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The species concept in a long-extinct fossil group, the conodonts

Le concept d'espèce chez un groupe d'organismes exclusivement fossiles, les conodontes

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ABSTRACT

Conodonts are an extinct group of organisms, known from the Upper Cambrian to the Triassic. They have no extant representatives, and tooth-like buccal elements are usually the only remains of the animal found in the sediments. Therefore, most of their taxonomy rests on these elements that are good stratigraphic tools for these ancient periods, due to their rapid morphological evolution. Conodont species are usually described species that are based on either clusters of elements corresponding to an entire apparatus (natural assemblages), or on the most frequently preserved element. These described species are acceptable stratigraphic tools, but hardly consider the dimension of the variation that a biological species can encompass through time and space. In order to tackle temporal, environmental and biogeographical changes, recent studies have shown that morphological variation should be taken into account by quantitative analyses, aiming at getting at the closest of what the former species might have been.

RÉSUMÉ

Les conodontes sont des organismes éteints, connus du Cambrien supérieur au Trias. Ils n'ont pas de représentants actuels, et seules leurs pièces buccales sont en général préservées dans les sédiments. Ainsi, l'essentiel de la taxonomie repose sur ces pièces qui sont de bons outils stratigraphiques pour ces périodes anciennes, en raison de leur évolution morphologique rapide. Les espèces de conodontes sont généralement des espèces typologiques basées sur des regroupements d'éléments correspondant à un appareil complet (assemblage naturel) ou bien sur l'élément le mieux préservé. Ces espèces typologiques constituent des outils stratigraphiques appropriés, mais elles ne prennent pas en compte la variation qui caractérise une espèce biologique à travers le temps et l'espace. Pour suivre les changements temporels, environnementaux et géographiques, des études récentes ont montré que la variation morphologique devait être prise en compte par l'intermédiaire d'analyses quantitatives, permettant d'appréhender au mieux ce que les espèces de l'animal conodonte ont pu être.

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1. Introduction

The species concept is a key issue in a wide range of topics dealing with organisms, either extant or extinct, because the "species" is currently regarded as a basic unit at the heart of the evolutionary theory. Yet, it is a multifacetted concept and a wide range of definitions hide behind this single term. A diversity of meanings for the species was already recognised by Darwin, who claimed in his *On the Origin of Species*: "No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species". This common idea beyond the species concept is that of a stable entity whose members share similarities and are clearly different from members of another such entities.

In order to give a testable basis to this concept, a biological definition of a species has been proposed; that is, a species is a group of organisms that is capable of interbreeding and producing fertile offspring of both genders. A species should be distinct from others with which interbreeding does not (normally) happen (Mayr, 1963, 1996). Although widespread in textbooks, this definition appears however rarely tested or even hardly testable in many cases. Hence, the current working definition has been shifted on looking for clusters of specimens sharing similarities, based on diverse data including genetics, genomics, chromosomal number, etc. (de Vargas et al., 2001; Ducroz et al., 1997; Michaux et al., 1998; Reutter et al., 2001a, 2001b). Noteworthy, an increasing number of genetic studies evidences that hybridization significantly contributed to the evolution of many species (Green et al., 2010; Mallet, 2005), showing that even in the modern context, and with a wealth of data, the species concept is far from being as defined in textbooks.

A further problem arises when dealing with fossil organisms. Beyond a certain age and depending on the taphonomical setting, ancient DNA is much too degraded and cannot bring any light about the genetic similarity between extinct and living taxa. Morphological similarities remain thus as the only basis for a "species" concept in most of the fossil record. When close extant relatives still exist, confrontation between genetic and morphological data can provide a robust basis to the interpretation for morphological clusters as "species" even in the fossil record (de Vargas et al., 2001; Paupy et al., 2010; Sáez et al., 2003). The analysis of modern populations, as well as their geographic variations, can provide clues about the range of morphological variation encompassed into the concerned species, which is precious information to interpret variations down the fossil record (Ellison et al., 2004; Irie, 2006; Mascort et al., 1999; Renaud and Schmidt, 2003).

The case of the conodonts, which are extinct organisms known only from the ancient fossil record, from the Cambrian to the Triassic, presents a further challenge to the definition of the palaeontological species. Since conodonts have no known close extant relatives, any identification of conodont species necessarily relies on the sole morphological similarity. Yet, depending on the conservation of the fossils and their abundance and the purpose of scientific investigation, it appears that a wide range of underlying assumptions influence the definition of conodont "species".

2. The conodont: an animal and its fossil remains

Conodonts were first discovered in the form of small denticles made of apatite, a kind of calcium phosphate similar to that of vertebrate teeth. They have been described first by H.C. Pander in 1856 and were interpreted as teeth of an unknown species of fishes. Understanding what the "conodont-bearing" animal might have been occurred much later, when remains including exceptionally preserved soft tissues of the animal were discovered (Aldridge and Théron, 1993; Briggs et al., 1983). Today, ten such specimens, showing traces of the soft tissues, are known. These were crucial for the understanding of the biology of the animal and its phylogenetic position (Aldridge and Théron, 1993; Briggs et al., 1983). Based on these remains, it became clear that the conodont-bearing animal was a small, vermiform active swimmer with fins, and what has been interpreted as sclerotic cartilages surrounding supposed large eyes suggested a predator feeding habit. A set of distinctive characters, including striated muscles, supports its attribution to "protochordates" (Aldridge and Purnell, 1996; Aldridge and Théron, 1993; Donoghue et al., 1998, 2006) and the presence of mineralized tooth-like elements and unpaired fin radials support the hypothesis that they were possibly early vertebrates (Purnell, 1995).

Although fundamental for a better understanding of what the animal may have looked like, these exceptional remains were nevertheless insufficient to estimate the morphological variation encompassed by a conodont species. Despite the exceptional preservation of soft tissues, these fossils were often incomplete, and this hindered advancement beyond a generic determination for most of these ten well-preserved specimens (Aldridge and Théron, 1993). However, they provided clear evidence that the separate conodont elements were composing a complex feeding apparatus, thereby corroborating earlier conceptions based on occasional findings of clusters of various elements on the surface of bedding-planes (Branson and Mehl, 1934).

Within the conodont-bearing animal, only the elements made of apatite that compose its feeding apparatus have a good potential for fossilisation. A classification of the elements into proto-, para-, and euconodonts has been proposed, based on the structure of the apatite, and suggests differences in the growth pattern of the elements (Bengston, 1976, 1983; Müller and Hinz-Schallreuter, 1998; Sweet, 1988). Bengston (1976, 1983) proposed that they represented successive stages of an evolutionary trend towards increasing complexity in conodont shape and apatite crystallite structure. However, protoconodonts have been recently suggested to be more probably related to chaetognaths (Donoghue et al., 2000; Szaniawski, 2002). The evolutionary relationship between para- and euconodonts is still accepted (Szaniawski and Bengtson, 1993), and paraconodonts would represent an ensemble of primitive conodonts. Even if only focusing on euconodonts (true conodonts), a large variety of elements existed at any given time in their geological record, because several taxa occurred together in the same time, and because the complex apparatus of each species was composed of several, different elements. A typical conodont apparatus

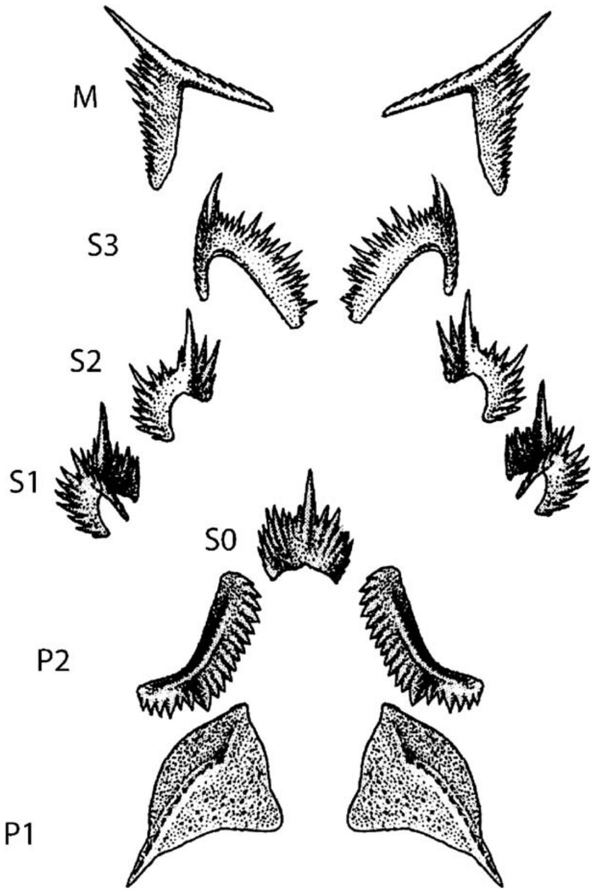

Fig. 1. Schematic representation of a *Palmatolepis* buccal apparatus. Multi-element reconstruction after Dzik (2002).

Fig. 1. Représentation schématique de l'appareil buccal d'un *Palmatolepis*. Reconstitution « *multi-éléments* » d'après Dzik (2002).

(Fig. 1) was composed of sharp, needle-like elements (usually a single pair), comb-like elements (usually seven to nine including a median one in the plane of symmetry) and robust platform-shaped elements (usually two pairs) (Purnell et al., 2000).

Defining species in conodonts should ideally be close to what a "biological" species would have been regarding the former entire animal, but should empirically rely on the morphology of the most frequent fossil remains, namely the elements possibly found as articulated apparatuses. By integrating more dimensions of the variation of the former animal, considering the entire apparatus seems the most seducing approach. Yet practical consideration aiming at gathering the largest possible number of conodonts for stratigraphic purposes led to the more and more frequent use of acid to dissolve the matrix of the sediments, from the 1840 s onwards. Consequently, conodont elements were more frequently found in isolation and conodont taxonomy turned into a parataxonomy, each kind of elements (needle-like-, comb-like-, or platform elements) receiving its own genus and species name, although potentially belonging to the same animal.

3. Species based on reconstructed apparatuses

A taxonomy based on the apparatuses appears a good basis for proposing species notion integrating a multi-facetted variation of the different elements. Finding really complete apparatuses is however quite rare. Approximately a hundred of such complete apparatuses are known from bedding-plane assemblages (Purnell, 1993, 1995), and only document few taxa out of the diversity of conodonts that evolved through time.

These exceptional cases of preservation provided important information about the composition of apparatuses, the relative position of the 7 to 8 types of morphologically distinct elements (needle-, comb-, and platform-like elements) in this apparatus (Purnell and Donoghue, 1997a; Purnell et al., 2000; Sweet, 1988), as well as the morphological variation of the elements across a set of apparatuses (Jones and Purnell, 2007). Unfortunately there is no rule for naming the types of elements and several authors proposed their own terminology for the elements depending on their position in the apparatus. Beyond this semantic discrepancy, a schematic representation of a typical apparatus (Figs. 1 and 2) would include two types of platform element, one medially located symmetric element, four to five comb-like elements, and one type of needle-like element (Purnell and Donoghue, 1997b; Purnell et al., 2000; Sweet, 1988).

Such complete apparatuses provided a basis for further interpretation of incomplete or disjoint clusters of elements that are occasionally found at the surface of bedding-planes (Johnston and Henderson, 2005). The composition of apparatuses can be further reconstructed from incomplete assemblages or even isolated elements, based on the fact that the different types of elements should be found in proportional numbers, and depending on the number of conodont-bearing animals initially present in the locality and the number of each type of elements in the original apparatus (Ishida and Hirsch, 2010; Orchard,

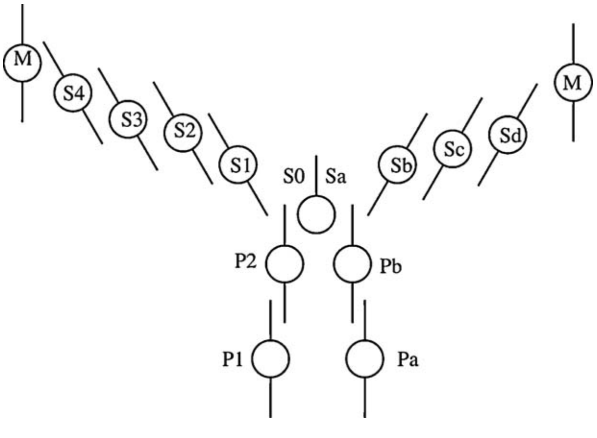

Fig. 2. Schematic map of the relative position of elements in the typological scheme of notation proposed by Purnell et al. (2000) on the left, compared with the proposition of Sweet (1988) on the right.

Fig. 2. Représentation schématique de la position relative des éléments dans le schéma typologique de notation proposé par Purnell et al. (2000) à gauche, et comparée avec la proposition de Sweet (1988) à droite.

2005). For instance each animal should have delivered two P1, two P2, one S0, two S1, two S2, two S3 and sometimes two S4, and two M (Fig. 2).

Such an approach, which bases the description of a species on the entire apparatus (Jones et al., 2009; Purnell and Donoghue, 1997b), has the advantage of being closer to the biological reality, and avoids the use of a taxonomy cluttered with a parataxonomy for each kind of element. It also has the advantage that a species can be recognised based on either the most distinctive, or the best preserved type of elements. Depending on the relative morphology of the elements composing the apparatus, the description of a species can rest mostly on the characteristics of the M, S, or P elements (Bultynck and Sarmiento, 2003; Corradini, 2009; Corriga and Corradini, 2009), notwithstanding the knowledge of the composition of the complete apparatus. In any case, a species is understood as an ensemble of specimens sharing morphological characteristics (denticulation pattern, ornamentation, overall shape of the elements...) exemplified by the holotype. A main problem is that even subtle differences often lead to a split of a continuous morphological variation (Gatovsky, 2010; Kirilishina and Kononova, 2010), leading to a definition of species as static and narrow entities close to the original typological definition of a species, based on similarities with the holotype. Such an approach reaches limits when the former biological entities were varying either in space or time or both: instead of integrating the dimension of the variation within a species, referring to the typological concept then lead to a proliferation of close static entities (Klapper et al., 2004).

Although widely applied for many periods of time, this approach based on the description of apparatuses sometimes meets with practical limitations, especially during the Devonian. First, such articulated apparatuses are rare during this time interval, possibly because of the dominant occurrence of carbonate deposits. In such sediments, dissolving the matrix for clearing fossils is a common practice that is highly efficient in delivering conodont elements even when rare, but these are then found in isolation. This contrasts with shale deposits that offer a good preservation potential for fragile clusters. A second problem that arises is that, despite attempts to reconstruct apparatuses based on the relative frequency of each type of element (van den Boogard and Kuhry, 1979; Dzik, 2002; Klapper and Philip, 1971; Metzger, 1994), many assemblages are dramatically skewed towards an overrepresentation of the platform elements (Carls, 1977; Dzik, 2002; Morrow, 2000; von Bitter and Purnell, 2005). This may be due to a marked morphological difference between the slender shape of the S and M elements, which contrasts with robust P elements during this time period, hence leading to a preferential deposition and taphonomical preservation of the P elements (Helms and Over, 2006; McGoff, 1991). Relying on a parataxonomy of isolated elements seems thus, for certain periods such as the Devonian, an approach that may be theoretically frustrating, but practically relevant.

4. The apparatus summed up as one of its elements

Devonian conodont assemblages are characterised by an overrepresentation of platform elements. These elements were both well preserved and highly variable across taxa of the same period and also through time. Therefore, focusing on platform elements only appeared as an acceptable alternative for such time periods and, accordingly, most taxonomic reviews bear on these elements that are extensively used for stratigraphic purposes (Branson and Mehl, 1934; Klapper, 1989; Ziegler and Sandberg, 1990). This amounts to considering only a part of the remains (here the platform element P1) as a marker of the evolution of the entire organism. Such an approach is not uncommon in palaeontology; for instance, most interpretations of small mammal assemblages only rest on tooth remains and, among the different teeth, on the few molars that display most of the diagnostic and informative characters (Gingerich, 1974; Michaux, 1971). This can be validated in the case of the small mammals by a comparison with the variation in modern, closely related species, and indeed, teeth appear as a useful source of characters for discriminating modern species (Chevret et al., 1993; Kan Kouassi et al., 2008; Michaux et al., 1998; Misonne, 1969).

Once it is accepted that considering a single element is a valid proxy for the entire animal, the problem remains to identify species within the variety of P1 elements of all size and shape in a given sample. Conodont species were traditionally identified on the basis of characters mostly related to the shape of the platform, but also including ornamental features such as nodes and costulations (Ziegler and Sandberg, 1990). As mentioned for the study of apparatuses, the concept of species implicit in this common practice is still close to a typological one, i.e. a definition that hardly encompasses the problem of the variation that might have occurred within a species.

This practice has led to the description of numerous Late Devonian genera and species. This approach was proven very efficient for recognizing stratigraphic zones and allowed the definition of a well-resolved time-scale for the Late Devonian, during which the duration of conodont zones is estimated at less than one million year, an exceptionally good resolution for such ancient period (Klapper, 1989; Ziegler and Sandberg, 1990). Going beyond the mere description of new species, some authors made efforts to bring a statistical support to their demarcation between species, by providing a quantitative assessment of how much specimens of different species were differing. Such efforts relied on the quantification of various morphological parameters (Barnett, 1971), including angles between either the carina and the most-developed end of the platform (Dzik, 2002) or the shape of the platform outline (Klapper and Foster, 1986, 1993; MacLeod and Carr, 1987; Sloan, 2000).

The proliferation of "species", and the effort to bring some statistical support to their demarcation, can be exemplified by the Late Devonian genus *Palmatolepis*. The identification at the genus level relies on indisputable morphological differences of the P element from other contemporary genera, but defining demarcation between species appears as a much more difficult and debatable task. More than a dozen of species have been described (Fig. 3), several of which being index species for some biostratigraphic zones. Most of the taxonomically relevant characters refer to the shape of the platform and,

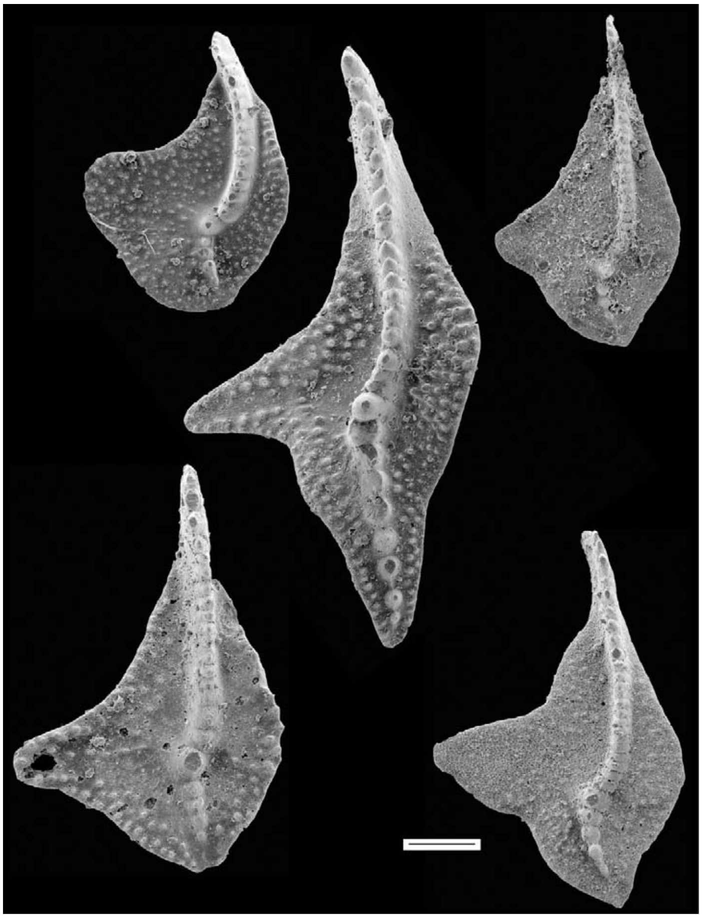

Fig. 3. Different specimens of the genus *Palmatolepis*, illustrating the morphological variation of the P1 element. Scale bar: 200 μm.

Fig. 3. Différents spécimens du genre *Palmatolepis* illustrant la variation morphologique de l'élément P1. Barre d'échelle: 200 μm.

accordingly, attempts at quantifying differences between species were based on an outline analysis of the platform shape (Klapper and Foster, 1986, 1993). Taking as an example emblematic species from the Late Frasnian, "species" appear indeed to differ statistically based on the shape of their platform (Fig. 4). This approach seems at first sight to provide indisputable support to the species that were defined to describe the range of existing variation of the platform elements during this period.

However, a closer consideration of such morphometric analyses raises some major issues about their true significance. The specimens included in such analyses corresponded to a subset of the total variation, and only documented "typical" elements of the considered species. Of course, if only groups of specimens chosen to be different are included in a discriminant analysis, differences between these groups will hardly fail to be significant (Fig. 4). Including in the same morphometric analysis specimens that document the whole variation existing during the same period (Fig. 5; Girard et al., 2004a, 2004b) dramatically changes the pattern: variation appears to be continuous and the described "species" only represent end-members of a large variation that might indeed correspond to the range of variation of the former biological species.

Indeed, the lack of well-defined clusters that would support the described species has been recognised by many authors, who mentioned transitional forms between species (Schülke, 1995; Scott and Collinson, 1959; Szaniawski, 1971; Ziegler and Sandberg, 1990). The lack of well-defined clusters also led to more than 80% of the specimens being left in an open nomenclature for some periods (Morrow, 2000; Sandberg et al., 1988; Schülke, 1998). As a further evidence of the fuzzy limits between described species, two parallel taxonomies have been proposed for the Late Devonian conodonts, with partially but not fully overlapping definitions of the species (Klapper, 1989; Ziegler and Sandberg, 1990).

Such facts challenge the significance of the described species that have been widely used mostly for stratigraphic purposes. Indeed, some authors suggest that the described species may represent end-members within a range of morphological variation of a single species at different stages of its evolution (Carnes, 1975; Scott and Collinson, 1959). We have provided further support to such a view by morphometric analyses of specimens from the Late Frasnian and Early Famennian, showing that identified specimens were in fact end-members of a continuous morphological variation that consistently show trends through

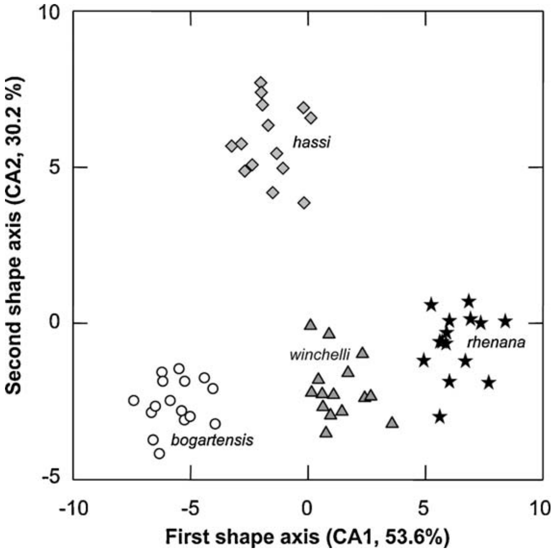

Fig. 4. Morphological differentiation between four species of Late Frasnian *Palmatolepis* species described by Klapper and Foster (1986, 1993), and represented on the first two axes of a discriminant analysis on the Fourier coefficients that describe the outline of the P1 element. Each dot corresponds to a specimen. Note that they do not represent the whole variation of an assemblage, but typical specimens of each species.

Fig. 4. Différenciation morphologique de quatre espèces du genre *Palmatolepis* du Frasnien terminal décrites par Klapper et Foster (1986, 1993), représentées dans l'espace morphologique décrit par les deux premiers axes d'une analyse discriminante, réalisée sur les coefficients de Fourier décrivant le contour de l'élément P1. Chaque point représente un spécimen. Remarque: ces spécimens ne représentent pas la variation totale d'un assemblage, mais des spécimens typiques représentatifs de chaque espèce.

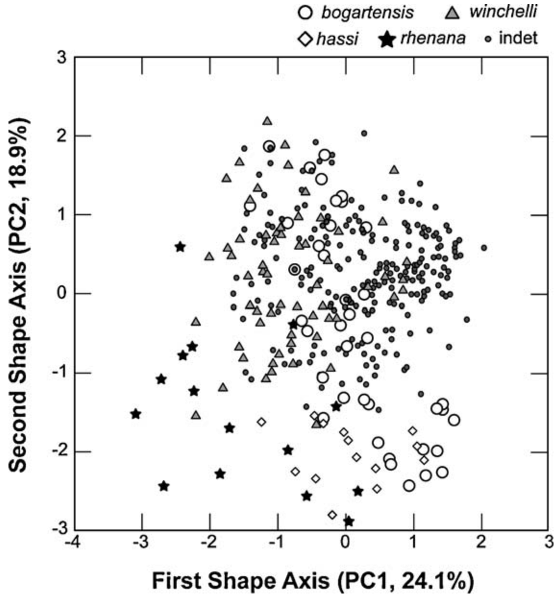

Fig. 5. Morphological variation of *Palmatolepis* P1 elements during the Late Frasnian, represented on the first two axes of a principal component analysis on the Fourier coefficients that describe the outline of the P1 element. PCs axes are calculated independently of any taxonomical a priori, to the contrary of canonical axes (Fig. 4). The specimens that are typical of four species (Klapper and Foster, 1986, 1993) have been superimposed to the total variation in a sample of the same age. They appear as end-members of a continuous range of variation. indet: undetermined specimens.

Fig. 5. Variabilité de forme des éléments P1 du genre *Palmatolepis* au Frasnien terminal, représentée sur les deux premiers axes d'une ACP sur les coefficients de Fourier décrivant le contour de l'élément P1. Les axes sont calculés indépendamment de toute détermination taxonomique a priori, contrairement aux axes canoniques (Fig. 4). Les spécimens typiques des quatre espèces (Klapper et Foster, 1986, 1993) ont été superposés à la variation totale d'un échantillon de même âge. Ils apparaissent comme des membres extrêmes au sein d'une variation continue. indet: spécimens indéterminés.

time (Girard et al., 2004b). Such analyses suggested that the former biological species was not corresponding to the described species, but to a larger entity that had to be defined on the basis of its continuous variation with no evidence of any particular cluster. This does not mean that any *Palmatolepis* assemblage was monospecific, since some clear-cut morphological clusters do occur during some time intervals, suggesting the co-occurrence of several former biological species (e.g., during the Latest Frasnian (Girard et al., 2007) and the Middle Famennian, (Girard et al., 2004a).

Such results suggest that studies focused on evolutionary patterns in time and space should better rest on a definition of species that still relies on morphology, but explicitly includes the dimension of the variation that might have occurred within the former biological species. Morphological species in this sense still correspond to "a unit or a group of units that differs morphologically from other units", but their definition should heavily rest on recognising the range of variation encompassed by the unit. This definition has been challenged in the modern biota by evidence that genetically distinct populations may look very similar (Hellborg et al., 2005; Nicolas et al., 2006; Rohfritsch et al., 2007; Van Daele et al., 2007), and contrarily, that important morphological differences sometimes exist between closely related populations (Paupy et al., 2010; Schneider et al., 1999; Shearin and Ostrander, 2010; Smith et al., 1997). Nonetheless, even in the modern biota, most species have been described solely on the basis of morphology, and were later frequently corroborated whenever genetic data became available (Colangelo et al., 2010; Macholàn, 2006). In the case of long-extinct animals, such as the conodonts, it seems to be the only operational way to define species in the purpose of evolutionary studies. The validity of such an approach is supported by the coherence of patterns emerging when considering species as variable entities instead of the described species that are static in space and time. (1) Their temporal trends are comparable from one outcrop to another one, and allow for large-scale correlations (Girard and Renaud, 2007). (2) They can be interpreted in terms of ecological response to environmental variations by correlating their variations in shape to palaeoenvironmental proxies (Balter et al., 2008). (3) Spatial variations in shape within the continuous range of variation of the species seem suitable for tracing fine-scale environmental variations and provincialism (Girard et al., 2007; Girard et al., in press). Such studies go far beyond mere stratigraphic purposes and, despite the unknowns about long-extinct fossils, hint at the processes involved in the short and long term evolution of conodont lineages in relation to their environment.

5. Conclusions

The species concept used in conodont taxonomy varies depending on several empirical factors. Any definition of species relies on morphology only, since no further biologically relevant information, such as genetic data, are available to support a given definition of species in these long-extinct fossil animals that lack modern close relatives. Practically, several definitions of conodont species nevertheless lie behind this common notion of morphological similarities. Depending on the abundance of more or less complete apparatuses, species were defined either on the basis of clusters of elements corresponding to an articulated apparatus (multi-element approach), or on a particular type of elements (usually the platform elements, best preserved and showing many diagnostic features), considered as diagnostic for the entire animal (mono-element approach).

In both cases, the most widely used definition of conodont species insists on close similarities between the members of a species, exemplified by the holotype; this definition is close to the traditional typological definition of a species. This notion does not properly address the variation that might have occurred through time and space within the actual biological entity, and might lead to artificially split a large and continuous variation that occurred within the actual species. This problem does not prevent the relevance of the described species as valuable stratigraphic markers: being considered as practical tools, these stratigraphic markers only reach their limit when, in an effort to refine the accuracy of the stratigraphic zones, index forms are chosen that are too rare in the assemblages. This is the case of *Palmatolepis linguiformis*, the index form of the Latest Frasnian conodont zone which is a highly informative index form because of its short occurrence in time, but whose practical value is greatly diminished by its rarity as it often represents less than 0.5% of the assemblages in well-studied areas such as Germany, France or Morocco (Girard et al., 2005). Despite their obvious practical value as stratigraphic markers, the significance of these “species” for evolutionary studies is often challenged, because they do not necessarily correspond to clear clusters within a large and continuous variation. For the purpose of studying patterns of temporal, geographic, and environmentally-driven variation, the definition of the species should thus be preferably shifted towards a definition that takes into account the variation that might have been encompassed into the biological species.

Whatever the definition of species, one should admit that any attempt to define a conodont species is doomed to remain hypothetical for such ancient fossils devoid of any unambiguous modern relatives. The exceptionally preserved but extremely rare remains of the whole animal, despite their importance for a better understanding of the animal’s biology and phylogenetic position, are too few to provide a further basis to definition of species through time and space. Confronted with these limits, any attempt to define species in conodonts should remain critical and oriented towards the aimed purpose, either stratigraphic or evolutionary problems.

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