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General palaeontology

Morphological and ontogenetic criteria for defining a trilobite species: The example of Siluro-Devonian Phacopidae

Critères morphologique et ontogénétique pour définir une espèce de trilobite : l'exemple des Phacopidae du Siluro-Dévonien

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ABSTRACT

The palaeontological species concept – a rather subjective concept – is based on morphological criteria and carries a notion of time. The delimitation of a species among trilobites does not break this rule and is based on morphological and ontogenetic features. Thus, among phacopid trilobites, characters such as the visual complex and the vincular furrow are diagnostic. Furthermore, quantitative studies of the morphological disparity and ontogenetic trajectories allow us better to define the species and its variability, and to identify the evolutionary patterns established in Phacopidae during 100 Ma of existence.

Mots clés :
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Phacopidae
Paléozoïque
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RÉSUMÉ

Le concept paléontologique de l'espèce – un concept relativement subjectif - repose sur des critères morphologiques et porte une notion de temps. La délimitation d'une espèce chez les trilobites ne déroge pas à la règle, se fondant sur des critères morphologiques et ontogénétiques discrets. Ainsi, chez les trilobites Phacopidae, sont diagnostiques des caractères tels que le complexe visuel et le sillon de fermeture. Par ailleurs, les études de quantification de la disparité morphologique et des trajectoires ontogénétiques permettent elles-aussi de mieux définir les espèces et d'appréhender les patrons évolutifs mis en place au cours des 100 Ma d'existence des Phacopidae.

1. Introduction

The definition of a species is a topic of debate within the biological community. There is a great variety of species definitions (Stuessy, 1990) currently in use by biologists according to their speciality. These include

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biological, genetic (Dobzhansky, 1951), phenetic, phylogenetic (Baum, 1992) and palaeontological definitions.

Over the last few decades the theoretically most important species definition has been the biological species concept. This concept defines a species as a group of interbreeding individuals that is reproductively isolated from other similar groups (Mayr, 1942). Members of a biological species have the potential to produce viable and fertile offspring under natural conditions.

Nevertheless, the biological species concept has its restrictions (Budd and Mishler, 1990; Sokal and Crovello, 1970), especially since the interbreeding criterion cannot be checked for fossil species. Therefore, the delimitation of fossil species is based on morphological criteria alone. The members of the same species share inherited features from a common ancestor. They have a certain morphological resemblance despite often significant morphological variability. Thus, morphological similarities and discontinuities are used for delimiting species. If the organisms are phenotypically similar, they are considered conspecific even although it is not possible to demonstrate any reproductive barrier. The palaeontological concept of species is more subjective and carries a notion of time.

In the present article, we will see how a phacopid trilobite species is defined according to discrete diagnostic features, on the one hand, and continuous features, on the other hand, before analyzing their developmental evolution during geological time.

2. Diversity and morphological disparity

2.1. Discrete diagnostic features

The highly mineralized parts are usually only preserved during or after fossilization. Consequently, the morphological analysis of trilobites is often limited to a study of cuticular structures covering the dorsal part (cephalon, thorax and pygidium) and its ventral invagination (cephalic doublure), plus the ventral part (hypostome).

2.1.1. Morphology

Phacopidae are an important component of marine benthos that existed for nearly 100 Ma. This family is globally represented and is characterized by its great diversity in genera and species. It is a family typical of Siluro-Devonian epicontinental platforms, present from shallower to deeper environments (Chlupáč, 1975, 1977).

The morphological diversity among Phacopidae is expressed especially in the shape of both the vincular furrow and visual complex and in the course of the facial suture (Fig. 1). Systematic clusters are based primarily on these characters.

2.1.2. Origin and phylogenetic development

Phacopids are clearly differentiated very early, in the Silurian. Chlupáč (1977) identifies two sub-families: Phacopidellinae Delo, 1935 characterized by a cephalic doublure without a vincular furrow and Phacopinae Reed, 1905 characterized by a cephalic doublure with a deep and continuous vincular furrow.

The ancestor of the main phacopid evolutionary lineage is represented from the basal Silurian by the cosmopolitan genus *Acernaspis* Campbell, 1967. From *Acernaspis*, the genus *Ananaspis* Campbell, 1967, is widely distributed, reaching its maximum development in the Late Silurian (Clarkson et al., 1977). The origin of Devonian Phacopinae mainly represented by the genus *Phacops* Emmrich, 1839 *sensu lato* must be sought in this group.

Phacopidae constitute assemblages adapted to unstable, high energy environments of shallow internal

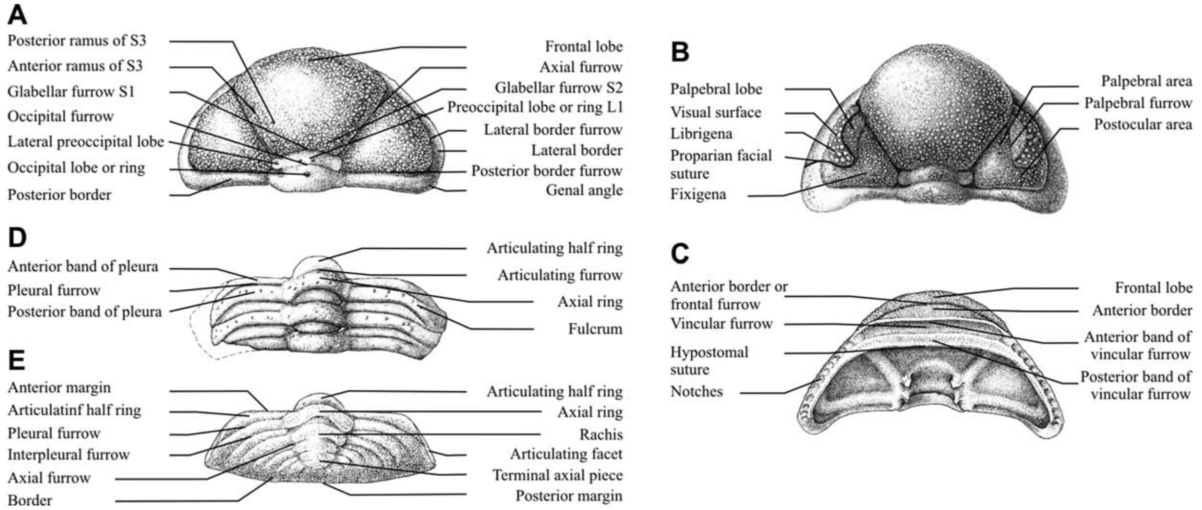


Fig. 1. Morphological terminology of Phacopinae trilobites based primarily on the work of Harrington (1959) and Clarkson (1998). A. Cephalon in dorsal view for a blind phacopine. B. Cephalon in dorsal view for a phacopine with well-developed eyes. C. Cephalon in ventral view. D. Three connected thoracic segments, in dorsal view. E. Pygidium in dorsal view (drawings by L. Meslin, Montpellier).

Fig. 1. Terminologie morphologique des trilobites Phacopinae, basée sur les travaux de Harrington (1959) et Clarkson (1998). A. Céphalon en vue dorsale d'un Phacopinae aveugle. B. Céphalon en vue dorsale d'un Phacopinae à œil développé. C. Céphalon d'un Phacopinae en vue ventrale. D. Trois segments thoraciques en connexion d'un Phacopinae en vue dorsale. E. Pygidium d'un Phacopinae en vue dorsale (dessins de L. Meslin, Montpellier).

platforms. Submitted to changes in the environment, these trilobites are characterized by a mode of dispersal and distribution, which accord with the evolutionary model of Punctuated Equilibrium (Eldredge, 1972; Eldredge and Gould, 1972). Representatives of this biofacies are characterized by their large size; large, wide and high reniform eyes with numerous lenses; a posterior band of the cephalic doublure curve, at least twice as wide (tr.) as the vincular furrow; a developed tuberculation; and a mutisegmentated pygidium.

Deeper biofacies are populated by Phacopidae with reduced sight, such as *Plagiolaria* Kegel, 1952 and *Struveaspis* Alberti, 1966 and blind forms such as *Ductina* (Richter and Richter, 1931) are rare.

After a maximum development in diversity and number in the Middle Devonian, most Phacopidae that were adapted to outer-shelf bottom habitats after the mid-Givetian Taghanic transgression, were severely affected by repeated rises of sea-level (Feist, 1991).

Numerous recent studies in macroevolution often indicate a high degree of differentiation very early in the history of monophyletic groups followed by a late peak of diversity. This pattern seems to occur in phacopid trilobites. Their origin may be found within the Pterygometopidae Reed, 1905 from Ordovician, on the basis of larval features.

2.1.3. *Diagnostic features: implications of the visual complex and vincular furrow*

This family is characterized by numerous genera and subgenera (according to the authors) but most of these are based on characters, which differ only slightly, especially for taxa from Lower and Middle Devonian.

The distribution of genera and sub-genera in tribes (Fig. 2) proposed by McKellar and Chatterton (2009) is

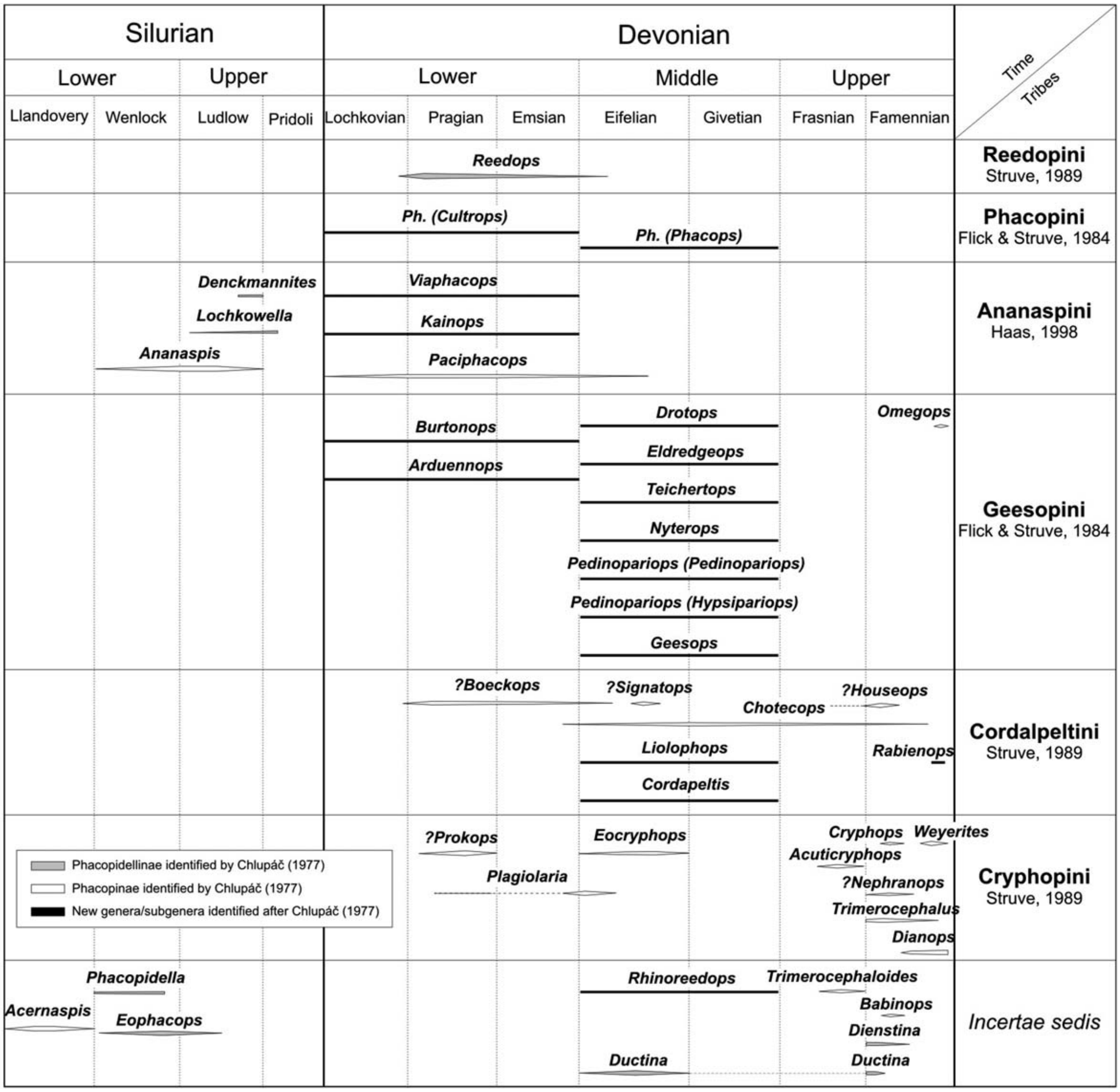


Fig. 2. Distribution of phacopid genera (or sub-genera) modified after McKellar and Chatterton's database (2009).

Fig. 2. Répartition des nombreux genres (ou sous-genres) de la famille Phacopidae, élaborée d'après les données de McKellar et Chatterton (2009).

based on the work of Flick and Struve (1984), Haas (1998) and Struve (1970, 1972, 1976, 1982, 1989, 1990, 1992, 1995). This distribution is in disagreement with the previous work of Chlupáč (1977): numerous members belonging to Phacopidellinae or Phacopinae are in the same tribe. Moreover, all taxa belonging to this family, listed in the exhaustive list of Jell and Adrain (2003), have not been taken into consideration.

2.1.4. *Delimitation of genera with well-developed eyes*

Earlier authors have often noted the heterogeneity of the genus *Phacops* and defined numerous subgenera (Chlupáč, 1977). Since then, many subgenera have been elevated to generic level such as *Omegops* (Struve, 1976) or *Chotecops* (Chlupáč, 1971).

Recently, McKellar and Chatterton (2009) performed a cladistic analysis in order to test the validity of many genera (or subgenera) widely recognized in Phacopidae from the Early and Middle Devonian and to provide a database for all subsequent analyses. Accordingly, these authors have obtained the tree of relationships presented in Fig. 3. The order of branches coincides rather well with the generic level; sometimes some genera seem not very stable and are paraphyletic. The position of *Viaphacops* within the *Paciphacops* clade led the authors to consider *Viaphacops* as a subgenus of *Paciphacops*. The clustering of taxa in tribes is not confirmed. Only a cladistic analysis including more taxa will confirm or otherwise the results obtained.

For example, the main features distinguishing *Chotecops* from *Phacops* are a less inflated glabella, tubercles absent on the glabella, the configuration of the preoccipital ring, flat palpebral lobes, a pygidium slightly segmented with shallow pleural furrows and flat ribs.

Otherwise, the species *Phacops (Phacops) granulatus* (Münster, 1840) from the Upper Devonian is atypical of the genus *Phacops sensu stricto* from the Middle Devonian. Its differs especially by a less inflated glabella, a preoccipital ring narrower and less convex in its middle part, distinctly demarcated from the glabella by a continuous preoccipital furrow S1, a visual surface smaller and more distant from the posterior furrow of the cheek (a feature shared by *Chotecops*), a tuberculation less pronounced, and a pygidium shorter than other representatives of the genus.

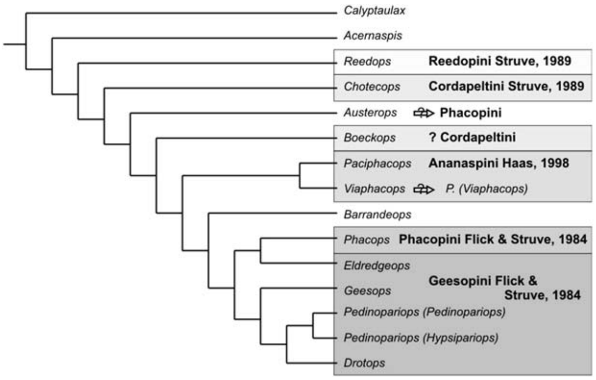


Fig. 3. Phylogenetic relationships of some genera and subgenera of Phacopidae from Early and Middle Devonian (simplified after McKellar and Chatterton, 2009).

Fig. 3. Relations phylogénétiques de quelques genres et sous-genres de la famille Phacopidae (simplifié d'après McKellar et Chatterton, 2009).

2.1.5. *Delimitation of genera with reduced eyes*

Traditionally, the configurations of the visual surface (small, elliptical with a small number of lenses) and the pygidium (wide and short) have been used to integrate different Late Devonian reduced-eye groups in one single taxon *Cryphops* (Richter and Richter, 1926). However, taking into account the discontinuous stratigraphic distribution and the ventral cephalic features, several genera have been distinguished (Crônier and Feist, 2000): the genus *Cryphops* characterized by the absence of the posterior band of the cephalic doublure; the genus *Acuticryphops* Crônier and Feist, 2000 characterized by a narrow and angular posterior band of the cephalic doublure, a feature shared with the blind genus *Trimerocephalus* McCoy, 1849; and the genus *Weyerites* Crônier and Feist, 2000 characterized by a curved posterior band of the cephalic doublure, a primitive feature shared with the genus *Phacops* (Fig. 4).

2.1.6. *Delimitation of blind genera*

The genus *Trimerocephalus* is characterized by the absence of eyes and its submarginal facial suture that cuts the anterior end of the cheeks. The genus *Dianops* Richter and Richter, 1923 differs by an interrupted (tr.) S1, a facial suture that goes through the lateral-frontal border, a pygidium longer (sag.), strongly convex without distinct segmentation. Phylogenetically, *Dianops* is the last representative of the phacopine evolutionary lineage, characterized by a gradual and progressive reduction of the eye until its final disappearance and a displacement of the facial suture to the margin. The diversity of these blind phacopids from Upper Devonian coincides with the expansion of pelagic facies at a worldwide scale (Chlupáč, 1975).

2.2. *Continuous characters and morphological variability at speciation boundaries*

In Phacopidae, the calcified compound eye is schizochroal. The biconvex and thick lenses, often relatively few and unusually large, are more or less separate from each other and they have their own corneal covering (Clarkson, 1975, 1979, 1998). Their size increases regularly from the top to the bottom, and they are ordered in dorsal-ventral rows (Clarkson, 1966).

The particular characteristics of the eye morphology and the pattern distribution of the lenses have been figured in numerous discussions about the possible dimorphism and polymorphism in Phacopidae, and have sometimes been used to separate genera and species (Beckmann, 1951; Lorenz, 1991; Thomas, 1998).

Thus, numerous specimens of *Acuticryphops* from the Canning Basin (western Australia) have allowed the analysis of the pattern of changes in lenses of a community from the internal platform; to make a comparative study with previously studied populations from external platforms: the Montagne Noire in France and Meseta Central in Morocco (Crônier et al., 2004); and to clarify the significance of asymmetries involved in the Late Frasnian,

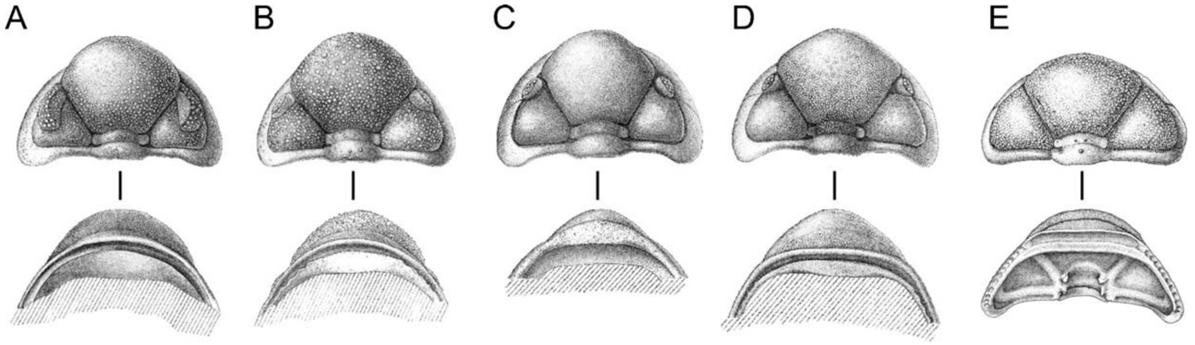


Fig. 4. Representation of some Late Devonian Phacopinae, respectively in dorsal and ventral views. A. *Phacops (Phacops) granulatus* (Münster, 1840). B. *Weyerites wocklumeriae* (Richter and Richter, 1926). C. *Cryphops cryptophthalmus* (Emmrich, 1844). D. *Acuticryphops acuticeps* (Kayser, 1889). E. *Trimerocephalus lelievrei* Crônier and Feist, 1997 (drawings by L. Meslin, Montpellier).

Fig. 4. Représentation de quelques Phacopinae du Dévonien supérieur, respectivement en vues dorsale et ventrale. A. *Phacops (Phacops) granulatus* (Münster, 1840). B. *Weyerites wocklumeriae* (Richter and Richter, 1926). C. *Cryphops cryptophthalmus* (Emmrich, 1844). D. *Acuticryphops acuticeps* (Kayser, 1889). E. *Trimerocephalus lelievrei* Crônier and Feist, 1997 (dessins de L. Meslin, Montpellier).

a crucial period preceding the extinction of the group (Feist et al., 2009).

The phenomenon of gradual reduction in the average number of eye lenses (Fig. 5) observed in the Montagne Noire appears contemporarily in Morocco (northern Gondwana) and Australia (north-eastern Gondwana). This reduction cannot be ascribed to the size of specimens or to the morphological variation of the cephalon. The successive populations testifying to the gradual reduction is concomitant with periods of pronounced deepening in terminal Frasnian, just before the Kellwasser extinction global event rather than regional effects.

This evolutionary trend observed in various independent lineages evolving during the Upper Devonian may result from an 'opportunistic' and adaptive strategy correlative with environmental constraints, insofar as it leads to a good fit between organisms and their environment (Crônier and Courville, 2003).

In addition, populations of the Montagne Noire and Meseta Central, and to a lesser extent the population of Canning Basin, located just below the Kellwasser event show a high coefficient of variation of the lens number (Feist et al., 2009). The visual complex that tends to disappear with depth increase during the Frasnian, would suffer

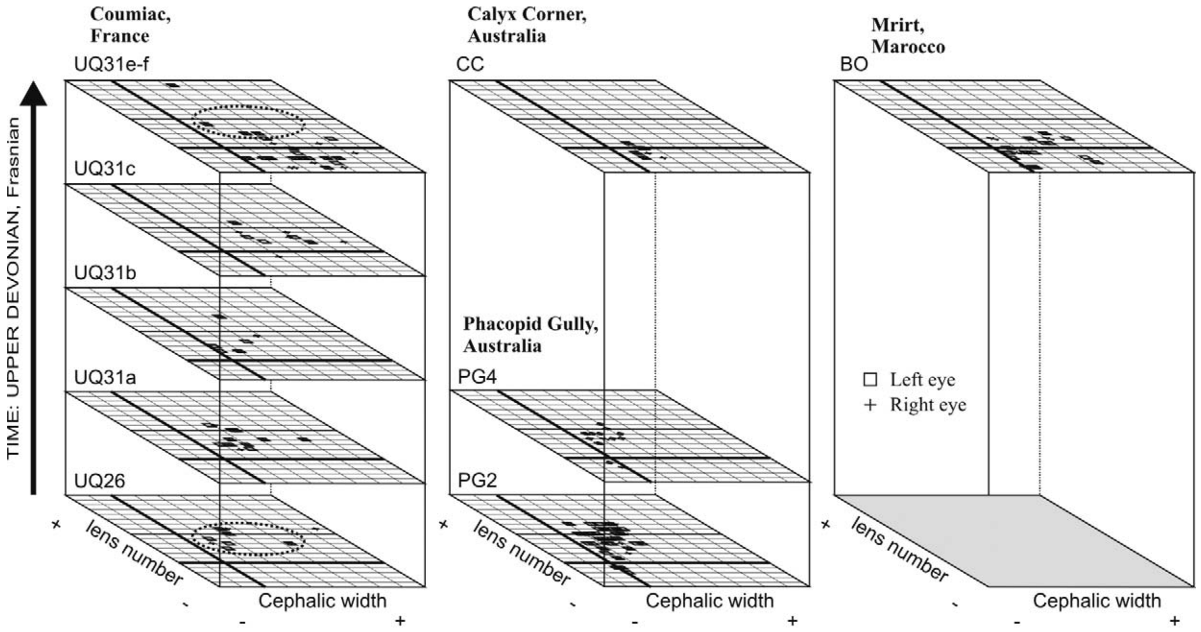


Fig. 5. Scatterplot of the lens number versus cephalic width in *Acuticryphops* from different levels of Coumiac quarry (UQ; Montagne Noire, southern France), Mrirt (BO; Central Meseta, Morocco), Phacopid Gully and Calyx Corner (PG, CC; Canning Basin, Western Australia). Size of each population: UQ26 = 14; UQ31a = 35; UQ31b = 28; UQ31c = 30; UQ31d-f = 62; PG2 = 49; PG = 19; CC = 6; BO = 23.

Fig. 5. Diagramme de dispersion du nombre de lentilles *versus* la largeur céphalique chez *Acuticryphops,* provenant de différents niveaux de la Carrière supérieure de Coumiac (UQ ; Montagne Noire, sud France), de Mrirt (BO ; Meseta Centrale, Maroc), de Phacopid Gully et Calyx Corner (PG et CC ; Canning Basin, ouest de l'Australie). Taille de chaque population: UQ26 = 14 ; UQ31a = 35 ; UQ31b = 28 ; UQ31c = 30 ; UQ31d-f = 62 ; PG2 = 49 ; PG = 19 ; CC = 6 ; BO = 23.

a relaxation of selection pressures leading to an increase in the variability of this organ and reflecting developmental instability (Debat and David, 2001). These disturbances that occurred during development seem to be linked to environmental stress, and in particular with rapid fluctuations in sea level around the terminal Frasnian.

There is a morphological intra-specific drift in *Acuticryphops* inducing a relatively important variability, which would be located at boundaries of speciation. The visual complex drift seems gradual and unidirectional (Crônier et al., 2004; Feist, 1995) for populations of the Montagne Noire represented by one species. For the same period, the populations of the Canning Basin are characterized by two species: *A. acuticeps* and *A. klapperi* characterized by different preoccipital lobes; the morphological drift would have affected other features (Feist et al., 2009).

3. Ontogenetic development and its regulation

3.1. Ontogenetic development and developmental program of segmentation

In this section, the term 'larval' will be used to designate protaspid instars, and 'juvenile' for meraspid and young holaspid instars. 'Early' ontogeny refers to the protaspid period and early meraspid period; and 'late' ontogeny to the end of the meraspid period and the holaspid period.

3.1.1. Exuviation

Like most arthropods, trilobites have a strongly indurated exoskeleton (Wilmot and Fallick, 1989) that protects the internal organs and the weakly mineralized ventral surface. Thus, these organisms could increase in size during the brief period following the loss of their old shell.

During moulting, the cephalic sutures (lines of weakness) usually functional at each moult, allow the shell to yield to the pressure during moulting (Hupé, 1953) by dissociation of the different cephalic parts (cranidium, librigenae, rostral plate and hypostome).

3.1.2. Ontogenetic development and articulation development

The ontogenetic development of trilobites was one of the best known among all invertebrates, at an early stage, due to Barrande's work (1852). During ontogeny, many features change substantially. Some radical morphological changes are related to behavioural or ecological modifications and occur in early ontogenetic development (Speyer and Chatterton, 1989). These changes correspond to the transition from a bulbous, probably pelagic larva ('nonadult-like' *sensu* Chatterton and Speyer, 1989; Speyer and Chatterton, 1990) to a trilobed benthic organism ('adult-like' *sensu* Chatterton and Speyer, 1989; Speyer and Chatterton, 1990).

Post-embryonic stages can be grouped into three successive periods (Fig. 6) defined on the development of the exoskeleton articulation (Whittington, 1957) or 'segment articulation' (*sensu* Hughes et al., 2006): protaspid (Beecher, 1895), meraspid and holaspid periods (Raw, 1925).

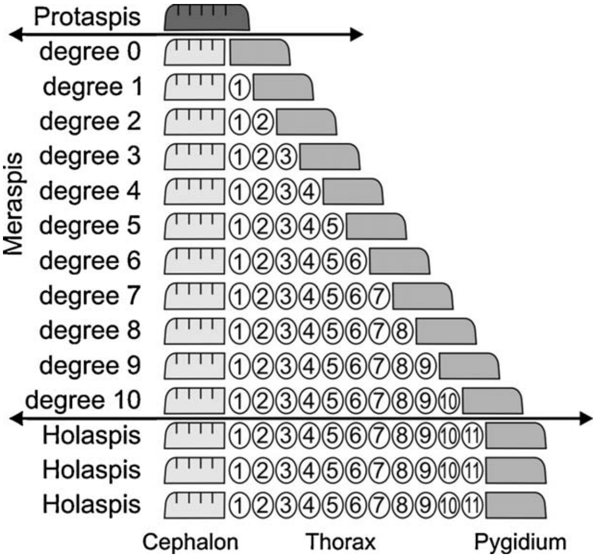


Fig. 6. Thoracic segmentation pattern based on the 'segment articulation' and defining three successive periods: protaspid period and its shield; meraspid period and its successive addition of articulated segments in the thorax up to 10; holaspid period with 11 thoracic segments in typical Phacopinae.

Fig. 6. Schéma représentant les trois périodes reposant sur l'articulation segmentaire : période protaspide et son bouclier ; période méraspide avec l'ajout successif de segments articulés dans le thorax jusqu'à 10 ; période holaspide avec les 11 segments thoraciques typiques chez les Phacopinae.

The protaspid period corresponds to the first instars divided into pre-metamorphic or anaprotaspid stages that correspond to dorsal shields with an axis surrounded laterally by furrows and divided usually into five cephalic segments; and post-metamorphic or metaprotaspid stages that correspond to dorsal shields divided transversely into a cephalon and a protopygidium (Chatterton and Speyer, 1997). This period begins with the appearance of the dorsal facial suture (Hughes et al., 2006).

The meraspid period begins with the emergence of a functional cephalo-pygidial articulation (Raw, 1925). Thus, the dorsal shield is divided into cephalon and 'meraspid (or transitory) pygidium'. This period is divided into degrees counted from 0 to (n-1), where n is the total number of thoracic segments present in the 'adult' individual. The degree p is the instar where p thoracic segments are individualized from the anterior part of the 'meraspid pygidium'. Typically at each moult, one thoracic segment is released from the anterior part of the 'meraspid pygidium'; but exceptions are known (Chatterton and Speyer, 1997). During this period, major shape changes transform the cephalon involving different allometric growth patterns (Crônier et al., 1998, 2005).

The holaspid period begins when the number of thoracic segments specific to the species is acquired, with the putting into function of the last articulation between the last thoracic segment and the posterior shield made of merged segments (Hughes et al., 2006). The term 'holaspid pygidium' is applied to this posterior shield or pygidial shield. The trilobite is still small and numerous successive moults will be required to reach an 'adult' size representing all large individuals in a population, whether they are sexually mature or not. The general shape during the holaspid period does not suffer significant shape changes (Crônier et al., 1998, 2005).

The ontogenetic development of Phacopidae is currently well known, especially since many are silicified, and of excellent preservational quality. Thus, there is good data for some meraspides and young holaspides of P*hacops sensu lato* for example (Alberti, 1972; Jahnke, 1969).

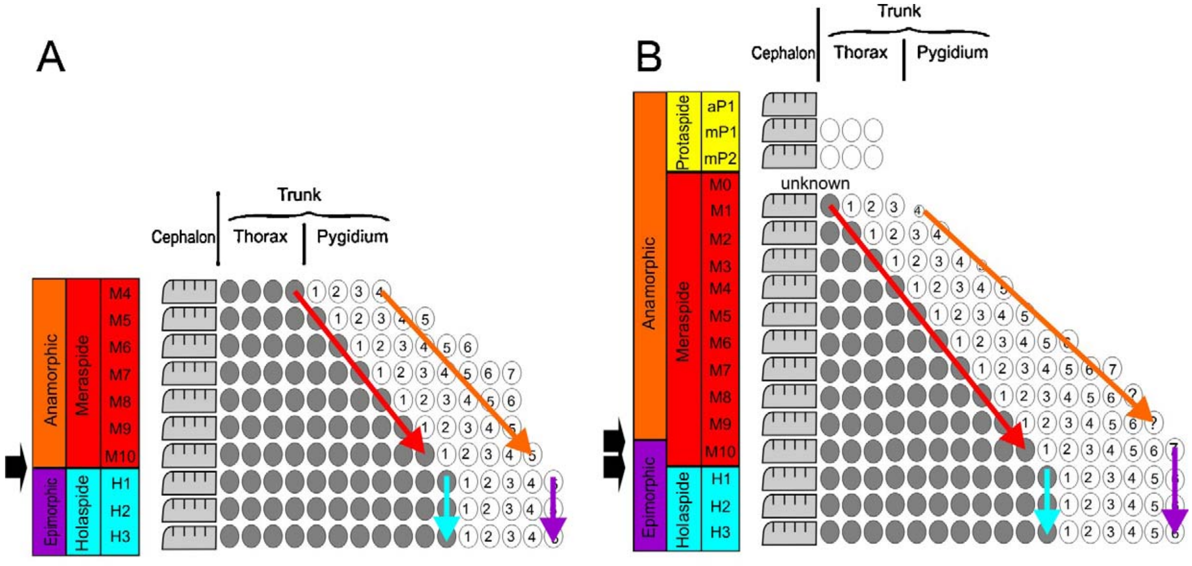
Additionally, protaspides are now known among Phacopidae (Crônier, 2007). Their morphological features especially for *Nephranops incisus incisu*s (Roemer, 1866) from Upper Devonian of Germany are: a highly arched form of smallest protaspides, a functional proparian suture, eye lobes far forward, a glabella widening anteriorly, four transglabellar furrows, a strong spinose occipital node, a distinct posterior and lateral cephalic furrows in older protaspides, and two distinct pairs of posterior spines. These different features are also present in other Phacopina, such as *Calyptaulax* Cooper, 1930 *Dalmanitina* Reed, 1905 and *Dalmanites* Barrande, 1852.

3.1.3. Developmental program of trunk segmentation

In addition to the development of articulations, the changes occurring during development depend also on the total number and the form of segments and on their relations with segment articulation. Thus, Hughes et al. (2006) have proposed a complementary descriptive ontogenetic scheme based on the generation of new segments or 'segment generation' within the thoraco-pygidium or trunk (differentiated in package of similar segments; Hughes, 2003b; Hughes et al., 2006). The trunk is divided into a set of articulated anterior segments constituting the thorax, and a set of merged posterior segments forming the terminal dorsal shield or pygidium.

In living arthropods, the number of segments after hatching determines the type of post-embryonic development (Enghoff et al., 1993; Snodgrass, 1956). In trilobites, the development is hemianamorphic (Crônier, 2010; Fusco et al., 2004; Hughes et al., 2006) with an 'anamorphic' addition of trunk segments during the early ontogeny, followed by an 'epimorphic' phase where the number of segment of the trunk is stable, although growth and moulting continue (Fig. 7). The hemianamorphic development, maintained for Trilobita, seems to be the basic situation for Euarthropoda (Hughes et al., 2006).

For a better understanding of segmentation, Hughes et al. (2006) have proposed a developmental program based on the decoupling or not between the different phases of segment generation and the different periods of segment articulation. They have identified five developmental patterns according to comparison of the boundaries of the different aspects of ontogeny. Thus, for some Phacopinae where the quality of preservation allowed recognizing various growth stages, the trunk development is synarthromeric in *Trimerocephalus lelievrei* and *Weyerites*



Weyerites ensae (Richter et Richter, 1926)

Nephranops incisus incisus (Roemer, 1866)

Fig. 7. Trunk segmentation pattern and ontogenetic stage boundaries based on 'segment generation' and 'segment articulation' in (A) *Weyerites ensae* (Richter and Richter, 1926) and (B) *Nephranops incisus incisus* (Roemer, 1866). P refers to protaspid stages, M, meraspid stages and their respective degrees and, H, holaspid stages and their respective degrees. Grey circles refer to articulated segments of the thorax; white circles refer to segments of 'meraspid' or 'holaspid' pygidium. Anamorphic phase corresponds to the setting up of new trunk segments; epimorphic phase to a constant number of segments despite of the continuation of moulting (see arrows).

Fig. 7. Patron de la segmentation du tronc et limites des stades ontogénétiques basées sur la génération et l'articulation segmentaire chez (A) *Weyerites ensae* (Richter et Richter, 1926) and (B) *Nephranops incisus incisus* (Roemer, 1866). P désigne les stades protaspides ; M, les stades méraspides et leur degré respectif ; H, les stades holaspides ; les ronds gris, les segments articulés du thorax ; les ronds blancs, les segments du pygidium « mérapide » ou « holaspide ». La phase anamorphique correspond à la mise en place de nouveaux segments du tronc, la phase épimorphique à un nombre constant de segments malgré la poursuite des exuviations (voir flèches).

ensae (Richter and Richter, 1926): the onset of the holaspid period coincides with the epimorphic phase (Fig. 7A). This mode seems to be rare in the fossil record requiring a synchronous transition between the maturity in segment generation and segment articulation (Hughes et al., 2006). By contrast, *Nephranops incisus insisus* has a hypoprotomeric development (Fig. 7B): the onset of the epimorphic phase begins before the holaspid period (Crônier, 2010). This mode seems to be the most widespread where the transition in segment generation and segment articulation ranges freely over a large number of stages (Hughes et al., 2006).

As underlined by Hughes et al. (2006), the mode of trunk development varies widely among trilobites, even among quite closely related species in Phacopinae (Crônier, 2010). This variability in the relationship between the onset of a stable articulation and the stable number of segments at a very low taxonomic level offers the opportunity to explore evolutionary changes of the trunk segmentation. These changes are important insofar as some major innovations in the evolution of trilobites require specific and unchanging relations between the appearance, the articulation and the form of segments (Hughes, 2003a, 2003b).

3.2. Ontogenetic trajectories

3.2.1. Discontinuous and isometric growth

Until recently, analyses of ontogenetic transformations were limited to univariate or bivariate quantitative analyses in order to characterize the dynamic growth of sclerites during ontogeny.

Like many arthropods, growth by successive moults leads to various instars typically, though not invariably clustered into instar groupings. Thus, a plot of two morphological dimensions (width versus length of a sclerite) shows a discontinuous growth curve; individuals are pooled in distinct dimensional classes.

On the basis of available material, for example, the growth series of *Nephranops incisus incisus* exhibits a conventional growth curve with discrete instars during early ontogeny (Crônier, 2007). Within the larval period, two stages are morphologically distinct, anaprotaspides and metaprotaspides (Fig. 8). The bulbous and smooth phacopid anaprotaspides (Fig. 8, A) are similar to the small protaspides of Pterygometopidae (Brenner, 2004; Chatterton, 1980; Chatterton and Speyer, 1997). The metaprotaspides exhibit two distinct morphotypes in which dorsal structures are notably present. All these larvae are inflated, more flattened dorso-ventrally in comparison with anaprotaspides, and subovoid (Fig. 8, B1) to subquadrangular (Fig. 8, B2) in overall shape. For the same range of length, B1 is narrower and B2 is widened. It is difficult to say if we can consider them to be successive instars or rather variants. Nevertheless, based on their morphology and size, these prostaspids could correspond to two successive metaprotaspid stages.

Among Phacopinae, the larval/juvenile ontogeny of *Weyerites ensae* and *Nephranops incisus incisus* are currently the best known. The growth series of *Weyerites ensae* is known from the meraspide degrees 3 to the early holaspide (Crônier et al., 1999, 2005), the growth series of *Nephranops incisus incisus* from the anaprotaspide to the early holaspide (Crônier, 2007). These growth series show a conventional and simple pattern of development ($y = ax + b$), comprising discrete growth stages.

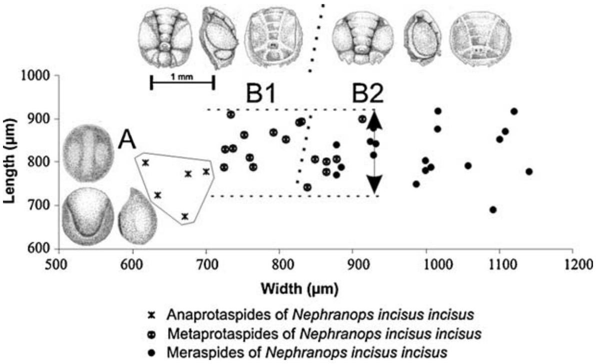


Fig. 8. Scatter plot of size (length *versus* width) of protaspid shields and early meraspid cephala showing distinct size classes in *Nephranops incisus incisus* (Roemer, 1866).

Fig. 8. Diagramme de dispersion de taille (longueur *versus* largeur) des boucliers de protaspis et des céphalons de méraspis précoces montrant des classes de dimensions distinctes chez *Nephranops incisus incisus* (Roemer, 1866).

Modified from Crônier, 2007.

However, in the absence of discrete morphological changes, especially for isolated cephala, size is the most reliable parameter for assigning each individual to particular instars. Such assignment can be performed through a hierarchical classification based on the cephalic width and/or length.

Thus, the growth series obtained, for example, in *Acuticryphops acuticeps* from the Upper Devonian, in Australia (Feist et al., 2009), shows a discontinuous and typical isometric distribution (Fig. 9). An extrapolation can be considered. Individuals with genal tips are compatible with the two smaller groups that could represent meraspid stages; individuals without genal point to holaspide. The growth rate, defining the coefficient of Dyar (calculated using the formula: $Y = ak^n$ where Y is the final size, a the initial size, k the coefficient of Dyar and n is the number of growth stages) was calculated between successive ontogenetic stages, according to cephalic width. The rate of 1.15 corresponding to an average biological value seems constant, according to the law of Dyar's Law (used as a null hypothesis of growth in insects), and comparable to that of living arthropods (Fusco et al., 2004).

The difference in size between instars can be tested by a multivariate analysis of variance (MANOVA). MANOVAs performed on the linear dimensions (width and length) of cranidia/cephala indicate the existence of a differentiation in size between stages (significant test).

3.2.2. Comparison of ontogenies

If the discontinuity in post-embryonic growth is due to changes in size and shape during ontogeny, it is only recently that these changes have been clearly quantified in Phacopidae (Crônier and Fortey, 2006; Crônier et al., 1998, 2005).

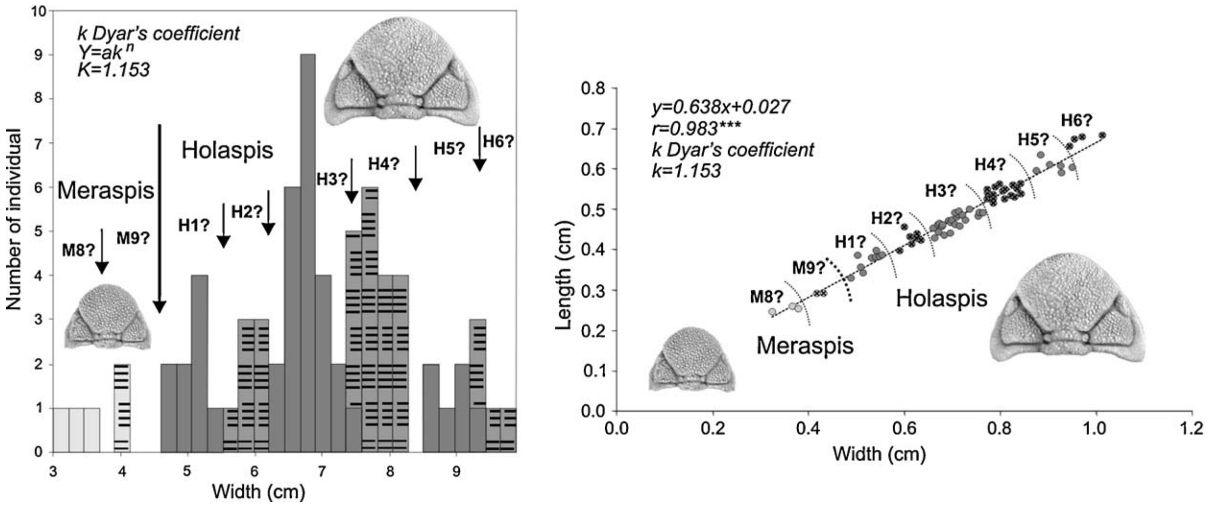


Fig. 9. Growth series in *Acuticryphops acuticeps* from the Frasnian of Australia showing a discontinuous and typical isometric distribution.

Fig. 9. Série de croissance chez *Acuticryphops acuticeps* du Frasnien d'Australie montrant une distribution discontinue et isométrique typique Modified after Feist et al., 2009.

The use of geometric morphometrics for studying the growth stages of a blind Phacopinae *Trimerocephalus lelievrei*, yielded a valuable reference database (Crônier et al., 1998). This makes possible a comparison with other related phacopine species (e.g. *Weyerites ensae*) in order to understand how the morphological diversity of ontogenetic stages is structured and to better understand the changes in terms of evolution and adaptation (Crônier et al., 2005).

Previous morphometric analyses based on an outline analysis showed a progressive shape change during the successive instars of increasing size (Crônier et al., 1998, 2005). Thus, significant morphological changes affect particularly the cranidium during the meraspid period. In early instars, this cranidium is relatively stocky with massive and long genal spikes. Then, during development, the cranidium expands and genal peaks are reduced (Crônier et al., 1998, 2005).

Furthermore, a comparison of size and shape changes showed that these two variables are related by an exponential growth model: main shape changes occur during the early meraspid period; increasing size during the late meraspid/holaspid period. This pattern observed in different phacopines suggests that the allocation of resources have been modified during ontogenetic development. It seems to be a general case among Phacopinae and even among unrelated taxa (Delabroye and Crônier, 2008).

Additionally, a relative comparison between the different ontogenetic instars for two ontogenies (i.e. *Weyerites ensae* and *Trimerocephalus lelievrei*; Crônier et al., 2005) showed a parallel shift of the nearly entire ontogenetic trajectories in the morphospace occupation and also with size increase (except for the initial growth assumed common: the two species share a common ancestor). The shape difference remains constant throughout the ontogenetic development. The preservation of such structural difference in these ontogenetic trajectories may be a manifestation of developmental constraints or linked to ecological/environmental adaptation: *Weyerites ensae* with longer (sag.) and narrower (tr.) cranidia is a reduced-eye form probably living on the bottom, *Trimerocephalus lelievrei* with shorter (sag.) and wider (tr.) cranidia is a blind form probably living buried in the sediment.

3.2.3. Development and its timing: role at a macroevolutionary scale

A complete understanding of ontogenetic development requires the knowledge of the variation in morphological features and of the timing and the rate of development among phylogenetically related species.

Amongst changes in developmental process known as heterochrony of development (Alberch et al., 1979; Gould, 1977, 1992; McNamara, 1986), paedomorphosis corresponds to juvenile ancestral morphologies displayed in adult descendants and is well established in trilobites of all ages. Additionally, some ontogenies carry quite a lot of information on mosaic heterochrony (Clarkson et al., 1997).

Only paedomorphosis has been observed in Late Devonian phacopids (Crônier et al., 2004, 2005). Such evolutionary trend concerns the progressive 'displacement' of the visual complex towards the outer margins and its 'reduction', accompanied by the 'displacement' of facial suture (Crônier and Courville, 2003).

These 'delayed effects' may correspond to evolutionary trends reflecting a 'balance' between intrinsic factors, depending of the ontogenetic potentialities limited in number, and extrinsic factors, depending on physical and/or ecological constraints (Dommergues et al., 1989).

In phacopids, paedomorphosis seems to lead to homeomorphic morphological changes, without creating new structural types. These homeomorphic changes occur in parallel with the extension of habitats during sea level rises in Devonian time (Crônier and Courville, 2003; Feist, 1995). They underline morphological trends that relay different taxa from epibenthic taxa of the internal platform with well-developed eyes to more distal epibenthic taxa with reduced eyes, or blind endobenthic taxa of the external platform. These morphological events that are correlated to transgressive maxima and coincide with the global anoxic episodes in deeper environments could be used for an ecophenotypic evaluation of palaeobathymetric trends.

However, even if the heterochronies of development seem to be common among Phacopidae, the concept of heterochrony is used here rather as a result (in order to describe the growth and its evolution) and not as a control mechanism of the developmental biology (Raff, 1996; Raff and Wray, 1989).

4. Conclusions

In phacopid trilobites, as many other fossils groups, the delimitation of a new species is based primarily on a descriptive comparison of distinct characters from the hard exoskeleton: shape and sculpture of the cephalon, glabella, pygidium, borders; number and shape of furrows, segments; size and shape of the visual complex; trace of facial suture and vincular furrow. Thus, specimens morphologically/phenotypically similar are considered conspecific.

However, a total invariance of characters delimiting a species is not acceptable. Thus, certain variability affects particularly the visual complex in phacopids, influenced by variable and unstable environmental factors such as those encountered in Upper Devonian (Crônier et al., 2004; Feist et al., 2009). A group of specimens that are more closely related morphologically to each other than to any other specimens with consistent and persistent diagnostic traits distinguishable by 'ordinary means' (Cronquist, 1988) delimit the boundaries of extinct species. The quantification of intra- and inter-specific variability in populations of phacopid trilobites must continue and should focus on reasonably continuous sedimentological series.

All these diagnostic features may be performed by a cladistic analysis in order to build a coherent α-taxonomy of Phacopidae, to propose phylogenetic relationships among taxa within the lineage, and to suggest a correlation between some morphological characters and the environmental conditions.

Moreover, in phacopid trilobites, consideration of ontogenetic series and their changes provides: additional qualitative and quantitative data on new growth stages and on new ontogenetic series; an understanding of morphological variability linked to developmental and/or environmental constraints. Without forgetting to establish a relevant phylogeny, trilobites, their ontogenetic series and structural changes appear to have a potential for the analysis of patterns and processes of evolution and provide a broader evolutionary perspective on Evolution. The study of ontogenetic development should permit the identification of the causes of patterns of decline in disparity over geologic time, especially before and after a major biological crisis (Zelditch et al., 2003). This drop in disparity may be due in particular to a decrease of available ecological niches (Valentine, 1995) or an increase of developmental constraints of organisms (Gould, 1991).

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