The flank bar-scales in Pycnodontiformes, Berg (1937): morphology, structure, evolutionary significance, and possible functional interpretation as venom apparatus

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Abstract

Bar-scales are unique, and they are found exclusively as a few ossified, dermic structures on the squamation of 31 genera of the order Pycnodontiformes, Berg (1937). These special scales are bar-shaped, very elongated, and prevalently restricted to the anterior half of the fish body. They are frequently associated with the dorsal shield scales that are arranged in sequences that extend along the flanks of the fish, from the near dorsal ridge, to the lower area of the vertebral column. This restricted topographic distribution on the fish flanks and their association with reduced ossification were the two pieces of evidence that induced previous authors to consider these bar-scales as anatomical structures that represent the extreme reduced stage of squamation of the anterior half of Pycnodontiformes fish. Here, I have examined in detail both the anatomic structure and the anatomic disposition of these bar-scales, and I have examined their micro-structure in detail under stereo-microscopy and scanning electron microscopy. In this way, I demonstrate that the bar-scales are filamentous ossified dermal structures that are frequently wrapped around themselves, due to a twist along their own major axis. Also, their internal structure is extremely specialized; indeed, in some cases (e.g., Coelodus costai, Nursallia tethysiensis, Palaeobalistum spp.), this is very well preserved. I demonstrate that these bar-scales have an internal structure with an interior cavity and a longitudinal channel. In another case (i.e., Proscinete penaluva), I demonstrate the presence of two deep grooves that run longitudinally along the anterior margin of each bar-scale. These aspects are consistent with the anatomical structures of the venom apparatus of some extant poisonous fish. These new data demonstrate that bar-scales represent a true apomorphy that was adopted by some Pycnodontiformes as true high specialization of some dermal well-ossified scales. Furthermore, I propose the hypothesis that these specialized scales had a role in fish defense or offence in their particular environments.

Introduction

In general, the anterior part of the body between the head and the unpaired fins (dorsal and anal) of many members of the order Pycnodontiformes (Berg, 1937) is covered by a sort of dermic carapace (Blot, 1987). This is reduced to a series of a low number of scales, many of which are elongated; these are known as the ‘bar-scales’. Frequently, these are associated with the dorsal ridge scales, and they can sometimes reach the ventral keel scales, which constitutes the pattern of squamation of this type of fish. These bar-scales are ossified anatomical elements of dermic origin that are characteristic of the pycnodont fish. No other fish, either as fossils or living, have these types of scales.

In 1996, Nursall classified the squamation pattern of pycnodont fish into five different models (Nursall, 1996). In two of these, the anterior part of the body was shielded by these special scales, defined as bar-scales. These two patterns were called ‘peltate’ and ‘clathrate’ (Fig. 1), with both characteristic of some genera of the order Pycnodontiformes, sensu Berg (1937), and in particular, of the subfamily Pycnodontinae, sensu Taverne & Capasso (2012). These peltate and clathrate patterns represent a sort of reduction of the squamation of Pycnodontiformes, with significant restriction of these ossified scales prevalently to the anterior part of the body, in the flank area between the skull and the unpaired fins. However, Poyato-Arriza & Wenz (2002) considered that the scheme of Nursall (1996) did not cover all of the patterns of squamation seen for pycnodonts, because this scheme only took into account the topographic distribution of the scales over the body, but not the grade of ossification of the scales. Indeed, to cover all of the patterns of squamation seen for Pycnodontiformes, Poyato-Arriza & Wenz (2002) considered that the various patterns found resulted from multiple combinations between the distribution and ossification of the scales. For this reason, they adopted a cladistics analysis that gathered the different characteristic states from Nursall (1996) and split them into these two characteristics, as the distribution of the scales over the body, and the pattern of ossification of the scales, also considering these two characteristics as linked. This thus defined, for instance, complete scales that can cover the whole of the body (Mesturus) or can be restricted to the anterior
half (*Apomesodon, Eomesodon*), and also partially ossified scales that can cover much of the caudal region (*Nursallia*) or can be restricted to the region in front of the dorsal and anal fins (*Pycnodus*). In this general context, it can be seen that these bar-scales are present exclusively in Pycnodontiformes that have squamation prevalently restricted to the anterior part of the body (such as on the flanks between the skull and the beginning of the unpaired fins), and that also have few ossified scales.

In synthesis, this squamation of the anterior shield in Pycnodontiformes appears to represent a combination of characteristics that relate to both the restricted distribution of these scales, as prevalently to the anterior part of the body, and to reduced scale ossification. This type of squamation is found in only a few genera of Pycnodontiformes (see Table 1), and it arises from coexistence of three anatomic elements: dorsal ridge scales; ventral keel scales; and flank bar-scales.

This body dermic lining was interpreted as part of the skeleton and not as a special pattern of squamation in the early studies that described the Pycnodontiformes. Indeed, Agassiz (1833-1844) and Pictet (1854), and also Heckel (1856), described the dorsal and ventral ridge scales and the related flank bar-scales as typical elements of the skeleton of the pycnodonts, which they referred to as the “single bones” ("osselets singuliers", in French).

Therefore, since the first descriptions of the species of the order Pycnodontiformes (Berg, 1937), the flank bar-scales were considered as typical of pycnodont fish. For instance, in 1856, in describing the species *Coelodus costai*, Heckel called these flank bar-scales “Firstrippen”, and attributed relevant taxonomic value to them for the new genus. Here, the intersection between the neural spines and the flank bar-scales gives the antero-superior region of the pycnodont body a lozenge shape (Fig. 2A), which Heckel defined as characteristic of pycnodonts (Heckel, 1856). So in this general context, the bar-scales represent scales that are more reduced, and apparently residual, with a few ossified and diffuse over the body of these fish (Fig. 2B).

For the anatomical significance of the squamation in pycnodonts, in particular, Agassiz (1833-1844) considered the anatomic unit represented by dorsal ridge scales/ flank bar-scales/ ventral keel scales as analogous of the “V-shape ossicles” of the Clupeiform fish, an interpretation that persisted into the XXth century. However, other authors, such as Henning (1906), underlined possible analogies with the dorsal and ventral shield of Acipenseridae and Dercetidae.

In the search for the true evolutionary significance of these dermal structures, many hypotheses arose. Poyato-Ariza & Wenz (2002) interpreted both the dorsal and the ventral ridge scales, as well as the flank bar-scales, as residual structures that were derived from an incomplete ossified dorsal and ventral shield. These were thus in continuous reduction along the evolutionary line of the monophyletic order of Pycnodontiformes, to result in a sort of vestigial structure. Notwithstanding this, Poyato-Ariza & Wenz (2002) gave very high taxonomic significance to various aspects of the scales of both the dorsal and ventral ridges. Indeed, the characters that they defined as 88 to 93 were devoted to the description of the dorsal ridge, and the characters they defined from 94 to 99 were devoted to the description of the morphology and disposition of the scales of the ventral keel. However, no characteristics concerning the flank bar-scales were taken into account in the taxonomic key of the cladistics scheme of this systematic approach to Pycnodontiformes.

In contrast, I believe that the flank bar-scales represent...
a unique bone structure that should be present also independent of the dorsal edge scales, as is well documented (e.g., in *Hensodon*; Capasso et al., 2010). For this reason, and with the aim being to clarify the true biological sig-

Table 1 – The scales that comprise the dorsal ridge and the flank bar-scales, in the genera of the order Pycnodontiformes Berg, 1937 (for those that have bar-scales).

<table>
<thead>
<tr>
<th>Genus</th>
<th>Nº dorsal ridge scales</th>
<th>Nº flank bar-scales</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Associated with dorsal ridge scales</td>
<td>Posterior to origin of dorsal fin</td>
<td></td>
</tr>
<tr>
<td><em>Hensodon</em></td>
<td>0</td>
<td>4-5*</td>
<td>Capasso et al., 2010</td>
</tr>
<tr>
<td><em>Iemanja</em></td>
<td>?</td>
<td>5-8 ?</td>
<td>Wenz, 1989</td>
</tr>
<tr>
<td><em>Pycnodus</em></td>
<td>7-8</td>
<td>6-7</td>
<td>Blot, 1987</td>
</tr>
<tr>
<td><em>Acrorhinichthys</em></td>
<td>8</td>
<td>8</td>
<td>Taverne &amp; Capasso, 2015</td>
</tr>
<tr>
<td><em>Paranursallia</em></td>
<td>8</td>
<td>8</td>
<td>Taverne et al., 2015</td>
</tr>
<tr>
<td><em>Polazzodus</em></td>
<td>9</td>
<td>9</td>
<td>Poyato-Ariza, 2010</td>
</tr>
<tr>
<td><em>Scalacurvichthys</em></td>
<td>9</td>
<td>9</td>
<td>Cawley &amp; Kriwet, 2017</td>
</tr>
<tr>
<td><em>Tergestinia</em></td>
<td>9</td>
<td>9</td>
<td>Capasso, 2000</td>
</tr>
<tr>
<td><em>Nursallia</em></td>
<td>8-9</td>
<td>8-9</td>
<td>Capasso et al., 2009</td>
</tr>
<tr>
<td><em>Stemmatodus</em></td>
<td>10</td>
<td>10</td>
<td>Bassani &amp; D’Erasmo, 1912</td>
</tr>
<tr>
<td><em>Haegelpycnodus</em></td>
<td>10</td>
<td>10</td>
<td>Taverne &amp; Capasso, 2018b</td>
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<tr>
<td><em>Stenamara</em></td>
<td>10-14</td>
<td>8-12</td>
<td>Poyato-Ariza &amp; Wenz, 2000</td>
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<td><em>Pseudopycnodus</em></td>
<td>11</td>
<td>11</td>
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</tr>
<tr>
<td><em>Oropycnodus</em></td>
<td>11</td>
<td>11</td>
<td>Poyato-Ariza &amp; Wenz, 2005</td>
</tr>
<tr>
<td><em>Libanopycnodus</em></td>
<td>11</td>
<td>10</td>
<td>Taverne &amp; Capasso, 2018b</td>
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<tr>
<td><em>Ocloedus</em> (Coelodus)</td>
<td>12-13</td>
<td>12-13</td>
<td>1-2</td>
</tr>
<tr>
<td><em>Neoprosinutes</em></td>
<td>14</td>
<td>14</td>
<td>Maisey, 1991</td>
</tr>
<tr>
<td><em>Akromystax</em></td>
<td>14</td>
<td>13</td>
<td>Poyato-Ariza &amp; Wenz, 2005</td>
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<td><em>Abdobalistum</em></td>
<td>15-17</td>
<td>15-17</td>
<td>Poyato-Ariza &amp; Wenz, 2005</td>
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<tr>
<td><em>Gyrodus</em></td>
<td>15-17</td>
<td>13-15</td>
<td>Poyato-Ariza &amp; Wenz, 2002</td>
</tr>
<tr>
<td><em>Prosicinetes</em></td>
<td>15-17</td>
<td>15-17</td>
<td>Poyato-Ariza &amp; Wenz, 2002</td>
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<tr>
<td><em>Turbomesodon</em></td>
<td>16</td>
<td>14</td>
<td>Frickhinger, 1994</td>
</tr>
<tr>
<td><em>Tepecichthys</em></td>
<td>16</td>
<td>14</td>
<td>Applegate, 1992</td>
</tr>
<tr>
<td><em>Brembodus</em></td>
<td>16</td>
<td>15</td>
<td>Taverne &amp; Capasso, 2015</td>
</tr>
<tr>
<td><em>Rhinopycnodus</em></td>
<td>19</td>
<td>14</td>
<td>Taverne &amp; Capasso, 2013</td>
</tr>
<tr>
<td><em>Turbocecintes</em></td>
<td>19</td>
<td>15</td>
<td>Ebert, 2016</td>
</tr>
<tr>
<td><em>Mesurus</em></td>
<td>18-22</td>
<td>18-22</td>
<td>Frickhinger, 1994</td>
</tr>
<tr>
<td><em>Palaeobalistum</em></td>
<td>18-20</td>
<td>16-17</td>
<td>Poyato-Ariza &amp; Wenz, 2005</td>
</tr>
<tr>
<td><em>Sigmapycnodus</em></td>
<td>21</td>
<td>21</td>
<td>Taverne &amp; Capasso, 2018b</td>
</tr>
<tr>
<td><em>Eomesodon</em></td>
<td>22-23</td>
<td>22-23</td>
<td>Frickhinger, 1994</td>
</tr>
<tr>
<td><em>Apomesodon</em></td>
<td>26-28</td>
<td>26-28</td>
<td>Poyato-Ariza &amp; Wenz, 2005</td>
</tr>
</tbody>
</table>

*, all the bar-scales in *Hensodon* are not associated with the dorsal ridge scales, which did not exist in this genus.
The significance of these flank bar-scales in Pycnodontiformes, I examined their anatomy in detail, as both a micro-morphological analysis and a histological analysis, across many specimens. The intention was thus to interpret the anatomical situation, the evolutionary significance, and the possible functional implications of these unique structures. On the basis of this detailed anatomical analysis, I also searched for morpho-functional relationships with similar structures in living fish, from the point of view of a comparative anatomy. Through this, I propose an alternative interpretation, with the hypothesis that these odd structures represent elevated specialization, with the potential function of a venomous apparatus.

**Anatomy**

As indicated, the squamation of the anterior part of the body in Pycnodontinae is the result of the coexistence of three elements: dorsal ridge scales; ventral keel scales; and flank bar-scales. These elements are variously assembled relative to each other, but in general, the following characteristics can be summarized for their anatomical situation and disposition.

**Dorsal ridge scales**

The dorsal ridge scales represent a more or less tight series of dermal shields that as a whole, forms the dorsal ridge (or dorsal ‘carena’), which extends from the posterior-superior corner of the skull roof to the first ray of the dorsal fin. The number of these scales varies depending on the species, from a minimum of zero (e.g., *Hensodon*), to a maximum of 28 (e.g., *Apomesodon*) (Table 1). The overlap of individual adjacent scales is also highly variable, as in some genera the individual scales are well spaced (e.g., *Coelodus*), while in others they overlap (e.g., *Acrorhinichthys*). In general, the size of individual dorsal scales decreases in the antero-posterior direction, although for some genera this situation is reversed, as for *Nursallia* (e.g., in *Nursallia tethysensis*, where the penultimate scale is the largest, as the last scale is less developed).

The morphology of these scales generally varies also within the same species, depending on the position of the individual scales along the dorsal ridge. For example, the first dorsal ridge scale is tightly articulated to the dermosupraoccipital bone posterior pit (as in all Pycnodontiformes), and the last scales assume a specific shape, depending on their relationship with the first axonost and ray of the dorsal fin. In general, the scales of the dorsal ridge have essentially a domed shape, where the concave part is turned inferior (i.e., internal) and the convex part is dorsal, so exposed to the outside. The convex surface defines the dorsal edge of the fish, forming the dorsal carena, from behind the dermosupraoccipital bone to the front of the living fish (Coelodus sp., from the Albian of Pietraroja).
the dorsal fin. There are variations to the morphology of the dorsal profile of the individual edge scales, which are also seen for different individuals within the same species, and in some genera, this has been interpreted as potential sexual dimorphism (Capasso et al., 2009). The convex surface of these scales forms the external surface and this can be completely smooth (e.g., Oclocedus) or variously ornamented by tubercles, spines, and reticulation (e.g., Polazzodus). Indeed, the dorsal (external, or superior) ridge of each dorsal scale can be flattened, although, more frequently, it is surmounted by one or more spines, each with rounded or acuminate pits, which are also of different sizes. Often, when these spines, or aculei, are present, they face backwards. The anterior and posterior margins of each dorsal ridge scale have one or more apophyses, in the form of spines or tubercles.

On the internal (inferior) face of the individual dorsal ridge scales, there are two articular pockets, one on each side, with the first (the most dorsal) pair of the flank bar-scales articulated. In some species, these pockets are duplicated, such that each dorsal ridge scale has two articular pockets on each side (e.g., Fig. 3A). In such cases, each dorsal ridge scale is articulated with two sequences of bar-scales on each side, as for Coelodus and Palaeobalistum. Heckel (1856) provided the first detailed description of the anatomic disposition of these true inter-scale joints in the genus Palaeobalistum (Fig. 3A), and Capasso et al. (2009) described these same articulations in Nursallia (Fig. 3B). In general, the first dorsal ridge scale that is closely set to the cranial bones is not associated with any bar-scales.

In some genera, as Acrorhinichthys and Akromystax, the connection between each dorsal ridge scale and the pair (or two pairs) of bar-scales is through the interpolation of further scales. In this way, the dorsal carena in this genus is formed by a double series of dorsal ridge scales, and at the same time, the extension of the bar-scales is reduced, to cover a more ventral area of the flanks of the fish (Fig. 4) (the last two additional scales are not associated with any bar-scales). This model of the relationship between the dorsal ridge scales and the flank bar-scales can be interpreted theoretically as a primitive situation, in which the ossification and extension of the anterior body shield is greater than the most advanced pycnodonts. However, the connection of the flank bar-scales with the dorsal ridge scales via a few complete scales is the same in Acrorhinichthys,

Figure 3 – Relationships (articulation) between the dorsal ridge scales and the two first (dorsal) bar-scales. (A) Palaeobalistum, as the lateral (left) and antero-posterior (right) views, from Heckel (1856). (B) Nursallia, as the lateral view, from Capasso et al. (2009).
the most specialized classical pycnodontiformes that is not yet a Pycnodontidae, and *Akromystax*, the most primitive member of the Pycnodontidae (Taverne & Capasso, 2015).

**Ventral keel scales**

The ventral keel scales are more numerous with respect to the dorsal scales, and in some genera there are 50% or 100% more in number. In addition, the ventral scales are more ossified, and individually they are larger and more robust, and in general they are also more ornate, with a number of spines or tubercles that are variously prolonged. All these characteristics define the sequence of the ventral keel scales as robust and well developed, as a compact ventral carena. The cloaca opens in the posterior part of this carena, and around the cloaca the ventral keel (or ridge) scales assume a specific shape, with a particular disposition and a unique function. Finally, the superior margins of each scale of the ventral keel supports one apophysis, or more frequently, a few. These were very robust, with many elongated in the dorsal direction. Indeed, the apophyses are so developed in the dorsal directions that in some species they almost reach the ventral margin of the vertebral column, and are associated with the bar-scales.

In the cladistic analysis of Pycnodontiformes proposed by Poyato-Ariza & Wenz (2002), a great number of characteristics were defined in the evaluation of the anatomical aspects, ossification state, and number and disposition of ventral keel scales. In particular, Poyato-Ariza & Wenz (2002) devoted their characters from 94 to 100 to the description of the morphology and relationships of the ventral ridge scales situated anterior to the cloaca, and their characters from 101 to 105 to the ventral scales around and behind the cloaca.

From the point of view of the aim of the present study, it can be noted that in the case of the peltate and clathrate patterns of squamation, while the dorsal ridge scales have close anatomic contacts with the flank bar-scales, the ventral ridge scales have less tight contact with the flank bar-scales. In particular, there are indeed true joints between the dorsal ridge scales and the flank bar-scales (see Fig. 4A), and at the same time, true articulation (i.e., anatomically structured as such) between the ventral ridge scales and the bar-scales has never been demonstrated in any pycnodontiforms.

Figure 4 – The dorsal ridge in *Acrorhinichthys*. Note the additional dorsal series of scales (SC), interposed between the dorsal ridge scales (Scu) and the bar-scales. From Taverne & Capasso (2015).
The flank bars represent the most reduced scales of Pycnodontiformes, both in terms of their weak ossification and in relation to their reduced topographical extension on the flanks of the fish. The bar-scales correspond to the “Firstrippen” (Heckel, 1856) of the German study, the “baguettes” of the French studies (e.g., Blot, 1987), and the “ossicini dorsali” of the Italian studies (e.g., D’Erasmo, 1915).

In terms of their classical anatomical appearance, the individual bar-scales have the form of a two-tipped, needle-shaped, ossified bar that is cylindrical in the central part, and conical in the two terminal parts. For their dimensions, an individual bar-scale can reach a total length of a tenth of the standard length of the fish (e.g., for a specimen with standard length 30 cm, the maximum length of the largest bar-scales will be around 3 cm); however, for bar-scales that are completely free from dorsal ridge scales, this proportional length can be doubled or even tripled (see below). Individual bar-scales are particularly elongated in the dorso-ventral direction, with a ratio of width:length that reaches around 1:15 in the middle section of the scales. They are also cylindrical, although they are invariably twisted along their major axe. This torsion is easily visible because the bar-scales have a striated surface (see below). In some genera, one or two very deep and very elongated grooves run longitudinally along the length of the central part of each bar-scale; this can be observed typically for Neoprosicinetes penalvai (see below).

The bar-scales are arranged in sequence along the dorso-ventral direction, which is here indicated as the “dorso-ventral sequence” (or simply 'sequence') for the single arrangement of each dorso-ventral series of bar-scales. The position of the bar-scales along the flanks of the fish form a true sequence in which the more dorsal bar-scale is connected with the more ventral bar-scale with a large overlap, as shown in Figure 5A. Here, two following bar-scales are seen to overlap for their pointed extremities; however, as a consequence of their torsion, the inferior pit of the dorsal bar-scale will stay anterior to the superior tip of the ventral bar-scale; and this alternative overlapping is repeated along each dorso-ventral sequence of the bar-scales (Fig. 5B). In some genera, such as Coelodus and Palaeobalistum, there are two sequences of bar-scales on each side of, and connected with, the same dorsal ridge scales. In general, these two
sequences on the same side have different lengths, as they are formed of different numbers of individual bar-scales. As a consequence, in these cases, four sequences of bar-scales are connected with each dorsal ridge scale.

In one particular case for the genus *Paranursallia*, there is articulation between the most superior parts of the first (dorsal) bar-scales of each sequence. Indeed, Taverne et al. (2015) demonstrated the particular morphology of the 'head' of the first bar-scales, whereby in the vicinity of the joint with the corresponding dorsal ridge scale these are enlarged, with two small and flattened extensions that serve to connect each bar-scale with the following bar-scale (see Fig. 6).

The most dorsal bar-scale is articulated with its corresponding dorsal ridge scale (if it has one), and in general, the most ventral bar-scale crosses the vertebral column, but does not reach the area of the ventral ridge scales. In some species, however, the most ventral bar-scale is associated with the very elongated apophysis of the dorsal margin of some more ventral keel scales, although true joints between bar-scales and ventral keel scales have never been described (contrary to the situation for the dorsal ridge area). The relationship of the bar-scales is through true articulation only with the scales of the dorsal ridge, although in some species the bar-scales do cover the flanks of fish also where there is no dorsal ridge, as for *Hensodon* (Capasso et al., 2010). Notwithstanding this, for the greater part of the species, the single dorso-ventral sequences of bar-scales form the flank of the anterior body squamation, and connect the dorsal ridge scales (through true joints) with the ventral keel scales (through the distant relationships between the most ventral bar-scale and the ventral apophysis of the ventral ridge scale) (Fig. 5B).

In the most primitive Pycnodontiformes, the bar-scales have a slightly different morphology. For example, in *Brembodus*, the individual bar-scales have a sort of flange, which is attached to the rear edge of the central, cylindrical part of each bar-scale (Taverne & Capasso, 2015). For this reason, each bar-scale of this type has two parts: the bar component of the scale, and the wing component of the scale (Fig. 7A). These 'winged' bar-scales should be interpreted as a primitive form, which should correspond to a more ossified squamation of the anterior flanks in Pycnodontiformes, or – in my opinion – a few specialized bar-scales, such as a transitional form between a 'normal' scale and a bar-scale. Winged bar-scales are also found for *Macromesodon*, as well as for *Microdon* (Blot, 1987). They have persisted also in some more evolved species, although they are just restricted to the most anterior area of the anterior half of the body, such as immediately behind the cranium; e.g., *Pycnodus apodus*, of the Eocene, for Monte Bolca (Blot, 1987)(Fig. 7B). On this point, I can also report the unpublished observation of Louis Paul Taverne, who stated that as for the members of the family Nursalliinae, there is variation within the same species between younger and larger specimens in terms of the
scales in the caudal region of the fish (e.g., the post-abdominal area). Indeed, in small individuals, there are only bar-scales, while the largest individuals show a thin bony wing on the posterior margin of each bar-scale that is sometimes weakly ornamented.

Bar-scales have been described for only 31 genera of Pycnodontiformes (in alphabetical order): *Abdobalistum*, *Acrorhinichthys*, *Akromystax*, *Brembodus*, *Coelodus*, *Eomesodon*, *Gyrodus*, *Haqelpycnodus*, *Hensodon*, *Imanja*, *Libanopycnodus*, *Mesturus*, *Neoproscinetes*, *Nursallia*, *Ocloedus*, *Oropycnodus*, *Paranursallia*, *Proscinetes*, *Palaeobalistum*, *Polazzodus*, *Pseudopycnodus*, *Pycnodus*, *Rhinopycnodus*, *Scalacurvichthys*, *Stemmatalus*, *Stenamara*, *Tepexichthys*, *Tergestinia*, *Turbomesodon* and *Turboscincetes*. Here, the number of dorso-ventral sequences of the bar-scales varies according to genus and species, from a minimum of four to five sequences, as in *Hensodon*, to a maximum of 17 sequences, as in *Proscinetes*, with the special case of *Nursallia*, where the 23 bar-scale sequences also overlap the caudal pedicle of the fish (see Table 1).

Each dorso-ventral sequence of bar-scales includes a minimum of two or three to a maximum of 10-11, again, depending on the species. These extend from the most anterior of the posterior position, along the cranio-caudal length of the body of the fish. The number will obviously depend on the total length of the sequence, which can cross the vertebral column to reach the ventral region of the fish, or can stay dorsal to the spine.

As previously indicated, the relationships between the inferior (ventral) face of each scale of the dorsal ridge and the first (dorsal) bar-scales have developed as true anatomical joints. In most cases, the superior pit of the first (most dorsal) bar-scale is housed in a special pocket dug into the ventral face of the corresponding dorsal scale (e.g., *Pycnodus, Palaeobalistum*) (Fig. 8).

The relationship between one bar-scale and the next, and for the following bar-scales, is not as true joints, but only of anatomical proximity. It is generally believed that some soft tissue was interposed between one flange and the next along the dorso-ventral sequences of the bar-scales in the living fish (see Fig. 5B). Thiollière (1854) described the relationship between two adjacent bar-scales as a “flute beak connection”, although I believe this terminology is not suitable as a description of the actual conditions and anatomical arrangements of one bar-scale to another.

Finally, in terms of the extension of the bar-scales along the flanks of the fish, it can be noted that in the majority of cases just the space between the cranium and the first ray of the dorsal fin is covered by more or less dorso-ventral sequences of bar-scales. However, in  

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**Figure 7** – The flank bar-scales in *Brembodus ridens*. (A) Bar-scale of the dorsal (left) and the ventral (right) flank areas; b.c., bar component of the scale; w.c., wing component of the scale. From Taverne & Capasso (2015). (B) In some cases the bar-scales can be the result of two components: the bar component, and the wing component, as in these two bar-scales that are typical of the immediately post-craniotemal area of the flanks (in *Pycnodus apodus*). From Blot (1987).

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**Figure 8** – True joints for connections between the dorsal ridge scales and the bar-scales. The dorsal pits of the first (more dorsal) bar-scale is housed in a special pocket dug into the ventral face of the corresponding dorsal scale. (A) In *Pycnodus*; from Nursall (1999). (B) In *Palaeobalistum*; from Heckel (1856).
some cases, the first one or two dorsal ridge scales are not associated with bar-scales. In some genera, the last two or three scales of the dorsal ridge do not support any bar-scales, while on the other hand, in some other genera, there are bar-scales also behind of the first axonost and ray of the dorsal fin. The species *Turbomesodon relegans* shows the first of these anatomical dispositions, as the last three scales of the dorsal ridge just in front of the start of the dorsal fin, are not associated with any bar-scales (Fig. 9A). The second anatomic disposition has been observed for just a few genera, where the bar-scales are extended caudally; the major examples here are *Palaeobalistum*, and especially *Nursallia*.

In *Palaeobalistum*, there are one to three incomplete sequences of bar-scales situated caudally to the first ray of the dorsal fin; however, these sequences are largely not complete, because they are constituted by only a few bar-scales, which are reduced in number but are more elongated dorso-ventrally (see Fig. 9B). These sequences are, obviously, not connected with the dorsal ridge scales (as there are no dorsal ridge scales in this region), and for this reason, this type of bar-scale sequence can be defined as 'free of dorsal ridge scales' (or
Figure 10 – The thickness of the individual bar-scales is greatly reduced toward the tail in *Nursallia tethysensis*, from Cenomanian of Hadjoula (Lebanon) (A), as also seen in a big specimen of *Sigmapycnodus Giganteus* from Cenomanian of Haqel (Lebanon) (B).
simply ‘free’). The most anterior (cranial) of these sequences contains three to five bar-scales, while the most posterior (caudal) of these sequences is constituted by only two or three bar-scales (Fig. 9B).

In the genus *Nursallia*, the sequences of these free bar-scales are greatly extended caudally, and also cover all of the space between the start of the dorsal fin and the caudal pedicle. In *Nursallia tethysiensis*, there are eight or nine sequences of these free bar-scales for the typical anterior area (between the cranium and the dorsal fin), with the additional of 13 or more sequences of these posterior to the beginning of the dorsal fin, and covering the flanks of all of the caudal pedicle of the fish. In this classic interpretation, the situation in *Nursallia* represents a sort of regression, which tends to form a caudal extension of the flank squamation in Pycnodontiformes, with a large reduction in the amount of ossification. Indeed, the more caudal sequences in *Nursallia* are constituted by one to three bar-scales, where the thickness of the individual bar-scales is greatly reduced toward the tail (Fig. 10A). In the recently described genus *Signapycnodus* the complete series of bar-scales is entirely free (Fig. 10B), because of the absence of the dorsal ridge scales (Capasso & Taverne, 1918a). This disposition appears to be interpreted as extreme specialization in the ‘use’ of bar-scales as a model of flank squamation in some Pycnodontiformes.

In at least one species, *Paranursallia spinosa*, the sequences of bar-scales along the flank of the fish are interrupted by the lateral line. Taverne et al. (2015) interpreted this interruption of the squamation as the fossil traces of a true channel that in the living fish housed the soft structures of the lateral line (Fig. 11).

**Structure**

There is no information in the literature concerning the micromorphology and histological structure of these bar-scales. For this reason, I examined the bar-scales of many species that have them under stereomicroscopy, to define the micro-structural details, both on the surface of the scales and on the interior parts, through the breaking of the natural fossils. In addition, a series of samples from various genera of Pycnodontiformes that have bar-scales (i.e., *Proscinetes, Nursallia, Coelodus*) were examined by scanning electron microscopy, as thin sections, both transverse and longitudinal. The aim here was to understand the histological structure and the internal anatomical disposition of these bar-scales. For the details on the materials and methods used for these studies, see Note #1.

Under the stereomicroscopy, it was possible to initially demonstrate that in some specimens where fortuitous breaks involved the bar-scales, they have an internal cavity. This cavity occupies the central part of each bar-scale, and extends longitudinally toward the two ends of the bone. Consequently, this inner chamber appears to have a fusiform, elongated shape, as in *Nursallia*. In other cases this cavity appears vastly open to the outside, as in *Coelodus* (Fig. 12A). In fact, these internal morphological details are of particular significance, above all because they have also been observed in specimens of the genus *Coelodus*. These come from the Albian field of Pietraroja (southern Italy), an extremely conservative deposit, where the very fine structures and soft tissues of many animals were also fossilized. This includes the case, for example, of the muscle and contents of the digestive system of a juvenile reptile, *Scipionyx samniticus* (Dal Sasso & Signore, 1998). Indeed, for a *Coelodus* specimen from Pietraroja, it was possible to remove the very fine sediment that filled the internal cavity of some bar-scales, and in this way it was possible to confirm the presence, shape, and dimensions of this internal cavity (Fig. 12A).

For *Proscinetes*, the observation of the surface of the individual bar-scales under stereomicroscopy showed a different pattern. Here, the surface of the bar-scales appeared to be invariably engraved deeply by two longitudinal grooves. Each of these grooves is wider and deeper in the central part of the bar-scale, while it tapers and becomes more superficial toward the superior pointed end of each bar-scale (Fig. 12B).
Figure 12 – (A) In this specimen from the genus *Coelodus* from Pietraroja, Albian, of southern Italy, the fine sediment that filled the internal cavity of two bar-scales was removed. In this way, it was possible to confirm the existence, shape, and dimensions of the internal chamber, partially opened to the outside, in the central part of each bar-scale (asterisks) in this genus. (B) In *Procinetes* (from Santana Formation, Brazil; Cretaceous), the observation under stereomicroscopy showed invariably that the surface of the individual bar-scales is engraved deeply by one or two longitudinal grooves. Each groove is wider and deeper in the central part of the bar-scale, while it tapers and becomes more superficial toward the pointed ends of each bar-scale.
The cross-sections of the bar-scales examined here showed three different patterns across the three pycnodonts, as reported below (Fig. 13).

**Type A – Bar-scales with internal cavity/ies**

Bar-scales showing an internal cavity that extended along the central and superior parts of the length of the spine, which was wider at the center of the bar-scales, and thinned toward the superior end. This internal cavity, which in these fossils is always filled with sediment (i.e., fossil matrix), can be single or double, as two side-by-side cavities that extend along each bar-scale, parallel to each other.

The cross-sections of the bar-scales from the genus *Paleobalistum* that were examined under stereomicroscopy always showed a single internal, central, regularly circular cavity that was filled with the fossil matrix (Fig. 14A). In contrast, the cross-sections of the bar-scales from the genus *Nursallia* showed two internal cavities, side by side (Fig. 14B).

**Type B – Bar-scales with internal cavity opened to the outside**

It is possible that, in some cases, the thickness of the ossified tissue surrounding the cavity (at least in some sections of the bar-scale) is so thin, or even absent, that the cavity is at least partly open to the outside of the bar-scale. In this way an anatomical arrangement of transition between the “internal cavity / ies” and the “external grooves” seems to be realized, as it has been seen in many bar-scales of the genus *Coelodus* (Fig. 12A).

**Type C – Bar-scales with external grooves**

The bar-scales without any internal cavities showed instead deep grooves that deepened at the surface of the bone and ran lengthwise along the whole surface of each bar-scale. The cross-sections of these bar-scales observed under stereomicroscopy showed that these deep grooves have different extensions, shapes and depths, although they were concentrated at the front of each bar-scale. This arrangement has typically been observed for the bar-scales of the genus *Proscinetes* (Figs. 12B, 12C, 15).

Under scanning electron microscopy at a relatively low magnification, all of the bar-scales (regardless of species of origin) showed a bone surface that was finely striated by very fine grooves, and longitudinal scraping that extended over the entire surface of each bar-scale (Fig. 16A). These cross-sections showed the same structures as seen under stereomicroscopy (Fig. 16 B, C), which included the internal chamber(s) in *Nursallia* and *Paleobalistum*, and two longitudinal grooves in *Proscinetes* (laterally at the anterior margins of the bar-scales).

The micro-chemical analysis under scanning electron microscopy initially helped to distinguish the fossilized bone from the fossil matrix. Indeed, for each cross-section of a bar-scale, a series of maps was constructed, where each represented the topographic distribution of a chemical element. The most interesting of these maps was the topographic distribution of phosphorus. The phosphorus was strictly linked to the presence of hydroxyapatite, which was derived from the original bone of the living fish. For this reason, the topographic distribution of phosphorus salts (the ‘red’ maps of Fig. 17) clearly distinguished the borders between the bones (with phosphorus) and the matrix (without phosphorus). All of these sophisticated analy-
ses provide important scientific support to the micro-morphological data on the internal and external structures of the bar-scales.

**Phylogenetic interpretation**

It is highly probable and very reasonable to believe that these bar-scales represent an extreme reduction stage of the squamation of the anterior half of the body of Pycnodontiformes. However, these new data about the structure of these bar-scales can also be interpreted in a different way.

Following the sequence shown in Figure 18, it is possible to identify all of the possible stages through which this reduction will have occurred. As a possible
starting condition, it is necessary to take into account the anatomical situation, for example, of the squamation that was typical of the anterior part of the dorsal area of the flanks in *Gyrodus*. Here, the dorsal shield consists of a strictly overlapping sequence of scales that are connected to the dorsal ridge scales, where a bar-like structure can only be seen as a detail on the surface (Fig. 18A). The first reduction stage will have developed in terms of both a decrease in the ossification of the individual scales (e.g., that assume a structure similar to those typical of *Brembodus*), and a reduction in the number of scales (e.g., *Acrorhinichthys*). Here, the bar-

scales will occupy only the central part of the flank, and the true well-ossified scales will remain only for some of the rows near the dorsal ridge (Fig. 18B). Finally,

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Figure 15 – Stereomicroscopy of a cross-section of a bar-scale of *Proscinetes* sp. showing two deep grooves (asterisks) of different extensions, different shapes and different depths, although both are concentrated at the front of the bar-scale.

Figure 16 – (A) Scanning electron microscopy of the bone surface of a bar-scale from the genus *Proscinetes*, showing a bone surface finely striated by fine grooves and longitudinal scraping. (B) Cross-sections of two adjacent bar-scales in the matrix under scanning electron microscopy show the internal chamber in *Palaeobalistum* sp.. (C) Presence of a couple of longitudinal grooves lateral to the anterior margin of the bar-scales in *Proscinetes* sp..
the bar-scales will have substituted also for the rows of scales near the dorsal ridge, and will be reduced in thickness (e.g., *Pycnodus*, Fig. 18D). Some other genera appear to be exceptions to this general trend, as for where the bar-scales extended back in a caudal direction, along the flank of the fish (e.g., *Palaeobalistum, Nursallia*).

However, the evidence from the structural analysis of the present study appears to demonstrate that the anatomy and disposition of the bar-scales can be inter-
interpreted not only as regression in ossification, but also, and maybe principally, as new specialization. Indeed, no other fish, either as fossils or living, have these very specialized scales. While the reductions in the dimensions and the loss of the articular relationships can be considered as characteristics that indicate the vestigial nature of the bar-scales, on the other hand, some of the other characteristics reported here appear to represent very advanced specialization. These signs of specialization can be summarized as the following characters: (i) the very elongated shape of each bar-scale in the dorso-ventral direction (which gives the individual scales a filamentous appearance); (ii) the acquisition of a sinuous shape along the major axis; (iii) the acquisition of a degree of torsion along the major axis; (iv) the extension of the overlap between the adjacent bar-scales along each sequence; (v) the internal structure of the bar-scales that shows a highly specialized anatomical arrangement, with a central internal ‘camera’, or chamber, connected to the outside through an upper narrow channel; and finally, where the internal cavity is not seen (e.g., Proscinetes), (vi) two very deep longitudinal grooves around the anterior margin of the external surface of the bar-scales. For these reasons, it is very difficult to interpret the bar-scales as simply vestigial scales, such as the last remains of the primitive more extended and more ossified squamation of some Pycnodontiformes.

This hypothesis of specialization should also be related to a possible additional function taken on by these special ossified dermic structures, at least in some Pycnodontiformes, and this needs to be consistent with the unique internal structures demonstrated for the first time in the present study. Theoretically, it can also be speculated that the bar-scales represent a selective advantage for Pycnodontiformes when in their correct environment. Thus, these new anatomical structures will have been linked to new possible functions as a dermic ossified apparatus of the fish, as discussed in the next section.

A new functional hypothesis

Recent studies have indicated that over 2,500 fish extant species (i.e., around 10% of all known living species) have venom glands (Smith & Wheeler, 2006; Wright, 2009). Therefore, on the basis of only this sim-
ple numerical data, it is difficult to believe that no fossil fish adopted venom as a defense or attack strategy.

Glandular cells are of dermal origin, as are scales, and in poison fish some of these glands of the epidermis are modified into poison glands. These glands secrete poisonous substances to protect the fish from their enemies, in terms of defense, and/or also for offence. Poison glands are generally positioned at the base of certain structures, such as a sting, the spine of a dorsal fin, or a tooth. However, the original anatomical model appears to provide an association between poison glands and scales, as both are of dermic embryological origin. Poison glands open at the tip of these structures, to inject poison during penetration into the victim. In extant poison fish, the venom glands are associated with specialized teeth (e.g., *Metiacanthus* spp., *Monognathus* spp.), fin spines (e.g., apistids, aploactinis, batrachoidids, caracanthids, gnathanacanthids, neosebastids, scatophagids, scorpaenids, sebastids, setarchids, signids, siluriforms, synanceids, tetrarogids), opercular spines (e.g., batrachoidids, trachinids), cleithral spines (e.g., uranoscopids), or modified scales (only in the acanthurids) (Williamson et al., 1996).

Focusing on these last fish, in which the venom activity is linked to modified scales, it can be noted that all of the 62 living species of the family Acanthuridae (i.e., the surgeon fish) have at least one, and possibly three or more, pairs of potent weapons. These are situated just forward of the base of the tail, such as on the caudal peduncle. These weapons are similar to a dagger, and consist of modified scales. Extensive tests have been inconclusive in terms of showing any sort of venom that is associated with this knife-like scale, but it is important to note that in one series of observations, every fish cut with these daggers formed from modified scales of the members of the sub-family Prionurinae died as a result of the wounds (Baensch, 1994). It is believed that some species of *Acanthurus* have venom glands while others do not. There is no doubt that these modified scales would have been used only as a method of protection against aggressors, as these fish did not eat other fish or other living prey (i.e., their diet consisted primarily of plankton, and they also grazed on algae). The modified scales that cover the caudal flanks of the pedicle in many species of Acanthuridae are true knives, and they have indeed been referred to as ‘scalpels’, because of their lancet-like morphology. These are associated with a special muscular apparatus that guaranteed the mobility of this special scale when the fish was excited (Williamson et al., 1996).

It appears difficult not to take in consideration the analogies between this anatomical structure of the living Acanthuridae and the impressive number and serrated external aspects of many Pycnodontiformes (e.g., *Coccodontidae*, *Gebrayelichthyidae*). Some fossil species, such as *Gladiopycnodus karami* and *Trevawasia carinata*, have a number of modified scales along their flanks that are also central crests that have razor-like processes, which are very similar to the scalpel-like scales of the extant Acanthuridae.

It is very difficult to collect paleontological evidence of poisoning apparatus or structures in fossil fish, and the only possibility here appears to be to provide detailed anatomic and micro-morphological analysis of the hard tissue, including bones, teeth, and scales. In the case of the bar-scales, the hypothesis of the poisoning function for the bar-scales is derived from the observation of a structure that appears to represent the internal or external housing for a venom gland.
Indeed, according to the current situation, the venom glands of present-day fish that are connected to dermal bones (which also belong to the scaly coating) can correspond to two distinct types: (i) glands located inside a cavity in the center of the bone (which correspond to type “b” of Halstead, 1988), eventually partially opened to the outside (Coelodus); and (ii) glands located close to the bone, and that appear in a deep longitudinal groove of the bone itself (here, the spine and glands are surrounded by a fine integument; this corresponds to type “c” of Halstead, 1988) (Fig. 19).

Of note, in extant Scorpaena spp., there is similarity between the disposition of the venom glands in the two grooves positioned lateral to the anterior margin of the dorsal fin spine (i.e., the so-called “Scorpaena-type venom apparatus” of Williamson et al. 1996) (Roche & Halstead, 1972) and the morphology of the bar-scales in fossil Proscinetes sp. (Fig. 20).

In addition, the sinuous shape of individual bar-scales is consistent with the idea that in the living fish these scales would have protruded outward, thus allowing at least the superior pointed end of each bar-scale to protrude. A correctly positioned muscle could also have provided some mobility to these pointed extremities of the bar-scales, similar to what still happens with the surgeon fish today.

These outer, mobile, and poisoned tips might also have provided good defense for fish that were to be engaged in the search for food. Moreover, this type of defense might have represented a huge advantage, especially as pycnodonts were not good swimmers and moved slowly and with difficulty, as Poyato-Ariza (2005) showed.

Finally, we can consider that the reduction from complete thick flank scales that formed a sort of a heavy armor in primitive pycnodonts, to the simple bar-scales in the more evolved forms will have had other benefits for the fish, including reduction of body weight and greater possibility of moving the body (Taverne, personal communication). Indeed, many studies have considered that the transition between thick and heavy ganoid scales to light cycloid scales is one of the major characteristics that can explain the success of the Teleostei over the most primitive Actinopterygii.
Conclusions

Previously, it was considered that bar-scales simply represent the extreme reduction stage of squamation of the anterior half of the body of Pycnodontiformes. However, the new data examined and discussed in the present study relating to the fine structure of bar-scales can be interpreted as specialization of these bar-scales of the squamation of some Pycnodontiformes.

These signs of specialization can be summarized in terms of the following characteristics: (i) the very elongated shape of each bar-scale in the dorso-ventral direction (which gives the individual scales a filamentous appearance); (ii) the acquisition of a sinuous shape along the major axis; (iii) the acquisition of torsion along the major axis; (iv) the extended overlap between the adjacent bar-scales along each sequence; (v) the presence of a central internal cavity, possibly partially opened to the outside, or properly connected to the outside through a narrow superior channel; or alternatively, (vi) the presence of two deep grooves running longitudinally along the central and superior parts of each bar-scale. All of these specialization features would appear to be linked with the acquisition of a new function.

My hypothesis is for a poisoning function, which is derived from these observations of the particular structures of the bar-scales that have an internal cavity or external groove that appears to represent the location of venom glands. Finally, this hypothesis appears to be consistent also with the sinuous shape along the major axis; (iii) the acquisition of torsion along the major axis; (iv) the extended overlap between the adjacent bar-scales along each sequence; (v) the presence of a central internal cavity, possibly partially opened to the outside, or properly connected to the outside through a narrow superior channel; or alternatively, (vi) the presence of two deep grooves running longitudinally along the central and superior parts of each bar-scale. All of these specialization features would appear to be linked with the acquisition of a new function.

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Finally, these new data and my new interpretation of the possible true evolutionary significance of these bar-scales mean that these anatomical structures need to be taken more into account in the systematics of pycnodonts. In particular, (i) the presence or absence of bar-scales, (ii) their number, and (iii) their extension along the flank of the fish can be considered as significant characteristics in the classification of Pycnodontiformes, as well as in the cladistic interpretation of the evolution of this monophyletic and very special group of extinct fish.

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### Nota 1

**Material, Methods and references of pictures**

The specimens studied here belongs to the Public Collection Capasso (CLC) in Chieti, Abruzzo, Italy. This collection is a public Collection and it is legally registered by decree of the “Ministero per i Beni e Cultural Attività” on the date of 11 October 1999, in accordance with the provisions of the law Italian 1089/39. The copies of this collection also meet the requirements of Article 30 of Italian law 42/2004 on conservation and accessibility to the study.

Figure 2A: https://en.wikipedia.org/wiki/Proscinetes#/media/File:Proscinetes cf elegans.jpg; Figure 2B: Public Collection Flavio Bacchia, Banne, Trieste, n. 24; Figure 9A: https://commons.wikimedia.org/wiki/File:Turbomesodon relegans.jpg; Figure 9B: CLC, n. S-355; Figure 10A: CLC, n. S-1117; Figure 10B: CLC, n. S-497; Figure 12A: CLC, n. I-51; Figure 12B: CLC, n. S-143; Figure 14A: CLC, n. S-355; Figure 14B: CLC, n. S-465; Figure 15: CLC, n. S-143; Figure 16A: CLC, n. S-143; Figure 16B: CLC, n. S-355; Figure 16C: CLC, n. S-143; Figure 17A: CLC, n. S-355; Figure 17B: CLC, n. S-143; Figure 20B: CLC, n. S-143. The Scanning Electron Microscope used is the Zeiss Gemini SEM 450 of the Centro di Microscopia Elettronica of the State University of L’Aquila, Italy. Directed by Prof. Luca Lozzi; all the SEM analysis on the quoted fossil fish samples were performed by Dr. Maria Giammatteo and Dr. Lorenzo Arrizza.