of nodes on the upper surface of the basal cavity. With the inclusion of *L. homopunctatus*, other features of P<sub>1</sub> elements that have previously been thought to characterize *Lochriea* – such as the distinctive subrectangular profile of the free blade in 'lateral' view and the variation in size of denticles along the blade – are no longer shared by all members of the genus, but may be useful in species recognition. Our analysis clearly demonstrates that M element morphology in particular is diagnostic for *Lochriea*.

*Lochriea homopunctatus* (Ziegler, 1960)

Figure 2

*Material.* See Table 1, and 'Material and methods' for locality details. Specimens illustrated in Figure 2 are deposited in the British Geological Survey.

*Diagnosis.* P<sub>1</sub> element characterized by expanded symmetrical or slightly asymmetrical lanceolate or lachrymiform basal cavity, the upper surface of which bears, on both 'outer' and 'inner' sides, an irregular row of nodes or ridges, forming a platform with 'shoulders' parallel to cavity margin. P<sub>2</sub> element has large discrete denticles, and the posterior process declines in height distally.

*Description.* P<sub>1</sub> elements have an expanded symmetrical or slightly asymmetrical lanceolate or lachrymiform basal cavity, the oral surface of which bears low nodes or short ridges on both 'outer' and 'inner' sides of the carina, forming a platform with 'shoulders' parallel to cavity margin. The oral surface of the cavity in small (presumably immature) specimens may be unornamented. In 'lateral' view, the carina is approximately twice the height of the platform; the height of the denticles decreases towards the 'posterior' end of the element, giving it a weakly arched oral profile. In oral view, the nodes of the carina may be fused, but they are not laterally expanded, even in large (presumably mature) specimens. The P<sub>2</sub> element is unarched in 'lateral' view and unflexed in oral view. It has short 'anterior' and 'posterior' processes of approximately equal length, the posterior process declining in height distally. Processes bear large discrete denticles. The basal cavity extends beneath both processes. In the specimens studied, the cusp is not markedly larger than adjacent denticles. The M element has a short, arched, 'posterolateral' process, which declines in height distally. It bears large 'laterally compressed' denticles, which decrease slightly in height and are increasingly inclined distally. The cusp is longer than the process and is compressed with sharp, straight sides and a sharply pointed tip. The basal cavity is small but extends beneath the 'posterolateral' process. The S<sub>3/4</sub> elements have an 'anterior' process that is shorter than the 'posterior', with the typical upswept distal termination of *Lochriea* species. The processes are 'laterally compressed' with flat sides. The cusp is wider and longer than any denticles on either process; it is 'laterally compressed' towards the base, but becomes more rounded in cross section towards the tip. The small basal cavity extends beneath the posterior process and may be flanked by recessive basal margin, especially 'anteriorly'.

*Remarks.* The platform ornamentation of the P<sub>1</sub> element differentiates *Lochriea homopunctatus* from other *Lochriea* species. P<sub>2</sub> elements of *L. homopunctatus* differ from those of *Lochriea commutata* in having straight posterior and anterior processes. It is possible, as other authors have suggested (e.g. Stone 1991), that conodont taxa with similar P<sub>1</sub> elements to those of *L. homopunctatus*, such as *Gnathodus symmutatus* and *G. mermaidus*, should also be assigned to *Lochriea*, but at present, this hypothesis lacks the support of evidence from non-P<sub>1</sub> elements, which remain unknown.

## DISCUSSION AND CONCLUSIONS

The taxonomic and phylogenetic issues that we have addressed in this study are not unique. Similar problems arise with some other biostratigraphically significant conodont taxa, and these would probably benefit from application of a similar approach. Disagreement surrounding the Mississippian–Pennsylvanian (Mid-Carboniferous) boundary provides a good example. This is defined at the First Appearance Datum of the conodont

*Declinognathodus noduliferus* at the Global Stratotype Section and Point (GSSP) at Arrow Canyon, Nevada, USA (Lane *et al.* 1999), and is supported by an explicit phylogenetic hypothesis that *D. noduliferus* evolved from *Gnathodus girtyi simplex*. P<sub>1</sub> elements in this section that are morphologically intermediate between the two taxa are interpreted as evolutionarily transitional forms, and the phylogenetic transition was used as evidence to suggest that the sequence is more complete than other GSSP candidates. This remains controversial. Riley *et al.* (1994, p. 288) did not explicitly question the phylogenetic hypothesis but noted that ‘the use of this evolutionary series as sole evidence for a complete boundary sequence should be treated with caution until the full stratigraphic range of all the taxa has been confirmed from other sections.’ Other authors have proposed alternative hypotheses of relationship for *D. noduliferus*: both Grayson *et al.* (1991) and Nemyrovskaya (1999), for example, suggested that *D. noduliferus* arose within a clade that includes the type species of *Gnathodus* (i.e. *G. bilineatus*) but does not include *G. girtyi*. Grayson *et al.* (1991) also raised doubts similar to those of Riley *et al.* concerning the evidence from conodont evolution for incompleteness of Mid-Carboniferous boundary sections relative to Arrow Canyon (and subsequent work on the section has demonstrated it is not complete (Barnett and Wright 2008)). Clearly, hypotheses of relationships of *D. noduliferus* and *G. girtyi* are in need of more robust testing.

Our analysis confirms that similarity in the morphology of P<sub>1</sub> elements, especially the relatively simple blade-shaped (carminate) P<sub>1</sub> elements that characterize taxa such as *Lochriea commutata*, *Lochriea saharae* and *Bispathodus stabilis*, is not a reliable guide to relationships between taxa, especially at supraspecific levels. This is because blade-shaped P<sub>1</sub> element morphologies are convergently acquired in numerous conodont clades and because reliance on the characters of only one of the six or seven morphologically distinct elements that together comprise the oropharyngeal skeleton of ozarkodinid conodonts ignores phylogenetically significant data. Even where P<sub>1</sub> element morphology is more complex, as is the case with *L. homopunctatus*, and where similarities with the morphology P<sub>1</sub> elements in other species are clear (e.g. with *Protognathodus* or *Gnathodus* species), P<sub>1</sub> element morphology may not be a reliable guide to relationships. Inclusion of characters from other elements provides a more complete sampling of morphological data and therefore increases the likelihood of differentiating between homoplasy and homology.

Our analysis also shows that, even when many or all the elements of a conodont species’ skeleton are known, it is difficult to determine *a priori* which elements carry phylogenetic signal. In our tests of competing hypotheses for phylogenetic placement of *L. homopunctatus*, the avail-

able data, including the P<sub>2</sub>, M and S<sub>3/4</sub> elements that we recognize herein, support the hypothesis that it is a species of *Lochriea*; shared characters of the M elements are particularly important, but additional data from other S elements, the S<sub>2</sub> in particular, are required before alternative hypotheses can unequivocally be refuted. Generalizations about the phylogenetic significance of particular elements – that is, whether they can be taken as indicators of familial, generic or specific affiliations – are unlikely to be reliable.

These conclusions apply not only to cladistic analyses of conodonts, but also to more traditional approaches to taxonomy. The advantage of the cladistic approach is that it allows relationships to be recognized that might otherwise be obscured because a taxon lacks what is thought to be a taxonomically diagnostic character. *Lochriea homopunctatus* provides a clear example of this. Recognition of the P<sub>2</sub>, M and S<sub>3/4</sub> elements provides new characters that support the hypothesis that it lies within a monophyletic *Lochriea*, even though its P<sub>1</sub> element has characters that were previously thought to exclude it from the genus. In such cases, where phylogenetic hypotheses and typological taxonomic concepts are in conflict, conodont workers must make a choice: either to modify taxonomic diagnoses to reflect the morphology of taxa that together form monophyletic groups (such that taxonomy reflects hypotheses of evolutionary relationships) or to persist with arbitrary taxonomic entities that reflect preconceived ideas of the taxonomic informativeness of morphological features. We would argue strongly that the former approach is better scientifically, but acknowledge that in cases where relationships are not well resolved, some pragmatic taxonomic conservatism may be appropriate.

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*Author contributions.* AO and MAP conceived research programme, conducted research, analysed data and wrote the manuscript. NJR provided samples and contributed to the manuscript.

*Editor.* Philip Donoghue

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Constraint trees used for Templeton and Shimodaira-Hasegawa tests comparing alternative hypotheses of relationships for *Lochriea* and for *L. homopunctatus*.].

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