A preliminary study on the ornamentation patterns of ganoid scales in some Mesozoic actinopterygian fishes

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INTRODUCTION

The ganoid scales are a synapomorphic groundplan feature of ray-finned fishes, the Actinopterygii (Schultze, 1977; Patterson, 1982), and these structures showed a much greater amount of variability in deep time. Today, only Polypteridae and Lepisosteidae retain ganoid scales and their study allowed biologists and paleontologists to clarify morpho-functional aspects of this kind of “exoskeleton”. Ganoid scales of these modern groups encompass features such as the general shape of scales, of body covering among lower actinopterygians and their morphology was greatly variable, if compared with the scales of Polypteridae and Lepisosteidae (e.g., Trinaustic, 1999a, b; Chen et al., 2012). This variability encompasses features such as the general shape of scales and the microrolline of ganoine covering, usually called “ornamentation”. Compared to the homogeneous aspect of modern ganoid scales, primitive groups of actinopterygians show a much higher variability in terms of scales shape and ornamentation of ganoine. The scales from fossil record exhibit a rhomboid to very elongate outline, from subcircular to squared. Their posterior margin may be from smooth to serrated and their surface potentially provide flexural constrains (Gemballa & Bartsch, 2002).

During the Paleozoic and Mesozoic and before the vast teleostean radiation, ganoid scales were the common type of body covering among lower actinopterygians and their morphology was greatly variable, if compared with the scales of Polypteridae and Lepisosteidae (e.g., Trinaustic, 1999a, b; Chen et al., 2012). This variability encompasses features such as the general shape of scales and the microrolline of ganoine covering, usually called “ornamentation”. Compared to the homogeneous aspect of modern ganoid scales, primitive groups of actinopterygians show a much higher variability in terms of scales shape and ornamentation of ganoine. The scales from fossil record exhibit a rhomboid to very elongate outline, from subcircular to squared. Their posterior margin may be from smooth to serrated and their surface...
may be from smooth to highly ornamented, with a microsculpture composed of longitudinal or transversal ridges, isolated tubercles, crests and grooves. The meaning of these characters is not fully understood and some speculative hypotheses were proposed, mainly involving functions related to swimming (Aleyev, 1977). One of the most widespread ideas is that the surface roughness of fish skin may have some hydrodynamics functions related to delaying the boundary layer separation or to the reduction of skin friction drag (Fletcher et al., 2014). The boundary layer separation can easily occur across smooth surfaces in regions of adverse pressure gradient, but experimental measures suggest that there is no separation (Anderson et al., 2001). The scales with ridges and grooves may possibly promote the formation of microflows (Sudo et al., 2002). This could be consistent with the generation of a turbulent boundary layer in which the separation is delayed, if compared to a laminar boundary layer. Some authors argued that ganoine ornamentation could have performed this function in extinct fishes (Burdak, 1986).

In spite of the poorly known evolutionary significance of morphological pattern of ganoine, the study of histology, crystallites arrangement and developmental aspects of the superficial hard tissues in the scales of lower actinopterygians has received fair attention as potential phylogenetic character and its structure has been described in detail for many fossil species (Schultze, 1966, 1977, 1992, 1996). These studies showed that ganoine is a shiny, acellular, non-collagenous, hypermineralized tissue of epidermal origin that covers the scales in polypterids (bichirs), lepisosteids (gars), and a variety of other osteichthians (Richter & Smith, 1995). It has been observed that ganoine growth proceeds in concentric accretion and the tissue is arranged in multiple stratified layers at maturity. The modulation in the accretion of ganoine produces the so called “ganoine ornamentation”. This ornamentation shows morphological convergences, as for example in the scales of certain Seminotiformes and Perleidiformes, which bear tubercles on the outer surface.

In the evolutionary history of fishes, the presence of convergent morphologies has been usually detected for various structures, such as fins or teeth (e.g., Donley et al., 2004; Andreev, 2011). Since the factors that influence their external morphology are strongly related to swimming and hydrodynamics, a certain amount of correlation between morphological features is in fact expected, primarily due to functional and structural constraints.

Thus, the aim of this study is to compare the pattern of ganoine ornamentation in some ganoid fishes and to test if there is an association between the general body shape and the pattern of ganoine ornamentation. Specific aims of this work are: 1) to describe the ganoid scales in terms of ganoine morphology and ornamentation, 2) to compare the different morphologies of scales using a quantitative descriptive approach and 3) to verify if there is a correlation between the body shape and the ganoine ornamentation pattern.

MATERIALS AND METHODS

Fourteen genera represented by sixteen different species of Mesozoic non-teleost actinopterygians with a complete ganoid squamation were investigated: Paralepidotus ornatus Agassiz, 1843 (according to Tintori, 1996); Gabanella agilis Tintori & Lombardo, 1996; Stoppania gaetanii Lombardo et al., 2008; Felberia excelsa Lombardo & Tintori, 2004; Endennia licia Lombardo & Brambillasca, 2005; Semolepis brembanus Lombardo & Tintori, 2008; Dapedium politum Leach in De La Beche, 1822; Dapedium noricum Tintori, 1983; Sargodon tunicus Pleninger, 1847; Ptycholepis gracilis Davis, 1884; Ptycholepis bollensis Agassiz, 1833; Eunathlus philopterus Agassiz, 1843; Luoxiongichthys hyperdorsalis Wen et al., 2012; Allolepidotus bellottii De Alessandri, 1910; Bobasatrania sp. White, 1832; Asialepidotus sp. Su, 1959.

Specimens belonging to these taxa were selected for study on the basis of quality preservation of their squamation pattern and scale morphology. The selected specimens are deposited in the following museums: Museo di Paleontologia del Dipartimento di Scienze della Terra “A. Desio”, Università degli Studi di Milano, Italy (acronym MPUM); Museo Civico di Storia Naturale di Bergamo, Italy (MCSNB); Museo della Vicaria di S. Lorenzo in Zogno, Italy (MVSLZ); Museo Cantonale di Storia Naturale di Lugano, Switzerland (MCSNL); Natural History Museum of London, United Kingdom (NHM); Geological Museum of the Peking University, Paleontological collection, Beijing, China (GMPKU-P).

When possible, holotype or paratypes were selected for the analysis. In other cases, specimens were selected on the base of their preservation degree of ganoid squamation and body features. The list of the studied specimens, with their inventory numbers is in Table S1 (Supplementary online material 1).

Morphology of ganoid scales and ornamentation

Since the aim of this study is the investigation of the ornamentation, the term “scales” is used herein to refer to the exposed portion of ganoid scales. The preservation, rich in details, of the external surface allows us to study the exposed portion of the scales in terms of ganoine morphology, which is the component producing the ornamentation pattern. Three analogous, non-specialized positions were selected along the body axis of the fishes to perform this study, in dorsal, lateral and caudal regions, respectively: positioning each of these regions, three scales have been selected. Scales from particular regions, such as those close to the base of fins or in the anal region, were excluded because factors other than general body shape could affect their morphology (e.g., functionality related to fin movements; adaptation to turbulences created by maneuvers during swimming performed using fins). The overall morphological difference measured in analogous positions along the body axis is considered as a tool to compare ornamentation patterns.

In order to describe morphological variability of scales, approaches based on landmarks are generally applied when there are anatomical homologous points to use as references in the analysis (e.g., Chen et al., 2012). On the contrary, the morphological variation of irregular structures is more difficult to evaluate. This is the case of the ornamentation produced by ganoid scales. Here, we describe the ornamentation of ganoid scales using several non-dimensional morphological descriptors, which do not require anatomical correspondence and are therefore useful.
to describe the organization of ganoine in terms of shape producing specific ornamentation.

For each scale, a picture was acquired using a digital camera installed on a stereomicroscope. The outline of exposed surface of scales and of the ganoine microrelief were digitized. Measurements were taken on the binary image obtained from the digitalization of the scales: maximum diameter, height and length, perimeter and area. A schematization of measurements is shown in Fig. 1. Several non-dimensional parameters were subsequently calculated from the measurements to describe morphology (Russ, 1992).

Morphological descriptors used are:

\[
\text{Height-Length ratio (HLr)} = \frac{\text{Height}}{\text{Length}}
\]

Height-Length ratio is calculated on the exposed part of the scales; for the measurement of the height, starting from the middle of the ventral edge of the scale, we traced a line parallel to the anterior edge, ending to the dorsal edge. For the measurement of the length, starting from the middle of the anterior edge, we traced a line parallel to the ventral edge, ending to the posterior edge.

\[
\text{Formfactor} = \frac{4\pi \times \text{Area}}{\text{Perimeter}^2}
\]

The Formfactor is the inverse ratio of the squared perimeter of an object to the squared perimeter of a circle of the same surface. The area and the perimeter are calculated on the ganoine outline. The smaller the Formfactor is, the more indented the outline is. In particular, since the main variability of scales outline is on posterior margin, which may be from smooth to serrate, the Formfactor provides information about the degree of serration.

\[
\text{Roundness} = \frac{4 \times \text{Area}}{\pi \times \text{MaxDiameter}^2}
\]

The Roundness is the ratio between the actual area and the area of a circle of the same diameter: the higher the Roundness is, the more rounded the scale surface shape is. The area and maximum diameter are calculated on ganoine outline because the use of this parameter is aimed to describe the ornamentation morphology.

\[
\text{Compactness} = \frac{\sqrt{4\pi \times \text{Area}}}{\text{MaxDiameter}}
\]

The Compactness is a numerical quantity representing the degree to which a shape is compact. It refers to ganoine coverage. The smaller the Compactness is, the more complex the ganoine pattern is.

\[
\text{Cover - coefficient} = \frac{\text{Covered Area}}{\text{Exposed Area}}
\]

The Cover-coefficient is the ratio between the area covered by ganoine and the total area of scale exposed. It shows a positive correlation with the ganoine coverage. This parameter may be also indicative of the relative lightening of scale coverage.

To compare the morphologies of different ganoid scales, we performed a Principal Component Analysis using the standardized values of morphological descriptors. Since the morphological descriptors are partially related to each other, it is necessary to plot a new set of variables (the Principal Components), which are orthogonal and represent an empirical and parametric morphospace. In this space it is possible to compare morphologies using the Euclidean metric. Subsequently, we performed a Hierarchical Cluster Analysis using Euclidean metric distances to group scales on the basis of morphology. In order to choose the best number of groups for subdividing the scales, we performed a Cluster Validation analysis (Internal Validation using Dunn, Silhouette and Collectivity test; Brock et al., 2008). All these analyses are performed using R 3.2.2 (R Development Core Team, 2015).

Body morphology vs. pattern of ganoine ornamentation

To establish the existence of a significant correlation between ganoine ornamentation and overall morphology of the taxa under investigation, the body shape was captured using the geometric morphometric approach (Zelditch et al., 2004), performing two different analyses. In the first one, homologous landmarks were selected on the basis of their functional or ecologic role following studies about the shape variation in extinct or modern fishes (Fig. S1). In the second analysis, 80 semilandmarks, equally spaced and aligned using the minimum bending energy criterion, were used to define the body outline.
The landmarks and semilandmarks were acquired and digitized using TPSDIG, version 2.17 (Rohlf, 2013a). Subsequently shape variables were extracted by applying Generalized Procrustes Analysis (GPA; Rohlf & Slice, 1990). This algorithm aligns landmarks configurations to a common reference (the consensus) after removing the effect of rotation, translation, and differences in size among specimens. Partial Least Square analysis (PLS; Rohlf & Corti, 2000) was applied to detect a possible association between shape variables and morphological descriptors of scales. The Partial Least Square analysis (PLS) extracts pairs of orthogonal latent variables from the correlation matrices of each block, using singular value decomposition. Each pair of latent variables (singular Warps; SW) maximizes the possible co-variation between the two blocks. In PLS models there are no predictors and predicted variables, but both blocks of variables (shape variables and morphological descriptors of scales) are equally weighted. A nonparametric permutation test (with 999 random repetitions) was performed in order to test if the covariation of latent variables and correlation coefficients were significant. GPA, PLS analyses and permutation test were performed using TPSRELW and TPSPLS, version 1.19 (Rohlf, 2010, 2013b).

RESULTS

Measures, shape descriptors and scales classification

The acquired measurements are summarized in the Supplementary online material 2. The largest scales exceed 50 mm² in exposed surface, and most of them belongs to the lateral body regions of large deep-bodied fishes such as Sargodon tomius and Stoppania gaetanii. The smallest scales belong to the paleonisciforms Ptycholepis and Bobasatrania, reaching less than 1 mm² in exposed surface. A summary of the shape descriptors ranges is presented in the Supplementary online material 1 (Fig. S2). Roundness and compactness show a wide range of overlapping values for the scales in the three different body positions of the investigated specimens. The Formfactor of ganoine coverage is more differentiated for the dorsal and lateral scales, compared to caudal ones, which present the highest values of this parameter. The Height-Length ratio shows lower values in caudal scales than in other body positions. The Cover-coefficient has a wide range of values both in lateral and dorsal scales, whereas in most of the caudal ones, this parameter is equal to 1.

The Principal Component Analysis of the non-dimensional shape descriptors results in the first two PCs, explaining more than the 82% of the observed variance, with the first PC explaining about 68% of the observed variance (Tab. 1). The Cluster Validation analysis highlights that the best scores are reached using a hierarchical cluster method. The number of clusters with the best score is 2 for Connectivity and Silhouette test, but it is grater for Dunn (see Supplementary online material 1: Tab. S2, Fig. S3). Looking the results of cluster validation and the characters of scales, we evaluated that a good compromise for the best grouping number is three (Fig. 2). The PCA reveals that along the first PC axis there is a decrease of Formfactor, Circularity, Compactness and Cover-coefficient, and an increase in the Height-Length ratio of the scales. The clusters follow the trend along the first PC axis.

The resulted clusters include these types of scales:

- **cluster A**: most of the caudal scales belongs to this group; they bear a complete cover of ganoine and have an aspect ratio close to 1, with a diamond shape (Fig. 3a). Variegated lateral and dorsal scales are included in this cluster, both those with an elongated aspect ratio, but with a smooth and complete cover of ganoine (Fig. 3b), and those with a sub-quadrate outline and a reduction of ganoine cover (Fig. 3e). The scales of this group are characterized by weak to developed ganoine serrations along the posterior edge, which vary in number and depth of the elements.

- **cluster B**: most of the scales exhibits an aspect ratio very different from 1; the scales are partially ganoine free in between the elements composing the ornamentation; scales strongly covered by ganoine show well developed and deep serrations with high number of elements (Fig. 3d); scales ornamented with longitudinal grooves tend to have a lower aspect ratio and show reduced coverage of ganoine in between the ridges (Fig. 3e).

- **cluster C**: this group contains scales ornamented by isolated elements of ganoine on the surface of scales; these scales have an high aspect ratio (Fig. 3f).

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<table>
<thead>
<tr>
<th>Principal components</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD</td>
<td>1.835</td>
<td>0.854</td>
<td>0.773</td>
<td>0.484</td>
<td>0.188</td>
</tr>
<tr>
<td>Proportion of variance</td>
<td>0.679</td>
<td>0.147</td>
<td>0.120</td>
<td>0.047</td>
<td>0.007</td>
</tr>
</tbody>
</table>

Tab. 1 - Summary of the results of Principal Component Analysis performed on the standardized values of morphological descriptors used to compare ganoid scales.
Correlation between body shape and ornamentation

PLS analysis supports the presence of an association between the morphological descriptors of scales and body shape in the actinopterygians analyzed. For the analysis in which landmarks were used to define body shape, the first pair of SW vectors explains the 82.15% of the covariance and their correlation coefficient is equal to 0.758. The permutation tests are significant for the correlation of vectors, but not for the amount of variance explained. For the analysis in which semilandmarks (i.e., outline) were used, the first pair of SW vectors explains the 93.73% of the covariance and their correlation coefficient is equal to 0.842. The permutation tests are significant both for the amount of variance explained by the first SW vectors pair and the correlation of vectors. A summary of the other latent variables is provided in Tab. 2.

DISCUSSION

Scale morphology and ornamentation of ganoine.

The external morphology of the studied scales is varied, both in scale shape and in ganoine coverage. We have included in the analysis:

1. diamond shaped scales, totally covered by ganoine, with a smooth posterior margin (Fig. 3a);
2. diamond shaped scales, totally covered by ganoine, with a serrated posterior margin (fig. 6C in Lombardo et al., 2008);
3. scales with HLR major than 1, totally covered by ganoine, with a thin serrated posterior margin (Fig. 3b);
4. scales with HLR major than 1, not totally covered by ganoine, with deep serrations along the posterior margin (Fig. 3d);
5. scales with HLR minor than 1, with longitudinal ridges of ganoine, with free grooves in between (Fig. 3e); 6. scales with HLR much more than 1, partially covered by ganoine, which tend to form isolated tubercles on the outer surfaces (Fig. 3f).

The clusters of scales based on shape descriptors are not totally consistent with the observed morphologies, since scales with different types of ornamentation are clustered together (Fig. 2). The cluster A is the most inconsistent, instead the B and C are progressively more and more consistent. This could be related to two factors:

1. the morphology of scales changes gradually along the body of fishes of a specific taxon and, as a consequence, it results as a continuously variable character, difficult to classify and clusterize;

Tab. 2 - Summary of the results obtained from PLS analysis between body shape block and morphological descriptors of scales data block for the 16 taxa of Mesozoic actinopterygians under investigation. The covariance and correlation values and the permutation test results are represented for the first five Singular Warps.

<table>
<thead>
<tr>
<th>SW</th>
<th>Covariance</th>
<th>Explained covariance</th>
<th>Correlation</th>
<th>Significativity of covariance (999 permutations)</th>
<th>Significativity of correlation (999 permutations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.251</td>
<td>82.15</td>
<td>0.758</td>
<td>( p \leq 0.11 )</td>
<td>( p \leq 0.03^* )</td>
</tr>
<tr>
<td>2</td>
<td>0.086</td>
<td>9.64</td>
<td>0.785</td>
<td>( p \leq 0.89 )</td>
<td>( p \leq 0.04^* )</td>
</tr>
<tr>
<td>3</td>
<td>0.071</td>
<td>6.63</td>
<td>0.717</td>
<td>( p \leq 0.53 )</td>
<td>( p \leq 0.06 )</td>
</tr>
<tr>
<td>4</td>
<td>0.024</td>
<td>0.76</td>
<td>0.663</td>
<td>( p \leq 0.99 )</td>
<td>( p \leq 0.19 )</td>
</tr>
<tr>
<td>5</td>
<td>0.016</td>
<td>0.34</td>
<td>0.766</td>
<td>( p \leq 0.99 )</td>
<td>( p \leq 0.06 )</td>
</tr>
</tbody>
</table>

| Landmarks | 1 | 0.334 | 93.73 | 0.842 | \( p \leq 0.046^* \) | \( p \leq 0.001^* \) |
| Outlines | 2 | 0.070 | 4.09  | 0.726 | \( p \leq 0.938 \)  | \( p \leq 0.053 \)  |
|          | 3 | 0.043 | 1.56  | 0.798 | \( p \leq 0.901 \)  | \( p \leq 0.06^* \)  |
|          | 4 | 0.023 | 0.45  | 0.542 | \( p \leq 0.932 \)  | \( p \leq 0.293 \)  |
|          | 5 | 0.010 | 0.08  | 0.702 | \( p \leq 0.994 \)  | \( p \leq 0.045^* \) |

**Fig. 4** - Cross plot of the first pair of Singular Warps (SW) representing body shape block (x-axis, a: body landmarks, b: body outlines) and morphological descriptors data block (y-axis) for 16 species of Mesozoic actinopterygians. 1) *Allolepidotus bellottii* (4431), 2) *Asialepidotus* sp. (GMPKU-P 3025), 3) *Bobasatrania* sp. (coll. Tintori), 4) *Dapedium noricum* (MCNB 3316), 5) *Dapedium politum* (NHM P1585), 6) *Endennia licia* (MPUM 8434), 7) *Eugnathus philpotae* (NHM P3576), 8) *Felberia excelsa* (MCSNL 5034), 9) *Gabanellia agilis* (MPUM 7751), 10) *Luxiongichthys hyperdorsalis* (GMPKU-P 1580), 11) *Paralepidotus ornatus* (MVSLSZ ST82916), 12) *Psycholepis bollensis* (NHM P858a), 13) *Psycholepis gracilis* (NHM P7789), 14) *Sargodon tomicus* (MPUM 7516), 15) *Semiolepis brebanus* (MPUM 9288), 16) *Stoppania gaetanii* (MPUM 9542).
2. the shape descriptors are not fully exhaustive and some features that contribute to morphological variability may be underestimated or not accounted for (e.g., the thickness of the ganoin coverage).

Despite the difficulty of creating consistent clusters, the PCA analysis of morphological descriptors represents a useful tool to compare scales, since it generates an empirical and parametric morphospace, where it is possible to quantify differences between scales. For the scales under investigation, we observed that cluster A is closer to cluster B than to C. This means that the ornamentation of a scale in A is more similar to a scale in B than in C (Fig. 2). For example, a lateral scale of *Asialepidotus* sp. (Fig. 3b) can be evaluated to be more similar to a caudal one of *Paralepidotus ornatus* (Fig. 3a) than to a lateral scale of *Stoppania gaetanii* (Fig. 3f) in terms of the organization pattern of ganoin. This is in agreement with the morphospace occupancy plotted in Fig. 5, where it is possible to measure metric distances between scales. As a consequence, the overall morphospace occupied by the scales of a single taxon can be considered an index of the differentiation of scales morphology. This allows to compare in a quantitative way the ornamentation pattern of different taxa. For example, *Gabanellia agilis* shows a relative homogeneous type of scales in the body positions analyzed. The scales are totally covered by ganoin and present posterior serrations. The main variability is mostly related to the change in aspect ratio of the scales. Instead, *S. gaetanii* has scales that gradually switch from high aspect ratio, with ganoin tuberculation, to smooth scales, with sub-squared outline, completely covered by ganoin. This results in a different morphospace occupancy for the scales of each taxon (Fig. 6), with *S. gaetanii* occupying a greater area because of the more differentiated scales morphology with respect to *G. agilis*. In addition, the position of the occupied area is informative about the type of scales ornamentation. In fact, it is noteworthy that *Bobasatrania* sp., which has homogeneous scales ornamentation composed of elongated ridges on scales surface, shows a morphospace area similar to *G. agilis*. On the other hand, *Bobasatrania* sp. has a type of ornamentation more similar to the lateral/ dorsal region of *S. gaetanii*, and this explains the position of the occupied area.

**Relationships between body shape and morphological descriptors of the scales**

The PLS analysis reveals that the overall scales ornamentation is better associated to the outline rather than shape defined by landmarks (Tab. 2, Fig. 4). Fishes with similar body shape show more similar trend for overall ornamentation pattern. This highlights that, even if the single scales are very different from each other, the pattern of ornamentation can be considered similar. In fact, fishes that have closer positions in the PLS (Fig. 4), possess similar organization of the ornamentation, irrespectively to the complexity of the ganoin organization on scale surfaces. For examples, *Gabanellia agilis* and *Ptycolepis* sp. are very close (Fig. 4, *G. agilis* = 9, *Ptycolepis* sp.= 12/13), sharing the streamlined outline of the body. *G. agilis* has scales totally covered by a thin layer of ganoin and with a weakly serrated posterior margin (Tintori & Lombardo, 1996). Instead, *Ptycolepis* sp. has thick ganoid scales, with longitudinal grooves along all the body (see Fig. 3e for lateral scale). For both taxa, the main changes are related to the aspect ratio of the scales, but the organization of ganoin ornamentation remains constant. Deep bodied fishes, such as *Stoppania gaetanii* and *Felberia excelsa*, have a more differentiated ornamentation, with a progressive change in the ornamentation of the scales along the body (Lombardo & Tintori, 2004; Lombardo et al., 2008). Taxa such as *Paralepidotus ornatus* and *Dapedium* sp. have a certain amount of change in scales ornamentation, with the dorsal and lateral being more ornamented and the caudal being smooth. This results in an intermediate position of these taxa (Fig. 4, *Dapedium* sp. = 4/5, *P. ornatus* = 11).

**Implications**

The relationship between body shape and ganoin ornamentation could be potentially extended to other non-teleost actinopterygians not examined in this study.
For example, the deep-bodied *Kyphosichthys grande* (Xu & Wu, 2012) possesses an ornamentation that varies along its body, as observed also in specimens of *Dapedium* from the Lower Jurassic Posidonia Shale of the Holzmaden area (Thies & Hauff, 2011). On the other hand, other fusiform taxa, with ganoid scales, have a relatively homogeneous ornamentation, such as *Isonichthys palustris* among the Semionotiformes or *Perleidus* among the Perleidiformes (Cavin & Suteethorn, 2006; Lombardo et al., 2011).

In this study, we have included representatives of different orders, which show distinctive traits of ornamentation. The paleonisciforms, *Bobasatrania* sp. and *Ptycholepis* sp., show a pronounced and complex ornamentation of scales, made of ridges and grooves, as observed in other genera of basal actinopterygians (see for instance the genus *Challaia* in López-Arbarello et al., 2010).

The deep bodied perleidiforms *Felberia excelsa* and *Stopania gaetania* have a complex ornamentation too, which changes drastically in the different positions analyzed. On the other hand, the fusiform *Gabanellia agilis* shows smooth scales ornamented only with posterior serrations. The Perleidiformes seem to bear a variety of types of ornamentation, as for example the genus *Colobodus*, which shows a very peculiar pattern of longitudinal ridges and grooves (Rusconi et al., 2006; see fig. 10 in Sun et al., 2008). The slender semionotiforms tend to have smooth scales ornamented with posterior serration. In the taxa developing a prominent hump-back region, such as *Paralepidotus ornatus*, the scales of this region bear tubercles (see for instance *Scheenstia zappi* in López-Arbarello & Sferco, 2011). Otherwise, deep-bodied taxa posses scales of dorsal and lateral regions completely covered by isolated tubercles (see *Sargodon tomicus*).

Even if there are differences in the specific types of ornamentation of different taxa, it is clear that there is a general association between ornamentation pattern of ganoid scales and the body shape. One possibility is that the observed trend could have some adaptive meanings. During the evolutionary history of fishes, repeated morphological convergences occurred to improve swimming performances (Fletcher et al., 2014). Since fishes work as an integrated unit and the association of morphological characters is expected to produce better performances, we can hypothesize that the ornamentation is related to the hydrodynamic forces shaping the general morphology of fishes. Several authors suggest that the microrelief of scales has some functions related to the control of water flow around the fish body (drag reduction, control of the turbulence, delay of boundary layer detachment, enhancement of float; e.g., Bone, 1972; Lang et al., 2008). This has been proven in part for placoid scales of sharks (Oeffner & Lauder, 2012), but, at present, only conjectures have been provided for ganoid scales (Burdak, 1986). The hydrodynamic function has to be verified, since ganoine produces structures that could have other roles. For example, *Dipteronotus olgiattii* (Tintori, 1990) possesses scales in which ganoine produces prominent spines, which could have a protection function. In addition, structural functions cannot be excluded. For example, it has been suggested that the ridges on the scales of *Bobasatrania* contribute to the body stiffness necessary for the swimming (Campbell & Duy Phuoc, 1983). However, complex ornamentations, such as random grooves or tuberculations, are difficult to relate to a specific function.

**CONCLUSIONS**

In this study, we have highlighted that the ganoid scales and their ornamentation can be studied using a comparative and quantitative approach. We have performed a preliminary study to solve the thorny question, which is the interpretation of structures that today are present in few taxa, but that were very common in Paleozoic and Mesozoic fish lineages, such as the ganoid scales, with their peculiar ornamentation, which is no longer observed in extant lineages. Applying this method, we have demonstrated that there is a general association between the body shape and the ornamentation pattern of ganoine in the investigated taxa, highlighting a possible function related to the hydrodynamics of swimming.

This finding is very important to better understand basal actinopterygians adaptations and paleobiology, since the ganoid scales are the most usual remains of these organisms. A quantitative test of our hypothesis would be desirable and the approach used in this study should be extended to other fossil materials and to other time intervals.

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