Phylogeny of Phosphatocopa

INGLEORE HINZ-SCHALLREUTER & ROGER SCHALLREUTER

EARLIEST records of phosphatocopes date back to the 19th Century when Barrande (1872) first described Beyrichia angelini (= Cyclotron angelini) from the late Middle Cambrian of central Sweden based on an unpublished figure by Angelin (1854). In the same year Jones (1872) figured another phosphatocope as a “larval trilobite” from the early Middle Cambrian of South Wales (Hinz-Schallreuter 1998, p. 104; 2000, p. 843, 870). In Germany, the first phosphatocope came from a northern glacial erratic boulder (geschiebe) and was described as an ostracode, Bythocyparis polita (= Hesslandona polita) by Steusloff (1895). However, it was not until 1964 the phosphatocopes were established by Müller as a group of their own by his discovery and study of a number of phosphatic ostracod-like carapaces in the course of conodont research in Upper Cambrian limestone nodules (Orsten) of southern Sweden. Because of their assumed primary phosphatic carapace nature, which Müller considered to be the main characteristic of this group, he introduced the term Phosphatocopina. The stratigraphically oldest record of a euphosphatocope is from the Lower Comley Series (Lower Cambrian) of Great Britain (Hinz 1987, 1993). In the following decade rich Middle Cambrian associations were described in detail from both Baltoscandia (Hinz-Schallreuter 1993a, c, 1998a, 2000; Hinz-Schallreuter & Koppka 1996) and Australia (e.g., Hinz 1991b, 1992, 1993b; Hinz & Jones 1992). Uppermost Middle Cambrian and Furongian faunas from Sweden and geschiebes of northern Germany were described by Gründel (in Gründel & Buchholz 1981), Hinz-Schallreuter (1993c, 2000) and Maas et al. (2003). A number of phosphatocopes (incl. Dabashanellida) have been recorded also from Great Britain (Williams & Siveter 1998), but comparably few are known from North America (Siveter & Williams 2007), Siberia (Melnikova & Mambetov 1990, Müller et al. 1995) and China (Huo & Shu 1985, Zhang 1987, Shu 1990a, Hou et al. 1992). The phosphatocope described by Müller (1973) from northern Iran seems to be a bradorid (Hinz-Schallreuter 2000, p. 843).

The phosphatocopes are useful as stratigraphic markers, not only for the uppermost Middle Cambrian and Furongian (Maas & Waloszek 2005), but also for the Middle Cambrian (Hinz-Schallreuter 2000, table 7) particularly in the “anomalous” biofacies in the Cambrian of Sweden, a facies without trilobites but dominated by phosphatocopes (Eriksson & Terfelt 2007).

The systematic position of this group has been under debate for a long time, with opinions ranging from Ostracoda (e.g., Müller 1964) or an early blind offshoot (“dead end”) within ostracod evolution (e.g., Jones & McKenzie 1980, p. 207; Hinz 1993) via Phyllopoda (see Hinz-Schallreuter 2000, table 5) to even Pseudocrustacea (Hou & Bergström 1997, p. 111).

Based on exoskeletal soft parts, Maas et
al. (2003) and Maas & Waloszek (2005) now consider the Phosphatocopa as ostracode-like sister group of Eucrustacea within the taxon Labrophora Maas et al., 2003.

RELATIONSHIP OF PHOSPHATOCOPES TO OTHER ARTHROPODS

After Müller’s sensational discovery of preserved soft integument in phosphatocopes (Müller 1979) Gründel (in Gründel & Buchholz 1981, p. 60) was the first to exclude phosphatocopes from Ostracoda. He based his argument on Müller’s observation of the biramous character of the first antenna (antennula). Later, more detailed studies of phosphatcope appendages led to a correction of the original interpretation, and phosphatocopes were defined in having “a strongly reduced first antenna and undifferentiated postmandibular limbs” (Müller & Walossek 1991, p. 283). As a consequence, phosphatocopes were regarded only as “ostracod-like” by the authors (Walossek & Müller 1992, p. 305, 309) and later regarded merely as stem-group derivatives of the Crustacea (Müller et al. 1995, p. 112). Hou et al. (1996, p. 1141) agreed with this while Siveter et al. (2003) consider phosphatocopes a

Fig. 1. Bivalved ostracod like arthropods from the Strenuella Limestone (Cobbold’s excavation no. 2), Atabanian, Comley, England. All stereo-pairs. A, Klausmuelleria salopensis Siveter, Waloszek & Williams, 2003, opened carapace (UB H 15) presumably of the second or third instar in ventral view with labrum and labium, length ~0.33 mm. B, Comleyopsis schallreuteri Hinz, 1993, holotype (UB H 18), carapace, dorsal view, length 0.46 mm. Note broad biconvex interdorsum with spines. C, Bradoria? sp., right valve (UB H 21), lat. view, length 0.38 mm. D, Dabashanella? sp., car. (UB H 16), lat. view, slightly lifted up dorsally, length 0.66 mm.
sister group of Eucrustacea within the new taxon Labrophora Maas et al., 2003, and not “stemline derivatives”. Based on their new species Klausmuelleria salopensis Siveter et al. (2003) distinguished within the Phosphatocopa (= Phosphatocopida) the sister groups Euphosphatocopa and the monotypic genus Klausmuelleria. Klausmuelleria salopensis is based on two larval specimens from the lower Cambrian Protolenus Limestone at Comley, Shropshire. The authors tentatively included a third specimen from the same locality and biozone, that had been described in open nomenclature by Hinz (1987, p. 59; fig. 1.1) and that also has a partly preserved soft integument. The separation of Klausmuelleria from the so-called Euphosphatocopa on a higher systematic level is the result of differences in soft part morphology (Siveter et al. 2003, p. 22, text-fig. 7) based on the observation that “... the body of phosphatocopine species is more or less similar” (Maas et al. 2003, p. 153).

In the only available instar of Klausmuelleria salopensis both the second antenna and mandible have a limb stem made of two parts, coxa and basipod, with their endopods having three podomeres (Siveter et al. 2003, p. 14). By contrast, Euphosphatocopa have only two podomeres at these limbs throughout ontogeny. Additionally, coxa and basipod are fused to a syncoxa in the second antenna from the first stage onward, a character, which shows the mandible later in ontogeny (op.cit., p. 24). Features of the carapace are not mentioned in the diagnosis (recte: definition, according to ICZN art. 13.1.1).The carapaces are presumably too small to exhibit morphological details. In Bidimorpha bidimorpha, the smallest investigated larvae measure 0.63 mm. They are distinguished from specimens that reach 2.44 mm by their much weaker lobation: of the five nodes developed on adults, only one (N1) is recognisable on small larvae (Hinz-Schallreuter 1993a, fig. 3.1, 5.1-2).

Siveter et al. (2003, p. 13,16,19) described Klausmuelleria as univalved and lacking a hinge-line or interdorsum. They compared it with the first stage of the bradorid Duibianella, which is also univalved (see Zhang & Pratt 1993, fig. 1A). Zhang (2007, p. 123) found that in Duibianella tuberosa, the instars 0, 1 and 2 are univalved and that instar 3 is “characterised by the appearance of a dorsum suture”. The univalve status of the shield is considered by Siveter et al. (l.c.) as a plesiomorphic feature.

Siveter et al. (2003) did not compare Klausmuelleria with the more closely related Comleyopsis Hinz,1993, the only contemporaneous euphosphatocope from Comley which has a very broad interdorsum (Fig. 1B). The interdorsum is considered by Hinz-Schallreuter (2000, p. 843,849) as the autapomorphic feature of the euphosphatocope carapace. However, the possibility that Klausmuelleria could be an earlier univalved instar of the bivalved Comleyopsis similarly to Duibianella had not been taken into consideration.

Siveter et al. also did not compare Klausmuelleria with the other univalved phosphatocope, Dabashanella of the Dabashnellina, which also seems to occur at Comley (Fig. 1D). They only mentioned (p. 13) D. hemicyclica Huo, Shu & Fu in Huo et al. 1983 (see Appendix) as being univalved.

Dabashanella has been regarded as an older synonym of Phaseolella Zhang, 1987 (Melnikova & Mambetov 1991, p. 59). The holotype of Phaseolella dimorpha is a partly broken specimen, which exhibits a well developed doublure typical of Phosphatocopa (Zhang 1987, fig. 12M). Features of the dorsal side are not described, but Zhang presented several thin-sections of specimens he assigned to Phaseolella dimorpha which, however, show different dorsal sculptures ranging from a univalved carapace without any commissure via a simple dorsal commissure to carapaces with broad interdorsum (Zhang 1987, fig. 12T-W). The latter specimen very much resembles the Lower Cambrian Comleyopsis schallreuteri (Hinz 1993, p. 12), first mentioned under open nomenclature by Hinz (1987, p. 59). Therefore, the genus Phaseolella seems to unite at least three different taxa (two phosphatocopes and a bradorid) and requires revision for future morphological comparisons at the generic and species level. Presently, the genus has to be considered a nomen dubium (Hinz-Schallreuter & Koppka 1996, p. 40).

The relevance of the above mentioned differences in soft part morphology for a separation on the suprageneric level is questionable. The number of endopodal podomeres might become reduced phylogenetically from early to middle Cambrian taxa and the fusion of coxa and basipodite to a syncoxa may also develop at least during the middle Cambrian. This assertion is strengthened by the different ontogenetic development of second antenna and mandible in the younger euphosphatocopes.

Siveter et al. (2003) distinguish two sister groups within the Phosphatocopa: Klausmuelleria salopensis and Euphosphatocopa. This is based solely on soft part morphological differences and therefore, neglects all records of other phosphatocopes or euphosphatocopes, respectively from the early and middle Cambrian.
TAXONOMY OF PHOSPHATOCOPES

On the use of suprafamily names. Names of orders and suborders were formed often by adding the suffixes –ida (order) and –ina (suborder) as exemplified by Moore (1961). However, in dealing with phosphatocopes, Siveter et al. (2003) and Maas et al. (2003) did not follow this practice. They arbitrarily use the endings for both superior and subordinate taxa. Martinsson (1962, p. 126) had already noted that such a practice may lead to conflict with informal family names in normal text (e.g., beyrichiids or bradoriids), and in certain cases it is unclear whether an order or family level taxon is meant. Therefore, neutral names should be given preference for taxonomic levels higher than the family rank and we suggest this practice should be applied for palaecope ostracods (e.g., Beyrichiocopa rather than Beyrichiida). Likewise we use the term Bradoridia instead of Bradoriida which is in accordance with Raymond’s (1935, p. 228) original use, and Phosphatocopa instead of Phosphatocopida. Additionally, this terminology does not fix the taxonomic rank in the nomenclatorial system.

The taxonomy of euphosphatocopes is still based on their carapace morphology despite the discovery of soft parts. The latter, however, lead to a better understanding of the relationships between phosphatocopes and other crustaceans, but prove to be insufficient for taxonomic differentiation within the group (Maas et al. 2003) on the basis of presently available material.

Williams & Siveter (1998, p. 27) stated that ‘‘….the distinctions between the phosphantocopid families are still based mostly on shell taxonomy and remain poorly constrained”. By contrast, in their detailed study on phosphatocopes from the Upper Cambrian of Sweden, Maas et al. (2003, p. 8) realised that ‘‘….body of all phosphatocopine species is more or less similar” and based their species concept on ‘‘traditional taxonomy” of carapace morphology. Consequently, the recognition of phylogenetic trends within the group results from differences in hard part morphology.

THE IMPORTANCE OF PHOSPHATOCOPE HARD PART CHARACTERS

Arthropods are characterised by an exoskeleton which developed from the cuticle. It consists of different portions subject to more or less sclerotisation. In crustaceans, an additional stabilisation may have been obtained by the incorporation of calcium carbonate and calcium phosphate (Westheide in Westheide & Rieger 2004, p. 412).

Phosphatocopes are usually preserved only with their hard parts, i.e. the carapace proper without other exoskeletal structures (e.g. appendages). To describe both morphogenesis and function the hard parts should correctly be referred to as “head-shield carapace”. For more convenience the simple descriptive term carapace has been maintained.

Interdorsum. The term refers to a special dorsal sculpture of bivalved phosphatocopes (= Euphosphantocopina Maas et al. 2003, = Euphosphantocopida Siveter et al. 2003) in contrast to univalved ancestral phosphatocopes represented by dabashanellids (e.g., Shu 1990, p. 323, Melnikova & Mambetov 1990 or 1991, p. 59). A possible explanation of interdorsum development was given first by Hinz (1993).

The original assumption of a primary phosphatic shell being the main character of this group has been replaced by the observation that many phosphatocopes developed a special dorsal structure between the two valves, which Müller (1964) termed dorsum. Since this term was preoccupied (Jaanusson 1957, p. 186) Hinz-
Schallreuter introduced the term interdorsum (Hinz 1991a, p. 233). Müller observed this sculpture on only one genus and accordingly considered it of less taxonomic importance. Meanwhile, interdorsa have been recorded from nearly all bivalved phosphatocope taxa occurring from the Early to the Late Cambrian (Fig. 2). Even if taxa from the late Furongian may display extremely narrow or rudimentary interdorsal sculptures (Figs 2K-O, 3), the phylogenetic context is fairly obvious and makes this feature the main autapomorphic character of euphosphatocopes, which are the sister group of univalve phosphatocopes. The evolution of the interdorsum within euphosphatocopes is expressed by the “Interdorsal Width Index” (IWI) calculated as follows (Hinz-Schallreuter 2000, p. 887):

\[ \text{IWI} = \left( \frac{\text{miw}}{\text{vl}} \right) \times 100 \]

where miw = maximum width of interdorsum and vl = length of valve

The highest index (>20) was found in Comleyopsis, the lowest (0.01) so far in Falites fala (Fig. 3).

Shell substance. Originally, the phosphatic nature of the carapace was considered to be primary (Müller 1964, Jones & McKenzie 1980, p. 210). This was questioned by Kozur (1974) who observed that the phosphate may be removed from the shell with hydrochloric acid and that the shape of the carapace is still preserved by its chitin content (Müller 1979, p. 11). Furthermore, secondary phosphatisation is frequently seen on phosphatocope shells which can preserve important features such as appendages but may also obscure features like the interdorsum (compare Hinz-Schallreuter & Koppka 1996, pl. 1, figs.1d, 2d). However, the fact that phosphatocope carapaces developed some sort of hinge structure with the interdorsum, which enabled the animals to open and close the valves, suggests that the valves might have been primarily stabilised by phosphate. The morphological change in interdorsal development from lower to upper Cambrian phosphatocopes might have been the result of an increasing degree of carapace mineralisation. The opening and closure of the carapace of Lower Cambrian taxa with convexly bordered interdorsa required a flexible shell unlike stratigraphically younger phosphatocopes with parallel-bordered interdorsa.

Additionally, the fact that phosphatocope
valves are documented with up to 10 mm length, while specimens with phosphatised appendages do not exceed 2 mm (e.g., Müller 1979, p. 21) in length suggests a primary nature of the phosphatic shell.

**Doublure.** Phosphatocope carapaces are characterised by a doublure extending along the inner side of the free margin. By contrast, this feature has been recorded from only few bradorid taxa so far (e.g., Zhang 2007, pl. 11, fig. 3).

**Ontogenetic turning point (OTP).** Ontogenetic studies of three genera (*Bidimorpha, Vestrogothia* and *Falites*), which represent three different subfamilies, reveal an abrupt change in shape (l:h ratio) during growth. It is best exemplified on *Vestrogothia longispinosa* Kozur (Fig. 4) with a recorded size range from 0.22-2.4 mm. The abrupt change occurs at a valve length of approximately 0.9 mm.

Presently, the OTP can be documented for six species of the abovementioned three genera. Whether or not this characteristic occurs in all phosphatocopes or only some taxa, is yet unclear, although it might be related to a fundamental change in soft part development. However, for probably taphonomic reasons in the Upper Cambrian Alum Shale Formation (comp. Müller & Walossek 1991, p. 284) soft body preservation with very variable degree of completeness has been documented only for rather small larvae despite the fact that adults of 10 mm length (Hinz-Schallreuter 1993, fig. 9.4) are almost 10 times larger than the recorded instars with soft integument preserved (e.g., Müller 1979, p. 21; Maas *et al.* 2003). The one dimorphic species, *B. bidimorpha* does not show any relation between OTP and dimorphism.

Another special feature of the phosphatocopes firstly observed by Hinz-Schallreuter (1993a, p. 340) is the ontogenetic reduction of the l:h ratio beyond the OTP. By contrast, in true ostracodes, the ratio increases or remains constant during ontogeny (Hinz-Schallreuter & Schallreuter 1998b, figs. 76 -77).

Apart from the interdorsum and the presence of a doublure, taxonomy within the group of Euphosphatocopa uses carapace features such as general outline, shape, development of the free margin, lobation, dimorphism, as well as ontogeny. Most of these characters are shown on Figure 5.

**DEVELOPMENT OF THE BIVALVE STATE IN PHOSPHATOCOPES**

Phosphatocopes belonging to Euphosphatocopa (= Euphosphatocopida Siveter *et al.*, 2003) are marked by a special dorsal structure, the interdorsum. Euphosphatocope carapaces are mostly considered to be bivalved, even if a proper dorsal separation of the two valves had not been achieved as, e.g., in Lower Cambrian taxa that have extremely broad and biconvex interdorsa like *Comleyopsis* Hinz,1993. Öpik’s (1968, p. 9) and Shu’s (1990b, p. 323) consideration of the interdorsum as a third valve is not followed, because a valve is characterised by a free margin, which is missing on an interdorsum.

The observation that phosphatocope interdorsa gradually decrease in width from the early to late Cambrian made Hinz-Schallreuter propose an evolutionary model for phosphatocopes starting from univalved shield-like carapaces to bivalved...
shells that developed via broad to extremely narrow interdorsa (Hinz 1993, fig. 2; Hinz-Schallreuter & Schallreuter 1998, fig. 101). She also assumed that bradorids originated from univalved ancestors. This hypothesis was supported when Zhang & Pratt (1993, fig. 1A-D) documented an early univalved stage in the ontogenetic development of the bradorid genus Duibianella and Zhang (2007) figured other examples (Kunmingella, Retaluta) of early univalved instars. This also

supports the assumption that not only bradorids but also phosphatocopes started ontogeny with a univalved instar.

The gradual reduction of the interdorsum during evolution was documented in more detail and quantitatively by Hinz-Schallreuter (2000) in calculating the IWI (interdorsal width index) and plotting it against the stratigraphical occurrence of the respective taxa. The respective diagram (Fig. 8) clearly shows the gradual decrease of interdorsal width accompanied by parallelisation of its lateral borders. Therefore, euphosphatocope evolution seems to start with the Lower Cambrian Comleyopsis having a very broad interdorsum with convex lateral borders. The Middle Cambrian taxa with more or less parallel-sided interdorsa are best documented from Australia. The Swedish material provides evidence of continued evolution into the Furongian. The respective interdorsa are characterised by further reduction to almost complete disappearance except for some rudiments.

The ancestor of Comleyopsis is probably a taxon lacking an interdorsum (Hinz 1993) like Klausmuelleria. The latter is considered by Siveter et al. (2003, fig. 7) as a sister-group of the euphosphatocopes.

**CARAPACE OF KLAUSMUELLERIA**

The first phosphatocope that does not display a bivalved carapace was a small larva figured by Hinz (1987) and later tentatively assigned to the “univalved” Klausmuelleria by Siveter et al. (2003). However, all three specimens assigned to Klausmuelleria were mounted on the dorsal side because of their preserved soft integument, thereby preventing a detailed study of possible dorsal carapace features. Secondary phosphatisation, which is rather strong on Klausmuelleria (Fig. 1A) but naturally also apparent on the material figured by Siveter et al. (2003, pls. 1-2) may conceal the presence of an interdorsum.

The effect of secondary phosphatisation has been well demonstrated on carapaces of Comleyopsis by Hinz-Schallreuter & Koppka (1996, pl. 1, figs. 1d, 2d): one of the carapaces displays the presence of a clearly developed interdorsum only on a tiny part of the dorsal side. Without detailed SEM photography this feature would have remained unrecognised and the carapace accordingly regarded as univalved.

With a length of 0.46 mm Comleyopsis Hinz-
Schallreuter 1993 is approximately ⅓ larger than *Klausmuelleria* and might represent a later instar (Fig. 1B). Both taxa came from the same locality and horizon at Comley, Shropshire. Other specimens documented by Hinz (1987) and Williams & Siveter (1998, p. 35) belong to bradorids and dabashanellids (Fig. 1C-D).

“Based on its size and morphology” Siveter et al. (2003, p. 18-19) compared their *Klausmuelleria* “with the earliest instars known from the uppermost Middle Cambrian/Furongian ‘Orsten’ phosphatocopes”. They concluded that the holotype (0.34 mm) is an “early, possibly the first, instar of the species”. The other two specimens known are of about the same size. They certainly represent an early ontogenetic stage but probably not the earliest one. The first instar of *Falites unisulcatus* (= *Hesslandona unisulcata* in Maas et al. 2003, table 7,15) ranges between 0.23 – 0.315 mm. The smallest specimens available to Müller (1979, p. 21) are about 0.125 mm long, and the smallest carapace of *Vestrogothia longispinosa* measured by Hinz-Schallreuter (1998a, table 9, pl. 3, fig. 9b) is only 0.22 mm long, while the largest appendage-bearing specimen measures 0.95 mm. Between 0.23 and 0.95 mm Maas et al. (2003) distinguished eight possible growth stages which, according to their figure 21, seem to reflect four different stages only (stages I, II, III–V, VI–VIII) with regard to presence or absence of appendages. Large specimens of the species attain sizes of 2.40 and ?3.22 mm (Hinz-Schallreuter 2000, p. 854).

The phylogenetic concept suggested by Siveter et al. (2003, fig. 7) reflects the present state of knowledge, but other possibilities as a result of different development within the Phosphatocopa should also be taken into account.

Just as carapaces of the bradorid *Duibianella* show a univalved to bivalved transition in early stages of ontogeny (Zhang, 2007), Lower Cambrian euphosphatocopes, likewise, may not have developed an interdorsum in the first instars. Similarly, *Klausmuelleria* may represent an earlier stage of *Comleyopsis* and thus could be classified as a true euphosphatocope. The fact that a distinct interdorsum could be documented...
on a carapace, only 0.22 mm long (Fig. 7), of the unequivocal euphosphatocopid Vestrogothia longispinosa (upper Middle Cambrian) may be the result of palingenesis. Alternatively, Klausmuelleria may belong to the ancestral phosphatocopoid group Dabashanellida, which lacks interdorsal characters, or may even represent a lineage separate from both dabashanellids and euphosphatocopes, in which case, knowledge of the dabashanellid body is necessary. Compared to Klausmuelleria, the known uppermost Middle Cambrian and Furongian euphosphatocopes possess a syncoxa formed by the fusion of the coxa and basipod, and the endopods are reduced from three to two. If it is later proven that Comleyopsis, and perhaps other pre-Furongian phosphatocopes, developed appendages like Klausmuelleria, the differences outlined above may represent an evolutionary characteristic within the Euphosphatocopida. Therefore, it would be important to know the ontogenetic development of euphosphatocopes in more detail, as well as of Klausmuelleria.

**CONCLUSIONS**

Maas et al. (2003, fig. 64) based their phylogenetic analysis of exclusively uppermost Middle Cambrian and Furongian euphosphatocopes and the Lower Cambrian Klausmuelleria (= Phosphatocopida sp. Siveter et al., 2001). According to their concept (Fig. 6), upper Furongian species such as Vestrogothia spinata and Falites fala with an extremely narrow rudimentary interdorsum directly developed from univalved taxa like Klausmuelleria and are followed by euphosphatocopes with a more or less broad interdorsum.

In combining evolutionary changes of the interdorsum expressed by the IWI with the stratigraphical occurrence of respective taxa, Hinz-Schallreuter (2000) came to quite a different evolutionary concept (Fig. 8): in Comleyopsis, the oldest yet known euphosphatocop from the Lower Cambrian, the interdorsum is very broad and laterally convex, while stratigraphically younger taxa from the Middle Cambrian have interdorsa that are narrower and gradually become parallel-sided, but still have converging cardinal portions. In the upper Furongian, the interdorsa become even narrower and completely parallel-sided to even rudimentary, having an IWI approaching zero in the youngest Furongian species Vestrogothia spinata and Falites fala. To us this evolutionary model seems to be more plausible. It is consistent with stratigraphical finds.
According to the present state of knowledge, two phosphatocope groups can be differentiated on the basis of their carapace morphology: the univalved dabashanellids and the bivalved euphosphatocopes. Whether Klausmuelleria represents a dabashanellid, a euphosphatocope or a third line in phosphatocope phylogeny, depends on the results of further research in this respect. As already outlined above, more detailed information about carapace morphology of Klausmuelleria as well as on the ontogenetic development of phosphatocope soft integument in general is required.

The conflicting results of Hinz-Schallreuter (2000) and Maas et al. (2003) may serve as another example demonstrating that cladistic analysis does not necessarily reflect the biological world (Schallreuter 2003), which had been documented by Campbell (1993). It also demonstrates that stratigraphic evidence must be taken into account in classification as was emphasised by Fortey & Rushton (2007).

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**APPENDIX: AUTHORSHIP OF DABASHANELLA**

The authors of *Dabashanella* and *D. hemicyclica* are Huo & Shu (in Huo *et al.*, 1983) not Huo, Shu & Fu (Zhang 1987, p. 1,16; Hou *et al*. 2002, p. 402,403; Siveter *et al*., p.13, etc.) nor Huo, Cui & Fu (Williams & Siveter 1998, p. 35). Cui is not cited to be responsible for the name, and Fu is not co-author of the paper presenting “the criteria of availability” and therefore, cannot be co-author of the species (ICZN art. 50.1). The correct citation is *Dabashanella* Huo & Shu in Huo, Shu, Zhang, Cui & Tong, 1983 (see Hinz-Schallreuter & Koppka 1996, p. 38).