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Constraints on using ontogenetic data for trilobite phylogeny

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In the latter half of the twentieth century, studies of ontogeny had a vital influence on trilobite systematics. Protaspid morphology especially has been regarded as one of the most significant criteria in classifying trilobites (Whittington 1957; Palmer 1962; Robison 1967; Fortey & Owens 1975; Chatterton 1980; Edgecombe *et al.* 1988; Fortey & Chatterton 1988; Speyer & Chatterton 1989; Fortey 1990, 2001; Edgecombe 1992; Chatterton *et al.* 1994, 1999; Lee & Chatterton 2003, 2007; Campbell & Chatterton 2009). Although it has been pointed out that a versatile morphological diversity of trilobite larvae could be independent of mature morphology (Bergström 1977; Lane & Thomas 1983; Thomas & Holloway 1988), protaspid morphology has been widely used for the higher-level classification of trilobites. For instance, the Order Phacopida was recognized by a morphologically distinctive protaspis with three prominent marginal spines in a characteristic disposition and a forwardly expanding glabella (Whittington 1957). Fortey & Owens (1975) claimed that one of the main characters of the Order Proetida was the protaspides having a preglabellar field. The protaspides of the members of the Order Asaphida were known to have a unique globular shape (Fortey & Chatterton 1988; Fortey 1990). This protaspis-based approach for suprageneric classification of trilobites has been proved to be successful so far and the morphological information from protaspides is expected to help elucidate many of unsolved conundrums in trilobite systematics (Fortey 2001).

Whittington (1957) proposed that great emphasis should be given to protaspid morphology in trilobite classification, and the application of this idea to the study of post-Cambrian trilobites has been quite successful (Whittington 2007). This is in part attributable to already distant phylogenetic relationship between the post-Cambrian trilobite orders. One of the seemingly intractable problems in trilobite phylogeny is to find the Cambrian 'roots' of post-Cambrian trilobites, and Cambrian ptychoparioid ontogenies are expected to help elucidate the problem (Fortey 2001). However, even though many protaspides of the Cambrian ptychoparioids have been reported (see Chatterton & Speyer 1997 for full list and Lee & Chatterton 2007 and references therein), trilobite phylogeny still seems to be far from being resolved.

The current state-of-play in trilobite systematics, in which protaspid morphology has played a significant role, is rooted in von Baer's rule, and this rule has been applied well to trilobites. Hence, ontogenetic studies are expected to reveal the currently unresolved phylogenetic relationships. Chatterton & Speyer (1997) mentioned 'as a rule, monophyletic groups based on characteristics of adult growth stages have similar larvae and life-history strategies so that larval morphology appears to be a useful indicator of relationship', implying that protaspides are more informative for systematics than later growth stages. However, von Baer's rule does not always apply well. Recently, Poe (2006) quantitatively tested von Baer's rule and raised doubts about the rule *per se*. A similar conclusion has been drawn for the phylogenetic use of the crustacean nauplius. Dahms (2000) pointed out significant differences in the morphology of nauplii of closely related species and emphasized that, for phylogenetic use, characters of the whole ontogenetic sequence including the adults should be considered and evaluated. These studies raise the possibility that protaspid morphology alone is not as useful as traditionally expected. With the application of von Baer's rule to trilobites aside, the validity of using protaspid morphology in trilobite classification has seldom been questioned from a logical perspective. Even if the hypothesis that trilobites with similar protaspides share a common ancestry is considered to have withstood the test of time rather well (Fortey 2001), there seems a logical pitfall that is derived from tradition rather than sound scientific reasoning.

Definition of the protaspis: timing of the first appearance of articulation

First and foremost, there is an intrinsic problem in comparing the protaspides of different clades, which may have been overlooked presumably due to a long protaspis-using tradition: i.e. there is no way to prove that the protaspis of one clade is in the homologous developmental stage to those of other clades. Alberch (1985) cautioned that it is difficult to have an unambiguous method of determining homologies among ontogenetic stages. This issue is complicated by the fact that the protaspid period is an artificial division rather than a naturally and biologically defined period. The term 'protaspis' was coined by Beecher (1895) to refer the earliest stage in trilobite development that has a tergite not separated into body sections: i.e. the cranidium is fused to the conjoined trunk segments (see Chatterton & Speyer 1997). It is self-evident that what defines the 'protaspid period' comes down to the timing of the first appearance of articulation. As soon as the first articulation appears, the trilobite is considered to enter the meraspid period and the timing of this articulation does not necessarily coincide among different clades of trilobites. Therefore, the protaspid period may encompass a different range of developmental stages with respect to size and trunk segmentation in different groups. Chatterton & Speyer (1997, fig. 147) clearly pointed out that the commencement of articulation occurs at different times in different clades, but this concept has rarely been considered seriously when using the protaspid morphology for trilobite systematics.

Hughes *et al.* (2006, figs 3–5) recently demonstrated that the segment number in the trunk region during the last stage of protaspid period is not always the same among different trilobite genera, which means that some trilobite genera went into the meraspid period when three or more segments were differentiated on the trunk region, whereas others did so when they had less than three segments on the trunk. Different articulation-appearing timing may be reflected in the various sizes of the protaspides of different clades, as illustrated by Fortey & Chatterton (1988, text-fig. 10): the protaspis of Odontopleurida is usually about 0.5 mm long, whereas that of Scutelluina may be well over 1 mm long. This casts doubt on the validity of direct comparison between those two protaspides.

Closely related species can also display different timing of first articulation. Figure 1 shows a hypothetical early ontogeny of four trilobite species. In the figure, species A, B and C have similar developmental pathways, but different timings of the first appearance of articulation. The protaspid period of these trilobites is the developmental stage 1 for species A, developmental stages 1 and 2 for species B and developmental stages 1, 2 and 3 for species C. In the conventional way in which the protaspis of the latest stage is used, the stage 1 of species A, the stage 2 of species B, and the stage 3 of species C will be compared and this may obscure our understanding of different developmental patterns shown by these three trilobites. Such a problem becomes more obvious when comparing the protaspides of certain trilobites, such as *Ceraurinella*

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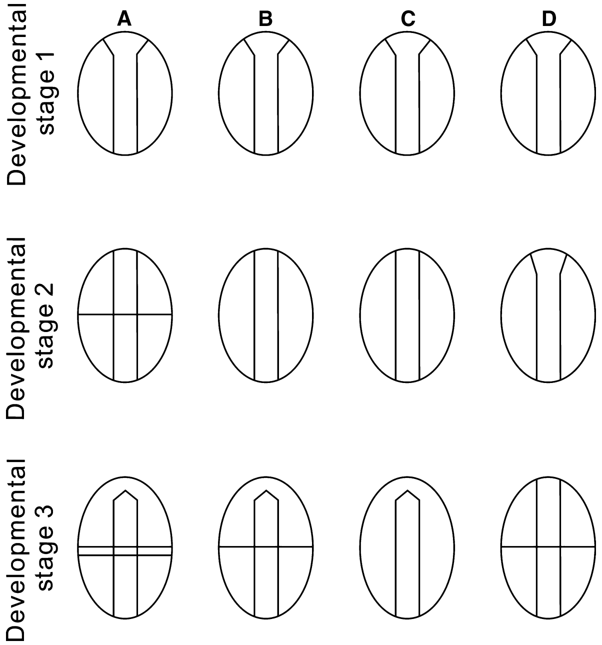

Fig. 1. Early development of four hypothetical trilobite species A, B, C and D. Species A, B and C have a similar early developmental pathway, but differ in the timing of the first articulation: i.e. developmental stage 2 in species A, developmental stage 3 in species B and later than developmental stage 3 in species C. Accordingly, if the protaspis of the latest developmental stage is used for comparison as done in the convention of trilobite research, the similar developmental pathway of the three species may be ignored, as the different timing of the first articulation has led to different protaspid morphology of the latest stage. The hypothetical species D has a similar timing of the first articulation to the species B, but differs in the latest protaspid morphology due to the delayed development.

nahanniensis Chatterton & Ludvigsen 1976; *Ceraurinella latipyga*? Shaw 1968 and *Sphaerocoryphe* sp. (Fig. 2). The protaspides of *C. nahanniensis* and *Sphaerocoryphe* sp. are similar to each other in morphology, whereas the latest protaspis of *C. latipyga*? has a quite different morphology. Such morphological disparity of two congeneric species, *C. nahanniensis* and *C. latipyga*?, must be attributable to different articulation timing, given the different numbers of trunk segments and different sizes: i.e. the protaspis of *C. nahanniensis* is ca. 0.5 mm long and has two trunk segments, whereas that of *C. latipyga*? is ca. 1 mm long and has five or six trunk segments. It can be inferred that the protaspid period was longer in *C. latipyga*? owing to a somewhat delayed appearance of first articulation. However, as the two species have similar developmental pathways, the illustrated protaspid cranidial morphology of *C. latipyga*? is seen in the meraspid cranidium of *C. nahanniensis* (Chatterton 1980; pl. 9, fig. 12; Fig. 2). In contrast, earlier appearance of articulation during ontogeny resulted in small, similar-looking protaspides of *C. nahanniensis* and *Sphaerocoryphe* sp. (Fig. 2), although subsequent development leads to profoundly different holaspid morphology, and hence assigned to different genera. Consequently, if one would compare the protaspid morphologies alone of *Sphaerocoryphe* sp., *C. nahanniensis* and *C. latipyga*? it is likely that *C. nahanniensis* and *Sphaerocoryphe* sp. will be considered more closely related. Different timing of first articulation in closely related species may not be uncommon. A difference between the number of transitory pygidial segments in degree 0 meraspis of *Ctenopyge* (*Eoctenopyge*) *angusta* Westergård 1922 and that of *Ctenopyge ceciliae* Clarkson & Ahlberg 2002 was illustrated by Hughes *et al.* (2006), and the difference may imply that the two *Ctenopyge* species had different timing of the appearance of first articulation.

The relationship between the Agnostina and the Eodiscoidea can be also viewed in the same sense. The relationship of these two groups, in which Agnostina descended from the Eodiscoidea, has been a matter of contention (Jell 1997). The lack of a calcified protaspis in Agnostina has been regarded as negative evidence for a close relationship between these taxa (Shergold 1991), whereas Fortey (1990) considered the absence of a protaspis as a secondary loss of calcification in protaspides of Agnostina. Arguments from both sides assumed that protaspides of the two groups would be in a homologous stage, thus allowing them to be compared. However, the appearance of articulation prior to calcification in Agnostina would simply result in the lack of calcified protaspis in the group. In this case, the possible protaspis of the Agnostina and the protaspis of the Eodiscoidea are not in a homologous stage: i.e. at the eodiscoid protaspis-equivalent stage, the Agnostina had already an articulation between cephalon and pygidium, and is considered a meraspid stage.

Changes in early developmental rate

Superimposed upon this problem is the change in the rate of development in early ontogeny. As noted by many authors (Bergström 1977; Lane & Thomas 1983; Thomas & Holloway 1988; Speyer & Chatterton 1989; Chatterton & Speyer 1997; Fortey 2001), trilobite larvae in the protaspid period were subject to dynamic morphological changes, which could, in turn, be susceptible to changes in the rate of development. In assuming no difference in the timing of the first articulation, some trilobites may have had rather fast morphological development in early stages, whereas for some other trilobites it may have been slow. In Figure 1, species D represents the ontogeny of a hypothetical trilobite that has a delayed rate of development, but has similar timing of articulation to the species B. In the ontogeny of species D, the last protaspid stage will be the developmental stage 2, which might be misleadingly considered similar to the protaspis of species A (developmental stage 1), although delayed development would lead to somewhat different adult morphology from those of species A and B.

In comparing proetide protaspides of different stages, Chatterton *et al.* (1999) claimed that the lack of preglabellar field in the telephinid *Carolinites* and some species of *Telephina*, a distinctive synapomorphy of the proetide protaspides, may be ascribable to either early separation of the meraspid pygidium or delayed differentiation of a protaspid pygidium. This means that the change of developmental rate is also a crucial factor in defining the protaspid morphology, along with the difference in the first articulation timing.

Metamorphosis-undergoing protaspis and phylogeny

In a general sense, metamorphosis during ontogeny seems to provide a good dividing point for ontogenetic stages, helping find homologous stages among ontogeny of different species. The globular, non-adult-like (*sensu* Speyer & Chatterton 1989), protaspides undergo a metamorphosis to attain adult-like morphology of the meraspis (life-history strategy I *sensu* Chatterton & Speyer 1997). Thus, there seemed to be no problem in considering the so-called 'asaphoid' protaspid morphology as a good synapomorphy of the Order Asaphida (Fortey & Chatterton 1988). However, Park & Choi (2011) revealed that the globular protaspis arose more than once in trilobite evolution: i.e. they demonstrated that the Superfamily Remopleuridioidea, which has a highly globular protaspis, was phylogenetically remote from the other 'asaphide' trilobites with a globular protaspis.

More importantly, the definition of life-history strategy I is predicated on the first articulation. Metamorphosis-entailing ontogeny is not restricted to the two lineages of trilobites

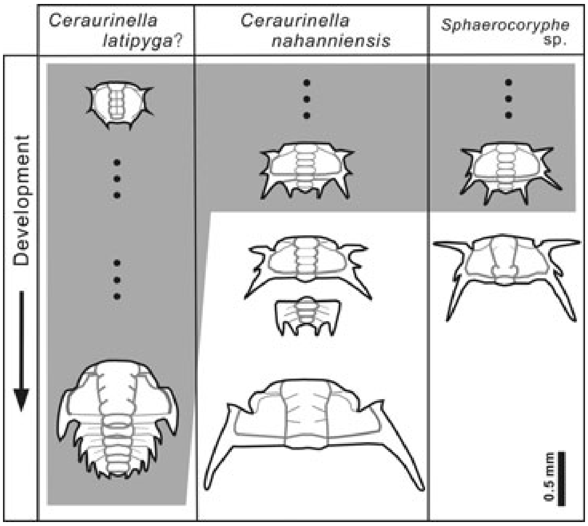

Fig. 2. The early development of three phacopide trilobites, *Ceraurinella latipyga*? *Ceraurinella nahanniensis* and *Sphaerocoryphe* sp. The shaded area represents the protaspid period. A row of three dots indicates the protaspid stages of which the matching protaspis is yet to be discovered. The earliest protaspid stages of *Ceraurinella nahanniensis* and *Sphaerocoryphe* sp. are currently unknown, whereas that of *C. latipyga*? has been reported. In contrast, the protaspid stage comparable to the known protaspides of *C. nahanniensis* and *Sphaerocoryphe* sp. is unknown in *C. latipyga*?. See text for more detailed explanation. The protaspides of *C. latipyga*? are drawn from Chatterton & Speyer (1997), figs 178.1, 3); the protaspis and meraspides of *C. nahanniensis* are from Chatterton (1980), pl. 9, figs 1, 5, 9, 12); and the protaspis and meraspis of *Sphaerocoryphe* sp. are from Chatterton & Speyer (1997), figs 177.1, 4).

mentioned above. Speyer & Chatterton (1989) stated that the early ontogeny of certain illaenid, calymenid, lichid and cheirurid trilobites also includes a globular protaspis. In addition, Chatterton *et al.* (1999) and Lerosey-Aubril & Feist (2005a, b) clearly showed that some proetide trilobites also have a non-adult-like protaspis that metamorphosed into an adult-like protaspis (life-history strategy II *sensu* Chatterton & Speyer 1997). If the first articulation appears earlier during the ontogeny of these trilobite lineages, say concurrently with the metamorphosis, there would be no adult-like protaspis during ontogeny, and these trilobites would be regarded to have life-history strategy I (Fig. 3A). Similarly, a delayed appearance of the first articulation may alter life-history strategy I to life-history strategy II (Fig. 3B). A simple change in the appearance timing of the first articulation would lead to a difference in the life-history strategy.

Nielsen (2000) stated that metamorphosis is nothing other than a strong acceleration (or compaction) of the transitory developmental stage: i.e. at first, the morphological changes associated with the transition from pelagic to benthic life are small, but as the two phases become adapted to different habitats, the morphological changes become more pronounced, and are eventually significant enough to be called a metamorphosis (Nielsen 2000, p. 127). In this respect, the presence of a metamorphosis in the ontogeny of many 'advanced' trilobites mentioned above may have been plesiomorphic. Many Cambrian ptychoparioids, which are rather 'primitive' trilobites, have a less globular (or slightly inflated discoid shape as described by Fortey & Chatterton 1988) protaspis at an early stage. With growth, it assumed typical adult-like morphology. The appearance of such adult-like morphology in a single molting event can also be regarded as a metamorphosis, although of lesser magnitude. Subsequently, the slightly inflated early protaspides in some lineages must have become better adapted to planktonic life with delayed timing of metamorphosis, which may have led to a comparatively large non-adult-like protaspis. Obviously, there are differences in the timing of metamorphosis in different lineages: e.g. early metamorphosis resulted in life-history strategy II, whereas delayed metamorphosis led to life-history strategy I. Therefore, it can be concluded that there is no logical reason to regard the pre-metamorphic protaspides of different species as a homologous developmental stage, even though the metamorphosis during ontogeny seems to provide a good dividing point of ontogenetic stages.

Better ways to use ontogenetic data for trilobite phylogeny

The relationship between ontogeny and phylogeny has long been an important subject in the biological sciences. What kind of role does ontogenetic information play in reconstructing phylogeny? Although it is an essential question, the answer has been surprisingly unsatisfactory (reviewed in Mabee 2000). Many of ontogenetic studies have been limited to revealing heterochronic evolutionary process between pre-supposed ancestral and descendant species (Gould 1977). Fink's (1982) classic study combined ontogeny-derived heterochronic evolutionary concept with cladistic approach, but his recapitulatory pattern-using method has rarely been applied since. Better ways of using ontogenetic data for actual phylogenetic reconstruction appeared in 1990s: they used ontogenetic growth pattern of a certain character for comparison (Cane 1994; Fink & Zelditch 1995) or differences in developmental sequences (called 'sequential heterochrony'; Smith 2001; Jeffery *et al.* 2002, 2005; Koenemann & Schram 2002; Schulmeister & Wheeler 2004; Smirthwaite *et al.* 2007). None of these studies are

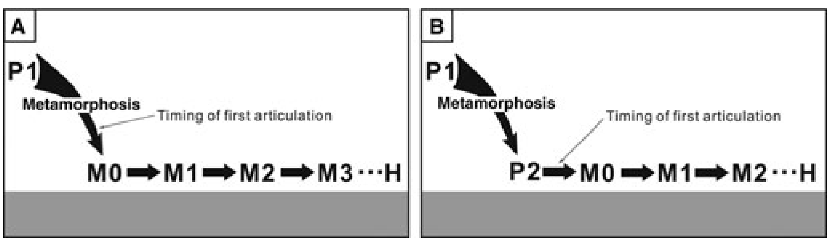

Fig. 3. Schematic diagrams showing the relationship between the life-history strategy and the timing of the first articulation. Both diagrams display ontogeny of two hypothetical trilobites entailing metamorphosis from planktonic to benthic at an early stage of development. P, M and H denote the protaspid, meraspid and holaspid periods, respectively. P1 represents a planktonic protaspid stage, whereas P2 a benthic protaspid stage. A, when the first articulation appears concurrently with the metamorphosis, there would be no adult-like protaspis during ontogeny, hence the life-history strategy I. B, delayed appearance of the first articulation would result in the presence of benthic protaspis (P2), hence the life-history strategy II. Modified from Chatterton & Speyer (1997).

limited only to one certain stage of ontogeny for reconstructing phylogeny.

Chatterton *et al.* (1994) stated that, ideally, information from all growth stages should be used for trilobite systematics. Nevertheless, in most papers dealing with trilobite ontogeny and taxonomy, great weight has been given to the protaspid and holaspid morphology. The meraspid period is the period of the most dynamic change of morphology, in which most features first assume their mature form. Hughes *et al.* (2006) demonstrated that some trilobites still added segments at the terminal part of the trunk even after entering the holaspid period, and probably underwent further allometric development in the holaspid period. In such cases, those holaspid stages may also provide useful information on ontogenetic development. Taking into account the fact that all the protaspides in the latest stages are not necessarily in a homologous stage to each other, using characters of the whole ontogenetic sequence in phylogenetic analysis is particularly important. For instance, if we compare the ontogenetic developmental series of hypothetical species A, B, C and D in Figure 1, one will be able to find that species A, B and C have similar developmental pathways, no matter how different protaspid morphology they have, whereas species D has a delayed developmental pathway, distinguishing it from species A, B and C. As the stage at which a particular character appears might be different, this kind of comparison should be applied to the whole ontogenetic series. Let us reconsider the phacopid protaspides. Despite its different-looking protaspis, *Ceraurinella latipyga*? grew up into a similar-looking adult to *C. nahanniensis*, whereas the similar-looking protaspis of *Sphaerocoryphe* sp. grew into a different-looking adult. If the whole growth series is taken into account, the different protaspid morphology of two *Ceraurinella* species would not complicate the classification.

In this respect, some recent works (Lerosey-Aubril 2006; Lerosey-Aubril & Feist 2006) are worthy of mention. Lerosey-Aubril (2006) presented differences in the morphologies of protaspides of closely related proetoid species, but he also found that the subsequent shape changes during the meraspid period were similar in those species. Lerosey-Aubril & Feist (2006) compared the post-metamorphic developmental changes for two proetide trilobites. Such an approach of considering the whole ontogeny would be a more reliable way to use the ontogenetic data for trilobite systematics. Webster (2007) provided a superb case of comparing the post-protaspid development of two closely related olenelloid trilobites. The procedure described by Chatterton *et al.* (1999) also has considerable value. Chatterton *et al.* compared several protaspid stages of different species; although a partial ‘growth series’, this enabled them to attribute some differences in protaspid morphologies of closely related taxa to heterochronic evolution, thus preventing different protaspid morphologies from misleadingly confusing the classification.

Incorporating the whole ontogenetic sequence also allows us to observe critical characters that might disappear with growth or to see the developmental mode of certain structures. This kind of information is significant in that it may give more integrative insight into the true relationship of organisms. Park & Choi (2009) observed a sudden disappearance of a pair of pygidial spines in the early holaspid period of *Tsinania canens* (Walcott 1905) and proposed that *T. canens* would have evolved from a trilobite group with a pair of prominent pygidial spines. Park & Choi (2009, 2010) showed that the development of a ventral median suture in *T. canens* and *Asioptychaspis subglobosa* (Sun 1924) during immature stages is different from the previously suggested developmental mode of the ventral median suture of the Order Asaphida, and concluded that the ventral median suture evolved multiple times in trilobite evolution. Accordingly they suggested that the current concept of the Order Asaphida be emended.

For more quantitative analysis involving many taxa, the cladistic approach with ontogenetic data would be the most desirable method. Although cladistics has been widely used in trilobite systematics, not many studies have applied ontogenetic information to the analysis: those that incorporated ontogenetic data are Fortey & Chatterton (1988), Edgecombe *et al.* (1988), Chatterton *et al.* (1990), Edgecombe (1992) and Campbell & Chatterton (2009); Waisfeld *et al.* (2001) also included some juvenile characters in their character matrix. When using ontogenetic data as a character provider for cladistic analysis, it is recommended that all the developmental stages be examined (e.g., Steyer 2000), so that possible false signals from using ontogenetic data of a certain stage will be compensated by desirable signals from other ontogenetic stages.

Conclusions

The morphology of the protaspis has been widely employed in trilobite systematics for the past several decades. Apparently protaspid morphology plays a key role in higher-level classification and in classifying problematic taxa, although the validity of its usage has rarely been tested owing to its long tradition in trilobite systematics. However, there is a fundamental problem in comparing the protaspides of different trilobites: i.e. protaspides of different taxa are not necessarily in the homologous stage to each other. Protaspid morphology is subject to differences in the timing of the first articulation between head and trunk and to changes in the rate of development. These complicate comparisons between different taxa. By putting excess emphasis on protaspid morphology for classification, information that can be provided by other developmental stages, such as the meraspid period or holaspid periods, is frequently underutilized. Hughes *et al.* (2006) pointed out that trilobite development is the combination of different attributes that develop sequentially, such as size, shape and segmentation. Understanding this aspect of trilobite development is necessary for the proper usage of ontogenetic data for trilobite phylogeny.

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