

Article

Morphological Disparity and Evolutionary Radiation of Early Actinopterygians Through the Devonian–Carboniferous Crisis

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Abstract

“Placoderm” and sarcopterygian fishes dominated Devonian waters. Following the end-Devonian crisis, actinopterygians rapidly became major contributors to vertebrate diversity. This transition constitutes the first major diversification event of actinopterygians. Here, we investigate the morphological diversification of Devonian and Carboniferous actinopterygians by quantifying disparity using two-dimensional (2D) geometric morphometrics, which estimates disparity from continuous data and brings geometric information related to the shape changes in several morphological features. In total, 13 landmarks and 203 semi-landmarks were digitized on the body shape reconstructions of 84 species, and 18 landmarks and 50 semi-landmarks were digitized on the reconstructions of the lateral view of the skulls of 86 species. When compared to variations in taxonomic diversity over time, the pattern of body shape variations is congruent, reaching a maximum during the Viséan, but the pattern of skull disparity is not entirely congruent, presenting a first increase during the Late Devonian. Changes in body shape are associated with locomotory properties, while changes in skull shape are associated with functional properties of the feeding apparatus. This pattern strongly suggests the diversification of actinopterygians to be driven by divergence in trophic strategies. This evolutionary radiation seems to be the result of an adaptive response to new ecological opportunities, triggered by big environmental changes in mid-Paleozoic oceans.

Keywords: end-Devonian crisis; geometric-morphometric; ecomorphology; Paleozoic; osteichthyans; palaeogeography; adaptive radiation



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1. Introduction

Actinopterygians, ray-finned fishes, are a group of osteichthyans that today represents the most diversified group of extant vertebrates, with more than 30,000 species [1]. They colonized almost all aquatic environments, and this ecological diversity is reflected in their impressive morphological disparity. However, the early history of actinopterygians is still poorly known. The oldest articulated specimen of osteichthyan is known from the Ludlow stage (Middle Silurian, 427.4 million years ago (Mya)) with the sarcopterygian *Guiyu oneiros* [2]. Nevertheless, the first articulated specimens of actinopterygians date back to the Lower Devonian (419.6 Mya) with *Meemannia eos* [3] and later genera like *Austelliscus* [4], *Dialipina* [5] and *Cheirolepis* [6,7]. At that time, the vertebrate community was dominated by “placoderms” (armoured fishes) and aquatic sarcopterygians [8], with only about twenty species of actinopterygians known from articulated specimens from the Devonian [9,10].

Osteichthyans evolved through various episodes of major changes in the aquatic environment [11]. The Late Devonian–Early Carboniferous transition is characterized by two successive biodiversity crises known as the Kellwasser [12] (Frasnian–Famennian boundary, 371 Mya) and the Hangenberg [13] (Devonian–Carboniferous boundary, 359 Mya) events that greatly modified aquatic biodiversity. Together, they constitute the end-Devonian mass extinction, one of the “Big Five” mass extinctions [12–14]. More than 50% of all vertebrate diversity was lost, including the extinction of dominant groups such as “placoderms” [8,15]. Simultaneously, the high tectonic activity levels lead to the formation of inland seas [16] and a large carbonate platform on the continental shelf [17] during the Early Carboniferous, which produced more diverse shallow aquatic habitats [18]. In addition, the re-emergence of coral reefs during the Early Carboniferous [19] brought new marine habitats with complex structures. These environmental changes associated with the loss of the majority of the dominant Devonian vertebrate groups may have contributed to the rapid diversification of chondrichthyans and actinopterygians that became major contributors to the aquatic vertebrate community during the Early Carboniferous [8,16,17,20].

Indeed, during the Early Carboniferous, actinopterygians experienced their first major and rapid diversification [8,21], which could be identified as an evolutionary radiation [22,23]. Evolutionary radiations are one of the most interesting evolutionary processes. Such events are characterized by a rapid increase in the diversification rate (i.e., difference between the speciation and the extinction rates) and an increase in the morphological disparity and the ecological diversity [24]. Several factors can trigger such events within clades [25–28]. The variation in the taxonomic diversity and the morphological disparity through time are two of the most fundamental parameters characterizing evolutionary radiations [29]; they bring complementary information about such events [30]. Therefore, exploring the patterns of morphological disparity through time and associated factors is crucial for characterizing evolutionary radiations.

The present study aims to investigate the event of rapid diversification of early actinopterygians and their putative evolutionary radiation by exploring body and cranial shape variation among Devonian and Carboniferous actinopterygians. As the taxonomic diversity of actinopterygians rapidly increased after the end-Devonian crisis, following major changes in the aquatic environment [8,22,31], we expect to detect increases in morphological disparity that matched the increase in taxonomic diversity, which could support a diversification of morphology triggered by the colonization of new habitats [32–34]. To support this hypothesis, we also hope to detect simultaneous increases in morphological disparity and in the expansion of the species’ geographic repartition. Finally, we expect to observe differences in the variation in body shape and cranial shape disparity through geological time. Indeed, the body shape of fish is mostly related to locomotory properties [33–35], while cranial shape is tightly connected to feeding strategies [36,37]. Even though body shape and trophic specializations are functionally related, body shape can also be related to habitat use and hydrodynamic performance, which may evolve independently from specialized feeding structures [31–33]. Therefore, we could assume that we would first detect an increase in body shape disparity early in actinopterygian history [38], followed by successive increases in the cranial shape, which could indicate the acquisition of various feeding strategies in lineages that already occupy distinct niches, differentiated by locomotor properties [37,39,40].

2. Materials and Methods

2.1. Taxonomic Diversity

To obtain an estimate of Devonian and Carboniferous actinopterygian taxonomic diversity, we gathered a list of 197 actinopterygian species from the primary literature and

published databases [41]. For each species, the first and last occurrence dates were noted (Figure 1, Supplementary Table S1). Our time scale sampling goes from the early Eifelian (Middle Devonian, 393.47 Mya) to the Late Gzhelian (Pennsylvanian, 298.9 Mya), which represents a 94.57 MY time span, and is divided into 11 stages (Eifelian, Givetian, Frasnian, Famennian, Tournaisian, Viséan, Serpukhovian, Bashkirian, Moscovian, Kasimovian and Gzhelian). The preservation state of actinopterygians from the Early Devonian did not allow for complete morphological analyses with geometric morphometrics. We analyzed actinopterygian diversity with the R package ‘divDyn’ (v.0.8.3) [42].

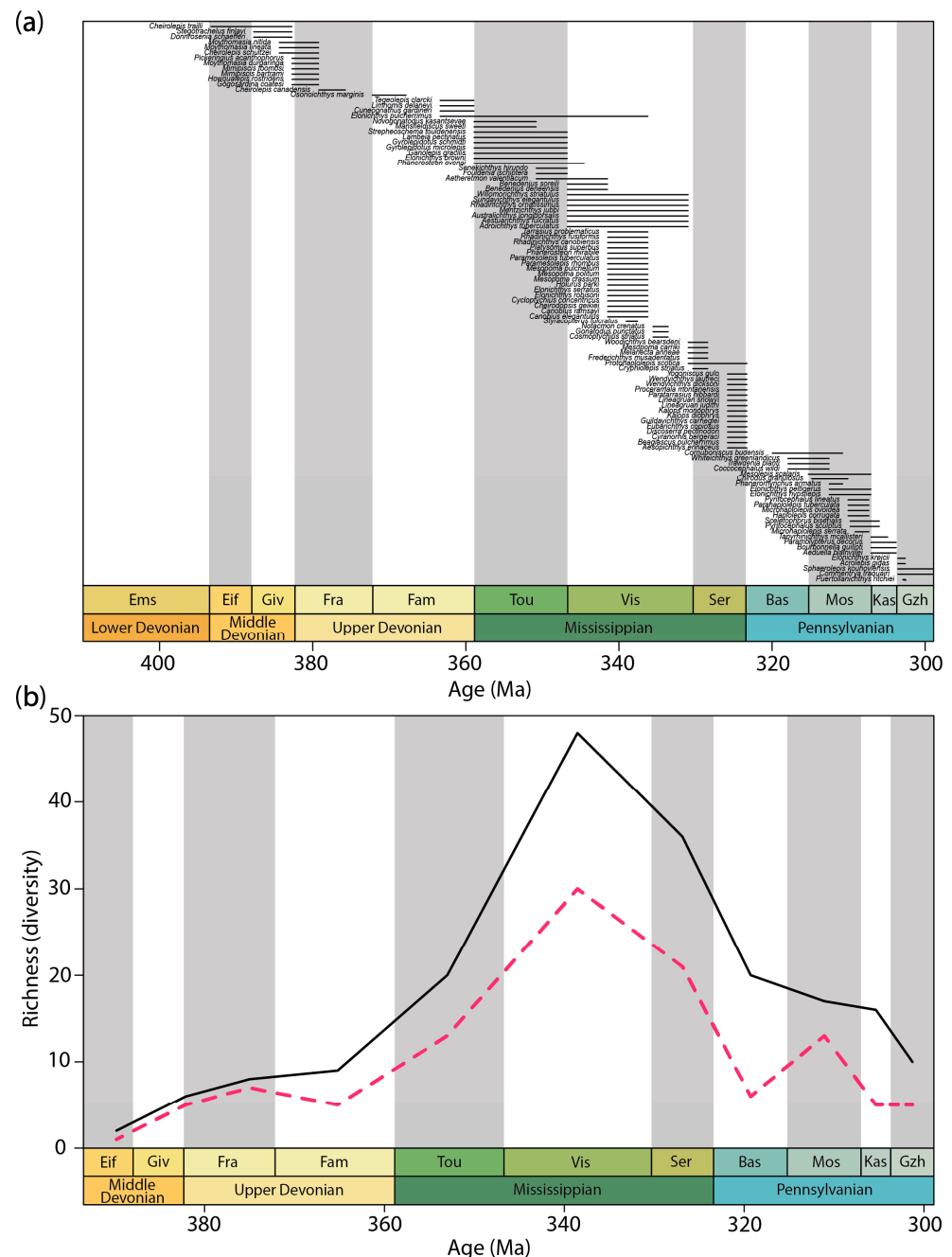


Figure 1. Occurrence and diversity of early actinopterygian species through time. (a) Occurrence of each of the 106 species of early actinopterygians analyzed; (b) diversity of early actinopterygians through time based on the richness calculated for each stage for the 106 species analyzed (dashed red line) and for the 197 species of early actinopterygians (black line). Bas: Bashkirian; Eif: Eifelian; Fam: Famennian; Fra: Frasnian; Giv: Givetian; Gzh: Gzhelian; Kas: Kasimovian; Mos: Moscovian; Ser: Serpukhovian; Tou: Tournaisian; and Vis: Viséan.

2.2. Morphological and Palaeogeographical Dataset

As the shape of fossil species is rarely conserved in three dimensions, we used two-dimensional (2D) datasets rather than three-dimensional data. We assembled two separate 2D datasets, including a total of 106 species, using palaeontological reconstructions of (1) the entire body shape ($n = 84$) and (2) the lateral view of the skull ($n = 86$) of Devonian and Carboniferous actinopterygian species (Supplementary Table S2). Using Adobe Photoshop (v22.0.0), we modified the reconstruction of the skull, when needed, to put the mouth in a closed position, controlling the morphological variation that could be induced by the opening of the mouth.

Only the species for which adult specimens were identified were compiled. We excluded from the analysis all species known solely from juvenile specimens. GPS coordinates of today's fossil locality were noted for each species, and their palaeocoordinates based on their respective ages were reconstructed with the R packages 'rgplates' (v.0.6.1) [43,44] and 'sf' (v.1.0-25) [45]. We used the maps from the PALEOMAP PaleoAtlas [46] for Gplates, available on Earthbyte.org, to plot the palaeodistribution of each species (Supplementary Figure S1a–c).

2.3. Landmarking Scheme

We used 2D geometric morphometrics to quantify actinopterygian morphological disparity by digitizing landmarks and semi-landmarks on palaeontological reconstructions. Even if reconstructions may have limitations due to the preservation of fossils and/or the subjective interpretation of structures, this approach allowed us to estimate disparity from continuous data and to obtain geometric information related to the shape changes in several morphological features of early actinopterygians. We digitized 13 landmarks and 203 semi-landmarks for body shape, describing the lateral outline of the body and the positioning and shape of the fins (Figure 2a, Supplementary Table S3). We chose to exclude information about the pelvic fins in this analysis because some species lack these fins. For the cranial shape disparity, we digitized 18 landmarks and 50 semi-landmarks on lateral reconstruction to describe the cranial outline, more precisely the orbital, cheek and lower jaw regions (Figure 2b, Supplementary Table S3). All landmarks and semi-landmarks were digitized using tpsDig2 (v2.32).

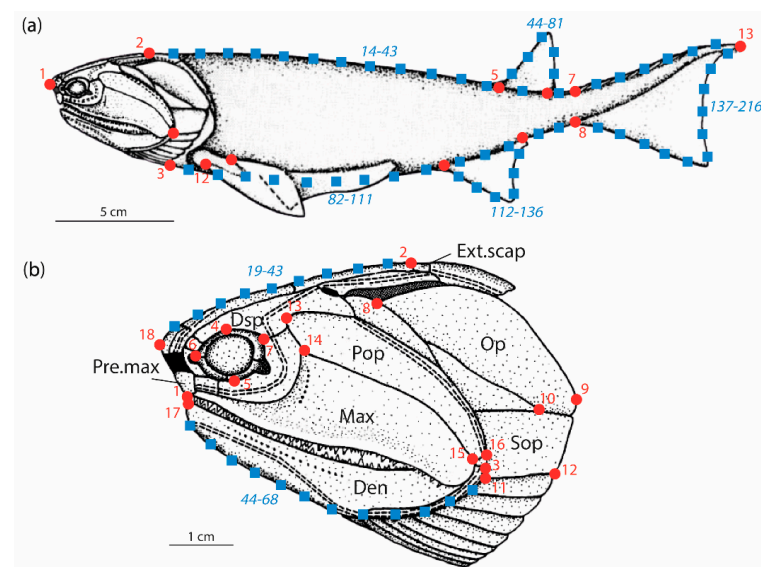


Figure 2. Landmarks (red circles) and semi-landmarks (blue squares) positioning scheme for geometric morphometrics analyses of (a) the body shape and (b) the lateral view of the skull; *Cheirolepis canadensis* (Arratia and Cloutier, 1996 [7], Figures 3A and 5A). See Supplementary Table S3 for a full description of the landmarks and semi-landmarks. Den: dentary; Dsp: dermosphenotic; Ext.scap: extrascapular; Max: maxillary; Op: Operculum; Pop: preopercular; Pre.max: premaxillary; Sop: subopercular.

Each set of landmarks coordinates was rotated, translated and scaled with a Procrustes superimposition using the *gpagen* function in the R package ‘geomorph’ (v.4.0.10) [47]. Semi-landmarks were slid using the Procrustes distance minimization criterion [48]. The multidimensional shape data were summarized using principal component analysis (PCA). The first three axes of each PCA were used to build morphospaces.

2.4. Morphological Disparity Analyses

We estimated morphological disparity using two different metrics, each reflecting different aspects of the distribution of multidimensional data in morphospaces: (1) the Procrustes variance, which measures the dispersion of taxa within the morphospace by estimating the difference among taxa based on the variance in the shape data, and (2) the weighted area of convex hulls, which measures the amount of global morphospace occupation for each group [49]. The latter one is more sensitive to extreme values and cannot be calculated for groups with two or fewer species. Nevertheless, it provides an intuitive metric for comparing the amount of morphospace occupied by each group.

Procrustes variance was calculated for each geological epoch and stage using the function *morphol.disparity* in the R package ‘geomorph’ (v.4.0.10) [47] that quantifies groupwise morphological disparity and assesses statistical significance for each pairwise comparison. Using the same set of grouping variables, the area of convex hulls in the multidimensional morphospace was estimated using a modified version of the *chull* function from the ‘grDevices’ [50] R package (v.4.3.2). We determined the number of PCs to retain for this calculation by using a scree plot that graphically represents the eigenvalues plotted against the corresponding PC number [51,52]. We chose to retain the first five axes for body shape, accounting for 75.52% of the variation, and the first four axes for cranial shape, which account for 78.64% of the variation (Supplementary Figure S2). We calculated the surface area for each pair of PCs and weighed each by the combined proportion of variance explained by the two axes (Supplementary Table S4).

As mentioned above, our time scale is divided into 11 stages. To be free from the time scale and to control potential biases in this subdivision (as stages are usually defined after major biodiversity or environmental changes), we also subdivided the total time interval into 11 equal time bins of 8.6 million years [53]. Then, we quantified the Procrustes variance for each time bin with the *dispRity* function in the R package ‘dispRity’ (v.1.9) [54]. The resulting two patterns of morphological disparity were highly congruent. To refine the presentation of our results, we present the morphological disparity along the stages from the international chronostratigraphic chart [53] in the main text. Species that overlapped two or more different stages were classified according to their stage of appearance.

All disparity analyses were performed in R v.4.3.2 using the packages ‘geomorph’ [47], ‘grDevices’ [50] and ‘dispRity’ [54].

3. Results

3.1. Body Shape Disparity

The first axis of PCA (PC1) explains 40.08% of the variation in body shape among 84 species, separating elongated and fusiform bodies, such as *Cheirolepis trailli*, from deep and short bodies, such as *Platysomus superbus* (Figure 3a).

PC1 also clearly discriminates between Devonian and Carboniferous species. Devonian species are all located in the left portion of the morphospace, characterized by an elongated and fusiform shape. On the contrary, Carboniferous species display various body shapes, spreading across all of the morphospace.

During the Devonian, body shape disparity increases slightly during the Frasnian, followed by a decrease during the Famennian. Subsequently, two successive increases in body

shape occurred during the Carboniferous; first, during the Mississippian and then during the Middle-Late Pennsylvanian, with a decrease during the Bashkirian (Figure 4). Overall, Mississippian species represent 56.83% of the total disparity, with the Viséan and Serpukhovian actinopterygians being the most disparate (Supplementary Tables S4 and S5), followed closely by the Moscovian species.

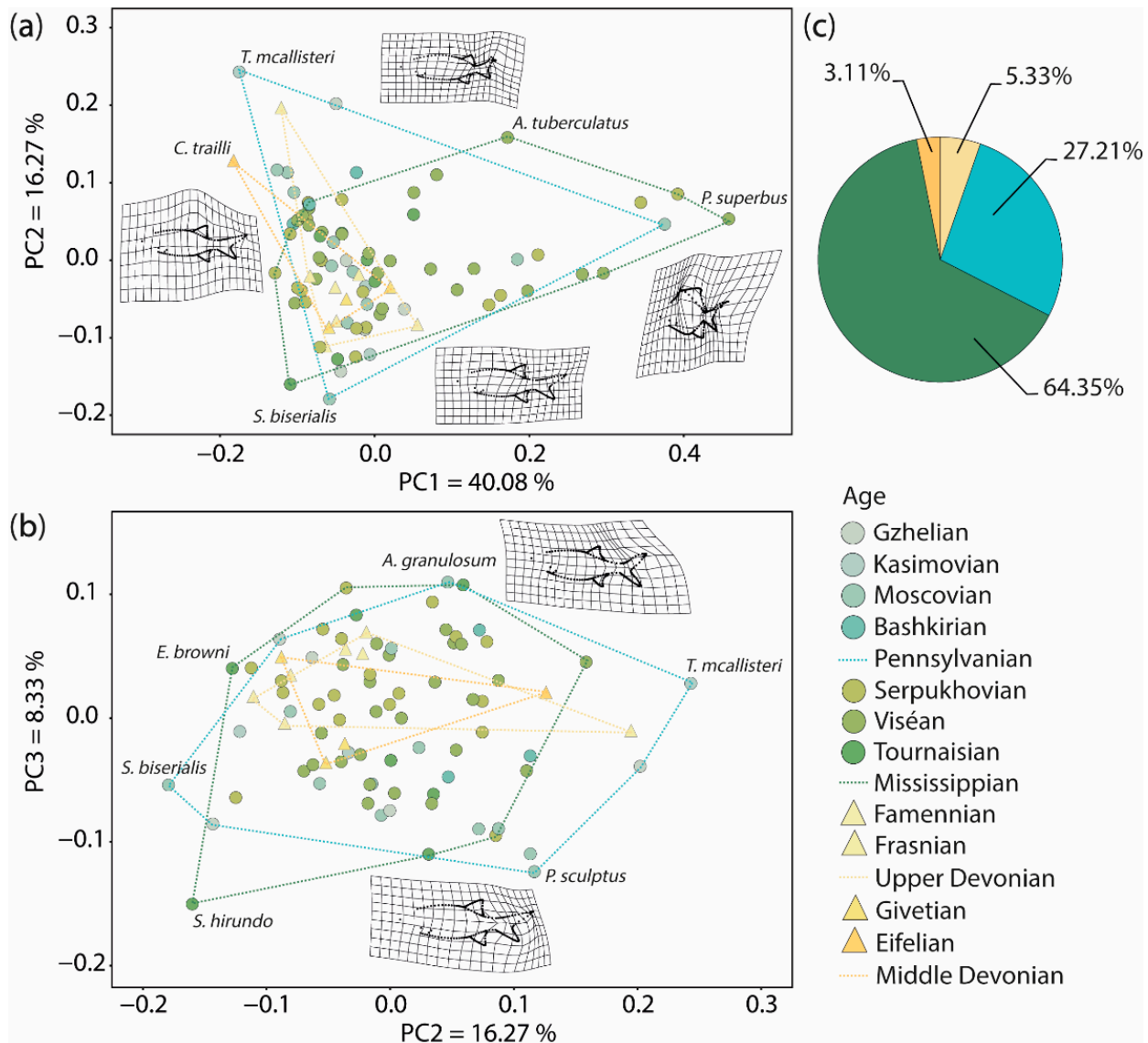


Figure 3. Body shape morphological disparity of 84 early actinopterygians per age. (a) Morphospace of principal components 1 and 2; (b) morphospace of principal components 2 and 3. Deformation grids show the differences between the extreme forms along each axis and the mean shape. See Supplementary Figure S3 for the deformation grids of each species; (c) The pie charts illustrate the proportion of total disparity each epoch represents based on its respective Procrustes variance.

PC2 represents a difference in the caudal fin shape, explaining 16.27% of the variation (Figure 3a). The tail is elongated in species such as *Scelotophorus biserialis* and rather short in species such as *Tanyrhynchichthys mcallisteri*. Finally, PC3 (8.33% of the variation) also seems to represent variation in the caudal region (Figure 3b). This third axis separates species with an elongated caudal peduncle, such as *Senekichthys hirundo*, from shortened caudal peduncle, such as *Amphicentrum granulosum*. The difference between Devonian and Carboniferous species is less defined in PC2 and PC3; Carboniferous species occupy a larger morphospace but lack a clear shift from Devonian species (Figure 3b).

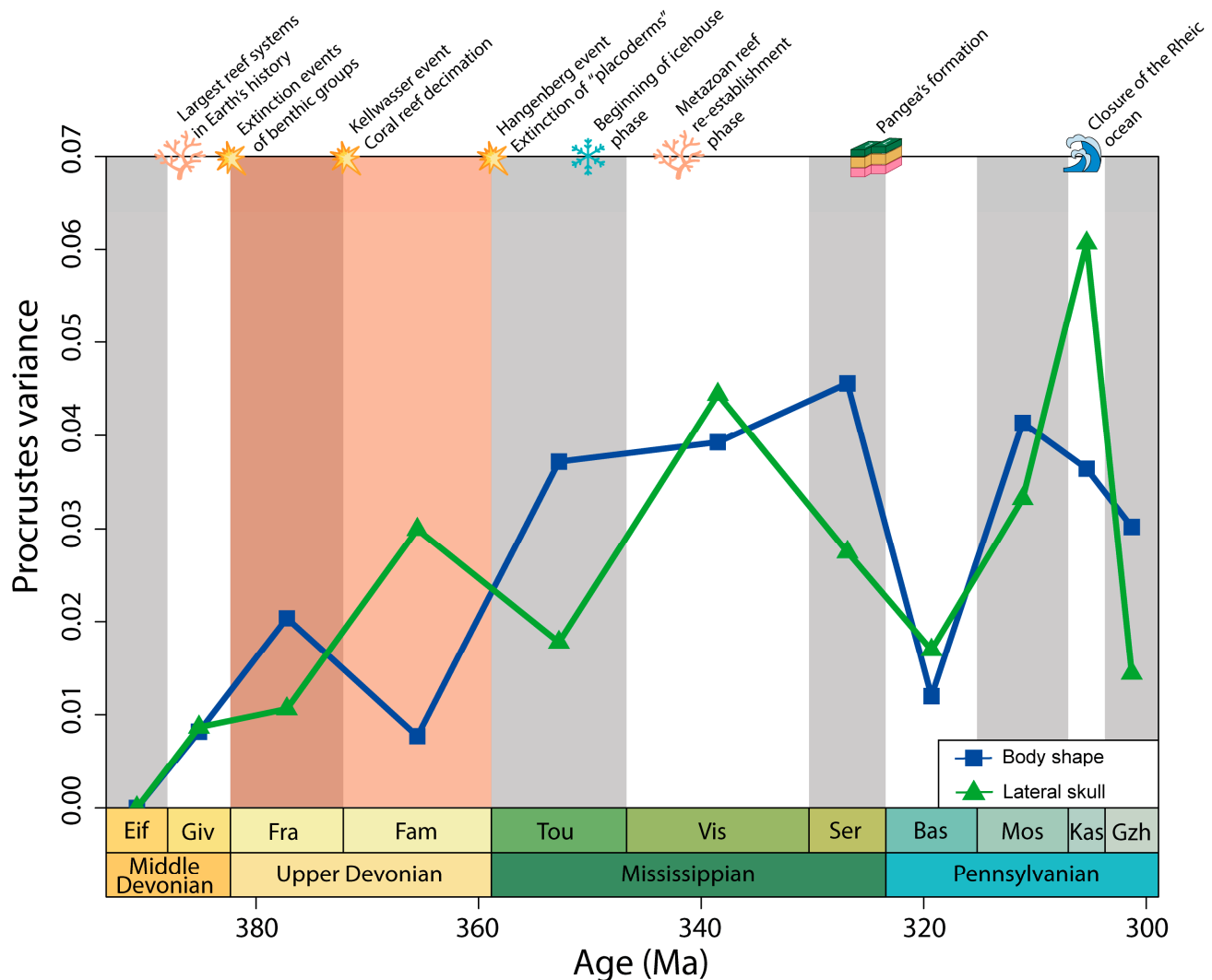


Figure 4. Procrustes variance for body shape (blue squares) and lateral skull shape (green triangles) disparity through time. Major Devonian and Carboniferous geological and biological events are represented: the largest reef systems in Earth's history [55], the extinction events of benthic groups [56,57], the Kellwasser event and coral reef decimation [12], the Hangenberg event and the extinction of "placoderms" [13,15], the beginning of the icehouse phase [58], the metazoan reef re-establishment phase [19], the Pangea's formation [59], and the closure of the Rheic ocean [59]. The coloured box, including the Frasnian and Famennian stages, corresponds to the end-Devonian mass extinction event.

3.2. Cranial Shape Disparity

PC1, explaining 48.15% of the cranial shape variation, represents the difference between short and deep skulls, such as in *Platysomus superbus*, and elongated, narrower skulls, such as in *Tanyrhynchichthys mcallisteri* (Figure 5a). Most of this variation seems to be explained by the epoch. Similarly to body shape, the skulls of Devonian species, all located in the left portion of the morphospace, are mainly characterized by an elongated shape, while Carboniferous species seem to explore diverse shapes, being spread across the entire morphospace.

PC2 (13.90% of the cranial variation) represents the variation in shape and orientation of the opercular series (Figure 5b). In species such as *Cycloptychius concentricus*, the opercular bones are narrow and more rectangular in shape, whereas in *Gyrolepidotus schmidtii*, they are more square. There is no remarkable shift in shape between Devonian and Carboniferous species across this axis.

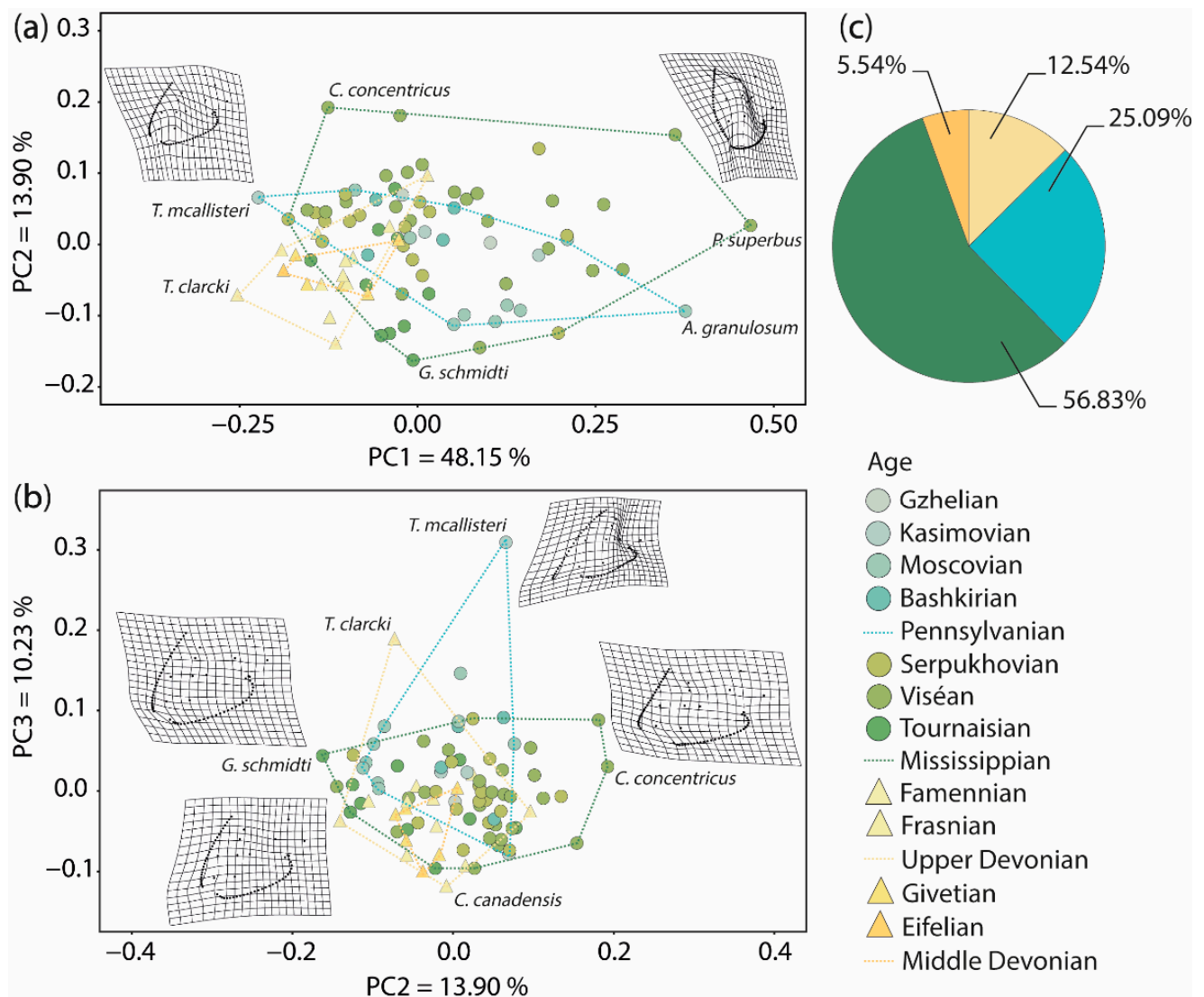


Figure 5. Lateral skull shape morphological disparity of 86 early actinopterygians per age. (a) Morphospace of principal components 1 and 2; (b) morphospace of principal components 2 and 3. Deformation grids show the differences between the extreme forms along each axis and the mean shape. See Supplementary Figure S4 for the deformation grids of each species; (c) The pie charts illustrate the proportion of total disparity each epoch represents based on its respective Procrustes variance.

Finally, PC3 (10.23% of the cranial variation) mainly represents a difference in the shape of the snout (Figure 5b). In *Tanyrhynchthys mcallisteri*, the snout is elongated and extends in front of the mouth (ventrally oriented mouth), whereas in *Cheirolepis canadensis*, the snout is short and terminal (terminal or dorsally oriented mouth). However, this axis seems driven by two species (*Tanyrhynchthys mcallisteri* and *Tegeolepis clarcki*) that differ greatly from all the others packed together. Thus, it seems to represent the variation in skull shape induced by extreme morphologies present in a few unusual species.

The disparity of the lateral shape of the skull shows three consecutive periods of increase and decrease through the Devonian and Carboniferous (Figure 4). A first increase in morphological disparity begins during the Eifelian and lasts until it decreases after the Famennian. The second increase starts right after the end of the Devonian and lasts until it decreases again after the Viséan. And finally, the morphological disparity of the skull increases during the Pennsylvanian and lasts until reaching its maximum during the Kasimovian.

3.3. Early Actinopterygian Taxonomic Diversity and Morphological Disparity Variation Through Time

The taxonomic diversity of actinopterygians presents one major increase during the Early Carboniferous, reaching maximum richness during the Viséan before decreasing during the Late Carboniferous (Figure 1b). This variation through time is congruent with what we observed for the morphological disparity of body shape, reaching a maximum during the Viséan (Figure 4). However, it is not entirely congruent with the pattern of variation through time of the morphological disparity of the lateral shape of the skull (Figure 4). The maximum skull disparity is reached during the Kasimovian, when the taxonomic diversity of actinopterygians decreases. We thus have a mismatch between the time of maximum taxonomic diversity and the time of maximum skull morphological disparity. Looking at the major geologic Devonian and Carboniferous events (Figure 4), we can see that the morphological disparity of the body shape dropped with the coral decimation induced by the Kellwasser event at the Frasnian–Famennian boundary and with the tectonic activity at the Mississippian–Pennsylvanian boundary, leading to the formation of Pangea. However, the main body shape disparity increases following the Hangenberg crisis and the loss of dominant groups of aquatic vertebrates (e.g., “placoderms”). Concerning the skull disparity, the Devonian pattern of variation is inverted compared to the body shape disparity. We detected an increase in disparity after the Kellwasser event during the Famennian and a decrease after the Hangenberg crisis. During the Carboniferous, the pattern of morphological disparity of the skull is similar to that of the body shape. A first increase occurred at the same time as the re-emergence of coral reefs, and a second one corresponded to the closure of the Rheic Ocean at the end of the Carboniferous.

3.4. Palaeogeographic Distribution of Early Actinopterygians

Even if the repartition of actinopterygians during the Devonian and Carboniferous varies in latitudes and longitudes, most species occupied waters near the equator or just south of the equator (Figure 6). Most of the variation observed in the species repartition is due to colonization of austral waters during the Late Devonian and Early Carboniferous, which was then limited by the southern ice cover during the Late Carboniferous, after which the species are again concentrated in the equatorial region of Pangea (Supplementary Figure S1).

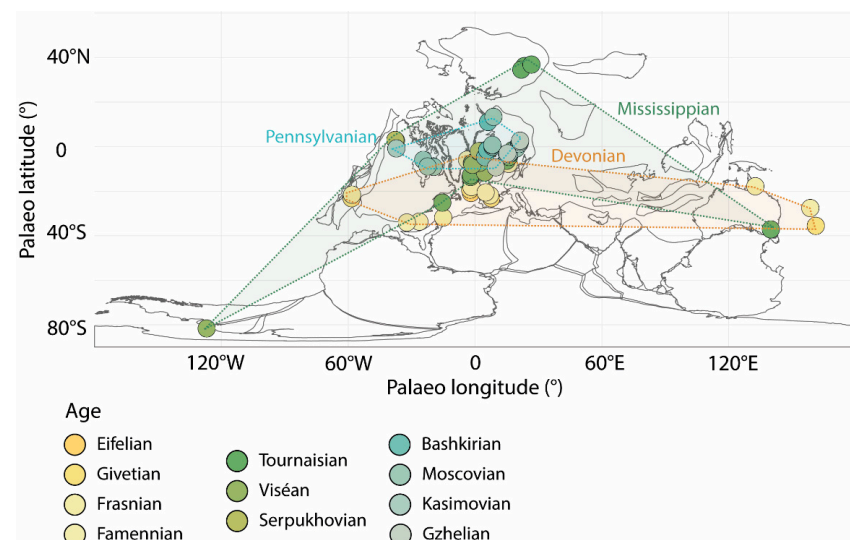


Figure 6. Palaeogeographic distribution of the 106 species of early actinopterygians analyzed based on the reconstruction of their palaeocoordinates. Each dot represents a species included in the analyses. The palaeogeographic reconstruction of the background represents continents 359 million years ago (Devonian–Carboniferous transition) and has been produced with the R package ‘sf’ [45] and ‘rgplates’ [43,44].

4. Discussion

The main goal of this study was to explore the putative evolutionary radiation of early actinopterygians by examining the patterns of morphological disparity of body and skull shapes during their first episode of diversification in the Devonian and Carboniferous periods. The variation in taxonomic diversity over time is congruent with the observed morphological disparity of body shape, which reached a maximum during the Viséan (Early Carboniferous), but is not entirely congruent with the pattern of skull disparity. Furthermore, we found patterns of morphological disparity in body and skull shapes to be inverted during the Devonian and similarly during the Carboniferous.

The variation in body shape was best explained by the difference between the elongated and fusiform shapes of Devonian species and the deep and short shapes of Carboniferous species. Most of the variation in skull shape corresponded to a difference between elongated and narrowed skulls, mostly found in Devonian species, and shortened and deep skulls, predominant in Carboniferous species. However, we also detected variation in skull shape not associated with the age of the fish but with differences in the orientation of the opercular series and the mouth.

4.1. Body Shape Disparity Explained by Locomotory Properties and Ecological Opportunities

The most remarkable shape shift in early actinopterygians concerns the emergence of new shapes during the Early Carboniferous. Short and deep bodies arose, such as in the Viséan *Platysomus superbus* [60], in addition to the Devonian elongated and fusiform shapes conserved in Early Carboniferous species, such as in the Serpukhovian *Fubarichthys copiosus* [61]. This change in the general body shape of fish is most likely related to a change in the locomotory mode. Indeed, while locomotion and feeding strategies are often related, the general body shape is primarily constrained by swimming performance [31,33,62], while trophic specializations are more reflected in cranial morphology [37,41].

Fishes move through a dense medium, which involves hydrodynamic constraints [63]. The fish must generate a force to move forward that limits drag [62]. There are two main methods used to generate thrust in extant fish that influence the type of swimming [33,62] that have been recognized among fossil fish [64]. The first one consists of using the undulation of the body and produces steady, straight-line swimming [33,62]. This type of locomotion is often associated with pelagic fishes living in open spaces and travelling long distances [65]. It requires an elongated body to generate sufficient undulations and a fusiform shape to limit drag by being more hydrodynamic [66,67]. The second method relies on median and paired fins to produce the force necessary to move in water [62]. Instead of maximizing the speed, this provides greater maneuverability [68]. This type of locomotion is usually associated with short and deep bodies that are laterally compressed, which help weave in and out between obstacles, and is mostly found in more complex habitats, such as reefs or kelp forests [33,35]. Although some deep-bodied fishes may have already been present during the Mid-Late Tournaisian [69] and associated with complex structure in wetlands [70], in this study, we found short and deep bodies to arise simultaneously with the re-emergence of the coral reef during the Early Carboniferous [19]. These new complex shallow marine aquatic habitats constituted new ecological opportunities for post-Devonian actinopterygians, which involved new constraints regarding locomotion and differed from what was needed in open waters. This is also supported by the difference in tail shape we observed, with variation in the caudal peduncle proportions. The variation in shape found in the caudal region was the second main source of variation in body shape in our analyses. The caudal fin shape has already been studied for its influence on fossil fish swimming [64,71] and habitat use [35]. Reef fishes tend to have shorter and deeper caudal peduncles, which help rapid starts by using the tail to promote thrust, whereas non-reef

fishes tend to have shallower caudal peduncles, which facilitate steady swimming [35]. Finally, this hypothesis is also supported by the size reduction in actinopterygians, observed by Sallan and Galimberti [72], after the end-Devonian crisis. This size reduction could be driven by ecological constraints, especially the emergence of more complex habitats. Indeed, in actual reef systems, small-sized fishes are usually associated with more complexity in the habitat [32].

Thus, the emergence of new habitats during the Early Carboniferous may have contributed to the rapid increase in taxonomic diversity and body shape disparity we detected during the Mississippian by triggering various types of locomotion [73].

4.2. Skull Shape Disparity Explained by Feeding Strategies and Ecological Opportunities

Similarly to body shape, the main source of variation in skull shape corresponds to a difference between elongated and narrow skulls, such as in the Devonian *Tegeolepis clarcki*, compared to shortened and deep skulls, such as in the Carboniferous *Platysomus superbis*. However, even if this axis of variation seemed again to be explained by the age of the species, a great amount of variation was not. The second and third axes of variation represented differences in the orientation of the opercular series and the mouth, which were not discriminated by age; Devonian and Carboniferous species overlapped. In species such as the Viséan *Cycloptychius concentricus*, the opercular bones are narrow and more rectangular in shape, whereas in the Tournaisian *Gyrolepidotus schmidtii*, they are more square. The opercular bones of fish are functionally involved with the jaws and the gill rakers, and differences in their shape could be explained by different feeding strategies [37]. Kimmel et al. [74] found a dynamic evolution in the opercular shape of teleosts, which could reflect adaptations to diverse ecologies.

Regarding the general shape of the snout, the variation was driven by extreme morphologies carried by a few unusual species. In the Kasimovian *Tanyrhynchichthys mcallisteri* and the Famennian *Tegeolepis clarcki*, the snout is elongated and extends in front of the mouth (ventrally oriented mouth), whereas in the Frasnian *Cheirolepis canadensis*, the snout is short and terminal. Again, the emergence of new shapes in the Carboniferous morphospace could be related to the different aquatic habitats after the Devonian, which was accompanied by a diversification in feeding strategies [36,39].

Thus, the rapid increase in the skull shape disparity of early actinopterygians is most likely to be an adaptive response to the emergence of new habitats and the loss of competitors during the Early Carboniferous.

4.3. Is There an Early Adaptive Radiation of Actinopterygians?

The main findings of this study regarding the variation in shape of early actinopterygians strongly support the adaptive radiation of the group after the Hangenberg crisis, associated with new habitats and new feeding strategies. We detected major morphological modifications that are most likely adaptations to new ecologies. This radiation may also have been triggered by climatic and geographic factors, which modified the aquatic environment through the Devonian and Carboniferous periods. The post-Hangenberg crisis was marked by the loss of dominant groups of vertebrates [8] and accompanied by profound environmental changes [13]. The beginning of the Late Palaeozoic Ice Age [58] and the formation of Pangea during the Carboniferous [59] deeply impacted the oceanic dynamics and may have played a key role in the evolutionary dynamics of actinopterygians during the Carboniferous. The Carboniferous period is a transitional time between the Devonian greenhouse world and the Late Palaeozoic Ice Age [75]. Liu et al. [76] found that the progressive cooling happening during the Tournaisian and the Viséan (Early Carboniferous) had increased ocean circulation and nutrient upwelling on the continental shelf, which

intensified ocean productivity. In recent marine systems, upwellings are known to play a key role in fish assemblages by increasing primary productivity near the coasts [77,78]. In our analyses, actinopterygian diversity and morphological disparity increased during the Early Carboniferous. This rise broadly coincides with Early Mississippian cooling and geochemical evidence for intensified ocean circulation and episodic nutrient upwelling, processes that can enhance nutrient delivery to continental shelves and stimulate marine primary productivity [76,79,80], thereby expanding the ecological opportunity for actinopterygian diversification.

Entering the Late Carboniferous, the collision of Laurussia and Gondwana formed Pangea [59]. This major geological event impacted aquatic diversity by eliminating vast continental shelf environments and modifying ocean circulation [59,81]. In addition, the southern ice cap covered most of the southern region of Pangea, which may have limited the geographic distribution of species and led them to be located around the equator. This may explain the drop in both species diversity and morphological disparity observed in our analyses at the beginning of the Pennsylvanian. The majority of the species included in this study come from formations on the Euramerica continent, which could introduce sampling biases into the species' palaeodistribution interpretation [73,82]. The observed pattern remains meaningful, but must be interpreted cautiously given the uneven sampling among latitudes. Indeed, actinopterygians may have spread to high latitudes early during the Middle Devonian [4], and their absence in the fossil record seems to be mostly due to the lack of systematic collecting efforts [4]. High latitude sites such as the Minusinsk Basin, which have been systematically studied, include several species of actinopterygians [83,84]. Thus, increasing the sampling effort in such regions would contribute to refining palaeodistribution models of early actinopterygians and clarify key evolutionary transitions in the group by revealing a preserved cryptic diversity [82], which could test the stability of the trends observed here.

Finally, the time of the first increase in skull disparity does not correspond to the time of the first increase in body shape disparity. Indeed, skull shape appeared to diversify before body shape, during the Late Devonian. This discrepancy between the two systems is congruent with what Sallan and Friedman observed [22] and with Igielman et al. (2025) [85], who found a substantial jaw disparity among early actinopterygians from the Devonian and exposed great mandible and dentition variations. Furthermore, the early history of the clade remains uncertain due to the limited number of fossils from actinopterygian species from the Late Devonian. Giles et al. (2023) [86] demonstrated that recent new species described from the Late Devonian may suggest a diversification of the group before the Mass extinction event, which may have acted as a bottleneck event for the surviving lineages, which rapidly diversified during the Early Carboniferous. Still, our findings challenge the "radiation-in-stages" proposed by Streelman and Danley [38] as a general model for vertebrate evolution in which the first stage of radiation is triggered by divergence in habitats, usually associated with the apparition of new ecomorphs, and then followed by a divergence in the trophic strategies associated with modifications of morphological elements of the feeding system. Our results support a trophic divergence, witnessed by early skull and jaw diversification in the group, as the first factor for the diversification of actinopterygians at the Devonian–Carboniferous transition.

5. Conclusions

The mid-Paleozoic period was a time of remarkable changes in actinopterygian evolutionary history. The transition between the Devonian and the Carboniferous constitutes the time of the first actinopterygian diversification, which most likely corresponds to their first evolutionary radiation. By exploring their morphological disparity, we found

strong support for an adaptive radiation triggered by new ecological opportunities. Major geographic and climatic events marked this transition, with the beginning of the Late Paleozoic Ice Age and the formation of Pangea, which directly impacted ocean circulation and aquatic habitats. Actinopterygians may have then thrived in the new habitats, developing adaptations to new life modes. We found that trophic divergence is most likely the main diversification factor, with morphological variation associated with the feeding apparatus and locomotion mode. Further investigation of aquatic habitats and interspecific interactions could help strengthen our understanding of this event, which marks the first diversification of the most diverse group of extant vertebrates.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18020083/s1>, Figure S1a–c: Palaeodistribution of the actinopterygian species analyzed based on their actual GPS coordinates; Figure S2: Scree plots; Figure S3: Deformation grids of all species compared to the mean body shape; Figure S4: Deformation grids of all species compared to the mean skull shape; Table S1: List of the 197 basal actinopterygian species included in diversity analyses; Table S2: List of the 106 basal actinopterygian species included in disparity analyses and their respective actual GPS coordinates; Table S3: Description of landmarks and semi-landmarks for the body shape and skull analyses, respectively; Table S4: Convex hulls weighted surface area; Table S5: Morphological disparity analyses.

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