Squamation in *Andreolepis* from the Late Silurian of Sweden

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ABSTRACT

The origin of osteichthyans (bony fishes and tetrapods) dates back to the Late Silurian, but the early evolution of osteichthyans is poorly understood. *Andreolepis* is one of the oldest known osteichthyans, but exclusively documented by detached and fragmented dermal microremains. Nevertheless, *Andreolepis* has unequivocally been attributed to the osteichthyan stem group. A variety of isolated scales of *Andreolepis* from Gotland, Sweden provides a large dataset, which would potentially improve our understanding of the acquisition of the osteichthyan body plan. In the present study, various forms of *Andreolepis* scales were classified into ten morphotypes by landmark-based geometric morphometrics. Based on comparative anatomy and functional morphology, each morphotype was assigned to a specific area of the body and a squamation model of *Andreolepis* was established. In this model, scales are allocated to anterior-mid lateral flank scales, posterior lateral flank scales, caudal peduncle scales, pectoral peduncle scales, dorsal flank scales, dorsal fulcral scales, caudal fulcral scales, ventral flank scales, medioventral scales and cranial scales.

This is the first time that landmark-based geometric morphometrics have been employed for the rhombic bony scales of primitive osteichthyans. The landmarks used for the *Andreolepis* scales were aimed to be applicable in other taxa, as they were defined by presumed homologous structures (e.g. anterodorsal process, depressed field, posterior ridge, keel, peg and socket) in the rhombic scales of osteichthyans. These structures are articulation devices that play different roles in facilitating body movement. Their conspicuity exhibits regional difference and taxonomic difference, which may be a phylogenetic signal and an indication of mode of life. The morphology of *Andreolepis* scales probably represents the ancestral state in the evolution of rhombic scales. For example, both the dorsal and caudal fulcras were here interpreted as paired, which is likely to be plesiomorphic. The squamation model of *Andreolepis* would be a handy reference for further studies of basal osteichthyans.
INTRODUCTION

As early as in the Silurian, osteichthyans had diverged into two lineages, actinopterygians (ray-finned fishes) and sarcopterygians (lobe-finned fishes). Sarcopterygians fishes achieved great evolutionary novelties for the invasion of land and evolved into tetrapods at the end of the Devonian. Actinopterygians have radiated since Carboniferous and gave rise to teleosts in Triassic, comprising half of the living species of vertebrates. Although the crown osteichthyans, including bony fishes and tetrapods, dominate the recent vertebrates, the stem osteichthyans are poorly understood. Guiyu oneiros, the exclusive articulated osteichthyan from the Silurian was recently discovered in the late Ludlow of Yunnan, China and interpreted as basal sarcopterygians (Zhu et al. 2009). However, no articulated actinopterygians have ever been known earlier than the Devonian.

Andreolepis, one of the oldest known osteichthyans, was uncertainly referred to the basalmost actinopterygian. The type species A. hedei was originally reported by Gross (1968), based on some scales and a small bone fragment from the Hemse Beds, the middle Ludlow of Gotland, Sweden. In the next two decades, more scales, fragments of cleithrum and tooth-bearing plate were described by Janvier (1978). Since then, new localities from the Ludlow and the Přidoli of northern Europe and northern Asia have been documented, and a new species A. petri was identified (Märss 2001). Nevertheless, Andreolepis had merely been known from isolated scales, teeth, fragmentary dermal platelets and incomplete skull bones, and its phylogenetic status was still in doubt.

Until recently, Andreolepis was unequivocally assigned to the osteichthyan stem group (Botella et al. 2007). Fragments of Andreolepis dentary were yielded from Gotland and identified as characteristic osteichthyan jaw bone. But differing from the crown-group osteichthyans, it lacks of mandibular sensory-line canal, large conical teeth and linear shedding tooth rows. The tooth-like denticle organization represents the initial situation of osteichthyans. Therefore, the body plan of Andreolepis, which will considerably increase our understanding on the origin of osteichthyans, has caught increasingly great attention.

Although articulated specimens of the most ancient vertebrates are extremely rare, a mass of phosphatic micromaterial of dermal skeleton can be extracted from the rocks by chemical
methods (Karatajute-Talimaa 1998). Bony scale has long been a source of interest to explore the evolution of early vertebrates because it is one of the most universal and diverse exoskeletal microremains among ichthyoliths. In living vertebrates, the integumentary skeletal element is dominated by elasmoid scales, which are the thin and rounded scales found in most of the teleosts. However, early osteichthysans bear thick and rhombic scales that are covered with layers of a shiny tissue, ganoine or cosmine (Sire et al. 2009). The ganoine and cosmine covering over the dermal surface have traditionally served as the synapomorphy of early actinopterygians and sarcopterygians relatively. In terms of its enigmatic affinity, Andreolepis was supposed to share some features with acanthodians (extinct spiny sharks) and sarcopterygians, but it was generally considered as a primitive actinopterygian, mainly because of its rhombic ganoid scales (Gross 1968, Janvier 1978). Notwithstanding, the recent finds suggested that ganoid scale was the synaplesiomorphy shared by basal osteichthyans (Zhu et al. 1999, Zhu et al. 2006). Other undetected features of Andreolepis may turn out to be completely distinct from the crown actinopterygians (Botella et al. 2007). Andreolepis has become one of the spotlights that may shed light on the actinopterygian-sarcopterygian divergence.

In addition to morphology, histology and ontogeny of separate scales, investigation on the squamation is necessary for taxa known only from discrete dermal elements (Karatajute-Talimaa 1998). Scales of the osteichthyan fishes are overlapping, which has the hydrodynamic function to increase rigidity and reduce drag. The rhombic scales of early osteichthysans are equipped with a series of interlocking devices on the base, anterior process, peg, socket and keel. Such structures exhibit a marked regional difference, thus, different scale morphotypes can be distinguished from different body parts. Burrow (1994) has attempted to interpret the functional morphology of various scale forms and accordingly assigned detached scales of Ligulalepis toombsi from the Early Devonian to particular body regions. On the basis of both complete specimens and isolated scales, Trinajstic (1999a, 1999b) characterized the scale morphology and squamation of Moythomasia durgaringa and Mimia toombsi, the most widespread and documented actinopterygians from the Late Devonian. Even though articulated Devonian actinopterygians are rare and their scale cover
suffers from incomplete description, most of them imply a consistent squamation pattern (Long 1988, Burrow 1995, Friedman & Blom 2006, Long et al. 2008, Choo et al. 2009, Swartz 2009). Last but not least, the extant “ganoid” families Polypteridae and Lepisosteidae provide living forms for the plesiomorphic bony squamation. In the light of the previous knowledge on rhombic scale morphology, it is feasible to get a general picture of the squamation of Andreolepis.

New collections of numerous Andreolepis scales from the Hemse Beds have shown a variety of new scale forms, and a large dataset is accessible. It is an urgent task to redescribe and classify the scales of Andreolepis, establishing a squamation model, which will be a handy reference for further studies of primitive osteichthyans. Instead of artificial classification, the categorization was attempted to carry out by landmark-based geometric morphometrics (Bookstein 1991). It is the first time to apply this technique to the rhombic scale of early osteichthyans. The linear or angular measurements of traditional morphometrics are usually insufficient to preserve the geometric relationships among the variables of shape, but highly correlate with size. In contrast, geometric morphometrics captured the shape variation by comparing the graphical representations generated from landmarks, while the non-shape variation in position, orientation and size is eliminated by superimposing the configuration of landmarks in a common coordinate system (Adams et al. 2004). The corresponding landmarks are biologically definable with structural, functional, developmental and evolutionary significance, and thus the shape difference described by them allows biomechanical interpretations (Lele & Richtsmeier 2001). Combining the geometric morphometrics with the functional morphology analysis, a tentative scale squamation model for Andreolepis was built in the present work.
SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES Huxley, 1880
Order incertae sedis
Family Andreolepididae Märss, 2001
Genus Andreolepis Gross, 1968

Type species. Andreolepis hedei Gross, 1968
Other species. Andreolepis petri Märss, 2001

Diagnosis. The scales are elongated or deep rhomboidal. Large scales carry several nearly parallel ridges each terminating with a spike, or united ridges separated by narrow grooves either only anteriorly or over the whole surface, or one wide ridge with a few short slanting ridgelets on both sides. The longitudinal ridges are surrounded by pores of vascular canals. Lateral line canals are placed longitudinally in scales and open on the surface by pores. The overlapped area can be very wide, and the antero-dorsal process can be rather long. Viscerally the base can be smoothly convex or has a keel, or up to two elongate keels and a groove between them. The ridges consisted of orthodentine are covered by thin single-layered ganoin; bases of ridges of all generations and the base of the whole scale are built from cellular bone; the neck between the base and uppermost dentine layer are spongyous.

Distribution. Middle Ludlow of Gotland Island, Sweden; late Ludlow of Saaremaa Island, Estonia and western Latvia; Ludlow of northern Timan, the Novaya Zemlya Archipelago and the Severnaya Zemlya Archipelago, Russia; late Ludlow — early Přidoli of the Central Urals, Russia; early Přidoli of British Isles.
MATERIAL AND METHODS

Material examined
The material studied herein is from the Late Silurian (Ludlow) of the Hemse Beds, Gogs, Gotland, Sweden. Hundreds of scales from surface blocks and in situ rocks are deposited in Uppsala University and the Swedish Museum of Natural History, respectively.

Terminology
The descriptive terminology of discrete scales is not entirely corresponding in all the reference, and suffers from the lack of strict definition. Herein, the nomenclature in the text basely follows Burrow (1994) and Märss (2001) with some modifications. The key terms are summarized in Fig. 1A, B. The dorsal depression on the external side of the scale base and the ventral depression on the internal side are recognized as peg and socket here. Even though the typical triangular peg of Devonian osteichthyan scales are high and narrow, the low and broad-based peg indicated by the gently convex dorsal edge was regarded as well-developed in Andreolepis. In articulated scales, the peg is locked in the socket of the dorsal scale of the same scale row, forming the peg-and-socket articulation. The free field refers to the area where the ganoid crown grows up. The depressed field is the area overlapped by the scale of the anterior scale row. The posterior ridge at the posterior margin of the base is to overlap the anterodorsal process and the free field of the scale on the posterior scale row. The keel at the middle of the base is almost parallel to the anterior edge and the posterior ridge, extending to the convex margin of the socket. It houses Sharpey’s fibers to attach the stratum compactum and bears one or a few vascular openings connecting to the vascular net of dermis. The keel used to be called the primary ridge or primary keel (k) and the posterior ridge was called the secondary ridge or secondary keel (k’). Since the posterior ridge possesses neither Sharpey’s fibers nor vascular openings, it should be differentiated from the keel.

Photographic method
200 totally or mostly complete scales were picked from both collections. Each scale was photographed under the dissecting microscope, from both the crown and basal view, and the file names were labeled by a particular number. The images files were flipped for consistency with the anterior edge of scale to the left side and the dorsal edge to the upper side (Fig. 1A, B) so that all the scales underwent the morphometric analysis would be from the same side (left flank) of the body, even if they actually originated from both sides. The crown-view image of
a scale was set to 50% opacity and overlaid on the corresponding basal-view image. Hence, both the crown and basal structures were visible in a superposition image (Fig. 1C).

Landmark
To propose a set of landmark appropriate for the various forms of Andreolepis scales, some rules and limitations of placing landmark must be pointed out. The landmark approach applied here is for two-dimension projections that based on 2D images. In order to avoid possible distortion due to the orientation of photograph, all the landmarks were chosen on the basal plate of the scale, rather than on the elevated crown. Since landmarks are biologically or geometrically homologous points, it requires the number of landmark and definition of each landmark is exactly the same in all the specimens. In early osteichthyan, some major scale elements, such as the peg and socket, which usually characterize the location of the scale on the body may scarcely developed in some forms of scale. Nevertheless, absent elements were incorporated and discriminated in the analysis as well. Landmarks fail to obtain information
regarding the area between them, for instance, the change of a curve between two landmarks is missing. A rhombic scale and an oval scale with the same major and minor axes would be identified as the same shape. The sliding semi-landmarks, which have been introduced to assess the curved outline without true landmarks, suffer from lack of standardized protocol. In terms of *Andreolepis* scales, the pilot tests with semi-landmarks did not make significant difference from those without semi-landmarks. The oval scales of *Andreolepis* were able to be distinguished by other features even no semi-landmark was used. Moreover, since the structure of fish scale is relatively simple, a large number of landmarks and semi-landmarks are in danger of amplifying the noise over the signal. The graphical representation of the ctenoid scale of mullet was successfully achieved by only a few landmarks (Ibañez et al. 2007). Therefore, I tried to catch the shape of the ganoid scales of *Andreolepis* by as few landmarks as possible. Inevitably, there are a minority of specialized scales that could not be represented properly by such a few landmarks. They were ignored in the morphometric analysis but discussed later on.

The landmarks were defined base on the standard morphotype (Fig. 1), which is the most abundant form in our collections, because the major structures shared by most scale forms are all notable in this form. Nine landmarks were located on the superposition image of each scale: Landmark 1 – the tip of the anterodorsal process (the joint of the anterior and dorsal edge); Landmark 2 – the ventral endpoint of the posterior ridge (the joint of the posterior and ventral edge); Landmark 3 – the dorsal endpoint of the posterior ridge (the joint of the dorsal and posterior edge); Landmark 4 – the vertex of the anterior depressed field (the joint of the anterior and ventral edge); Landmark 5 – the anteriormost point of the free field grown from the base; Landmark 6 – the intersection of the margin of the free field and the posterior edge of the base; Landmark 7 – the intersection of the margin of the free field and the ventral edge of the base; Landmark 8 – the intersection of the keel (or the line of vascular opening) and the dorsal edge of the base; Landmark 9 – the intersection of the keel (or the line of vascular opening) and the margin of the socket.

Landmark 1 and 2 make up of the major axis of the rhombic scale and the baseline in Bookstein Coordinates and Sliding Baseline Registration. Landmark 1, 2, 3, and 4 capture the rhombic shape of the scale base. Landmark 5, 6 and 7 indicate the general boundary between the depressed and free field, where the ganoid ridge grows up with inter-grooves or furrows. Landmark 8 and 9 reflect the direction and location of the keel or the line of vascular
openings as well as the height of the peg and socket. Landmark 1, 5, 6 and 8 and Landmark 2, 4, 7 and 9 outline the general shape of the peg and socket. Landmark 1, 4, 5 and 7 represent the area of the anterior depressed field. If the scale has no peg, Landmark 3 and 6 will overlap and Landmark 5 will sit on the dorsal edge. Similarly, if there is no anterior depressed field, Landmark 4 and 7 will become identical with Landmark 5 on the anterior edge. If the socket is absent, Landmark 9 will move to the ventral edge.

**Geometric morphometric method**

The geometric morphometric was performed by the software of *thin-plate spline* (TPS) series from the website *Morphometrics at SUNY Stony Brook*, maintained by F. James Rohlf (http://life.bio.sunysb.edu/morph). An initial TPS file that listed the superposition images to be analyzed was built in the *tpsUtil* program. A set of landmarks were located and digitized for each scale by the program *tpsDig*. From the processed TPS file with the landmark data, the other program *tpsRelw* summarized the shape variables (termed warps) among the scales, producing a plot of two relative warps. When the scales were posited respect to the first and second partial warps, the highest percentage of total variance was explained by relative warps. The superimposition of consensus configurations (mean shape) was employed as the reference of the transformation grip displayed by the *tpsSplin* program.
RESULTS

In the relative warps, most of the morphological variation was revealed by the first six relative warps (Table 1). According to the clusters of spots along the first two relative warps (Fig. 2), which account for 56.19% of the total variance, the 200 scales were grouped into 10 types. The specimens situated at the boundaries between clusters were determined by their distance to both clusters combined with visual diagnosis. They might be the transitional scales between two types.

![Fig. 2 Scatter plot of distribution of individual scales in the space of the RW1 and RW2. Accordingly, the scales were classified into ten groups and set into different colors: black, Type 1; green, Type 2; pink, Type 3; orange, Type 4; navy blue, Type 5; brown, Type 6; sky blue, Type 7; red, Type 8; purple, Type 9; yellow, Type 10.](image)

The morphological variation trends of the scales along each relative warps were visualized by transformation grids (Table 2). The transformation grip of the negative extreme point of the RW1 axis represents the shape of a Type 1 scale, which has longer Landmark 1-3 and Landmark 2-4 distance (the dorsal and ventral margin of the scale) than the Landmark 1-4 and Landmark 2-3 distance (the anterior and posterior margin of the scale). Type 7 scales are separated from the other scales at the positive extreme of RW1, where the circumstance is
adverse to that at the negative extreme: the shape is generally elongated, and the relative distance between Landmark 3 and 6 is enlarged with Landmark 6 moving posteriorly. Obviously, the RW1 aligns specimens from a deeper shape to a longer one, possibly corresponding to the distribution mode of fish scales that anterior scales are deeper and posterior scales are longer.

The shape represented by the negative extreme of RW2, has Landmark 2, 4, 7 and 9 almost situate in a line and Landmark 5 fall on the link of Landmark 1 and 8. Whereas the positive extreme, occupied by Type 9 scales, shows long distance between Landmark 1 and 5 and between Landmark 4 and 7, indicating a wide anterior depressed field. What’s more, Landmark 1, 3, 5, 6, 8 and Landmark 2, 4, 7, 9 enclose a rather large peg-and-socket area. It is clear that RW2 polarizes specimens by the ratio of depressed and exposed areas, namely, the degree of overlap.

Landmark 3 and 6 are quite closed at the negative extreme of RW3, but super far from each other at the positive extreme. Landmark 9 shifts posteriorly from the negative to the positive extreme, and the keel indicated by Landmark 8 and 9 does not parallel to the anterior margin, which differentiates Type 6 scales from the other scales.

At the negative extreme of RW4, Landmark 3 and 4 locate more anterior. Consequently, the links between Landmark 5 and 6 and between Landmark 5 and 7 are shorter than those between Landmark 2 and 6 and between Landmark 2 and 7. In contrast, at the positive extreme, Landmark 6 and 7 become so backward relative to Landmark 5 that the depressed fields of the scale extend extraordinary posteriorly. RW4 characterizes Type 4 scales at the negative extreme and Type 9 scales at the positive one.

<table>
<thead>
<tr>
<th>Relative Warps</th>
<th>Singular Values</th>
<th>% Explained Variance</th>
<th>% Cumulative variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>RW1</td>
<td>2.15665</td>
<td>35.40%</td>
<td>35.40%</td>
</tr>
<tr>
<td>RW2</td>
<td>1.65259</td>
<td>20.79%</td>
<td>56.19%</td>
</tr>
<tr>
<td>RW3</td>
<td>1.36115</td>
<td>14.10%</td>
<td>70.29%</td>
</tr>
<tr>
<td>RW4</td>
<td>1.09646</td>
<td>9.15%</td>
<td>79.44%</td>
</tr>
<tr>
<td>RW5</td>
<td>0.85507</td>
<td>5.57%</td>
<td>85.01%</td>
</tr>
<tr>
<td>RW6</td>
<td>0.82611</td>
<td>5.19%</td>
<td>90.20%</td>
</tr>
</tbody>
</table>
Table 2. Transformation grids display shape changes from the mean to the extremes along each relative warp.

<table>
<thead>
<tr>
<th>Relative Warps</th>
<th>Negative Extreme</th>
<th>Positive Extreme</th>
</tr>
</thead>
<tbody>
<tr>
<td>RW1</td>
<td><img src="image1" alt="Diagram" /></td>
<td><img src="image2" alt="Diagram" /></td>
</tr>
<tr>
<td>RW2</td>
<td><img src="image3" alt="Diagram" /></td>
<td><img src="image4" alt="Diagram" /></td>
</tr>
<tr>
<td>RW3</td>
<td><img src="image5" alt="Diagram" /></td>
<td><img src="image6" alt="Diagram" /></td>
</tr>
<tr>
<td>RW4</td>
<td><img src="image7" alt="Diagram" /></td>
<td><img src="image8" alt="Diagram" /></td>
</tr>
<tr>
<td>RW5</td>
<td><img src="image9" alt="Diagram" /></td>
<td><img src="image10" alt="Diagram" /></td>
</tr>
<tr>
<td>RW6</td>
<td><img src="image11" alt="Diagram" /></td>
<td><img src="image12" alt="Diagram" /></td>
</tr>
</tbody>
</table>

Note: both the mean shape and extreme shapes represent theoretical specimens based on the analysis of the sample, and there may not be any real specimens in such shapes.
The scales isolated at the negative extreme of RW5 are Type 10 scales, which have the keel placed much more anteriorly than those at the more positive part. The ratio of the peg and the anterior depressed field is even higher.

Landmark 8 is remarkably anterior and posterior to Landmark 5 at the negative and positive extreme of RW6 respectively. It implies the difference of the relative position of the keel and the crown of the longer or deeper scales.
SQUAMATION MODEL

Main scale types
According to the grouping in the geometric morphometric analysis, the scales of Andreolepis in the sample were mainly assigned to ten morphological types from different parts of the body. Each type was characterized by size, shape, sculpture and symmetry, as well as the relationship between scales, such as degree of overlap and interlocking devices. The location of each scale type was concluded from the functionality of those characters. Any taxa with data of rhombic scale squamation, especially the Devonian actinopterygians, were used as comparison.

Type 1 – anterior-mid lateral flank scales (Fig. 1, 3A-B, 4A, 5)
The scales are rhombic with well-developed peg and socket. Both the keel and the posterior ridge are strong, and in some scales the margin of the socket is so prominent that it appears as another transverse rib. The depressed field occupies 2/5 to 1/2 of the scale, but the free field hardly overhangs the posterior edge of the bony base. The ganoid crown is sculptured by multiple interridge deep grooves over the whole surface with a few posterior serrations (Fig. 3B,L), or only by fine furrows at the dorsal and anterior margins with a largely smooth surface and posterior edge (Fig. 1A, 3A). The lateral line scales that penetrated by a sensory canal from the anterior junction of the depressed and free field hold the most conspicuous anterodorsal process, with the anterior margin shrinking at the level of the opening of the canal.

The scales are generally big, deep and thin. As the typical scale, this group contributed the largest proportion (33%) of the selected scales. A higher proportion was expected to present in life, since the seriously broken ones were excluded in the morphometric analysis. It is very likely that this type of scale covers a large area of the trunk.

Type 2 – posterior lateral flank scales (Fig. 3C, 4B, 5)
The scales are similar to Type 1 scales, but much smaller and lower. The anterodorsal process, posterior ridge, keel, peg and socket are even weaker. The depressed field is narrower only taking up to 1/5 of the scale and the free field is less sculptured. The ventral edge of the rectangular scale is gently concave down and the vertex of the dorsal and posterior edge become blunt.
Fig. 3 Crown and basal view of each scale type. (A, B) Type 1 scales with different sculpture; (C) Type 2; (D) Type 3; (E) Type 4; (F) Type 5; (G) Type 6; (H) Type 7; (I) Type 8; (J) Type 9; (K) Type 10; (L) first row scale; (M) inversion line scale. Bar, 1mm.
Fig. 4 Squamation model of *Andreolepis*. (A) lateral view of Type 1 scales; (B) lateral view of Type 2 scales; (C) lateral view of Type 3 scales; (D) lateral view of Type 4 scales; (E) lateral view of Type 5 scales; (F) dorsal view of Type 6 scales; (G) dorsal view of Type 7 scales; (H) lateral view of Type 8 scales; (I) ventral view of Type 9 scales, flanked with Type 8 scales; (J) lateral view of scales around the inversion line, scale rows on the left are from Type 2 scales, scale rows on the right are from Type 3 scales. Grey area, ganoid crown; Solid line, base structures visible from the crown view; dotted line, base structures visible from the basal view. Anterior to left.
This type of scale probably locates at the posterior part of the trunk where the body tapers. When they extend to the inversion line, they are elongated with their overlapped areas and sculpture reduced and the posterior ridge invisible.

**Type 3 – caudal peduncle scales** (Fig. 3D, 4C, 5)
The scales are diamond-shaped but can be quite elongated or narrow. Peg and socket is absent, while the anterior and dorsal depressed field is rather narrow, extending caudally. It leaves the free field almost occupying the whole surface of the scale. The free field is smooth, but some scales have a fine furrow at the anterior tip. The base is thick and convex with a poorly defined keel or without keel.

These scales allow stiff and sthenic movements and probably come from the dorsal lobe of the possible heterocercal tail which functions as a propeller. The lack of peg-and-socket articulation and the broadening of the keel in scales of caudal fin is the plesiomorphic condition for actinopterygian and remains consistent from *Moythomasia* to *Polypterus* and *Lepisosteus* (Trinajstic 1999a, 1999b, Pearson 1981).

**Type 4 – pectoral peduncle scales** (Fig. 3E, 4D, 5)
The scales are small and rhombic. The posterior part of the scale is elongated as the convex posterior margin and the concave ventral margin are considerably longer than the anterior and dorsal margin. The anterior depressed field constitutes 1/4 of the scale. The dorsal depressed field terminates in front of the dorsal-posterior vertex. There is no socket and posterior ridge but only a fine keel on the base.
As the earliest osteichthyan, *Andreolepis* may possess a fine-scaled lobe to support the pectoral fin, which is a primitive actinopterygian character also observed in *Cheirolepis* from the Devonian (Long 1995). Well-preserved Carboniferous ray-finned fish specimens showed that the muscular lobe of pectoral fin was covered with elongated rhombic scales (Poplin & Lund 2000, Poplin & Lund 2002). Type 4 scales are most likely the scales that lie on the lobe of pectoral fin.

*Type 5 – dorsal flank scales* (Fig. 3F, 4E, 5)

The scales are lowered than the lateral flank scales and concave down at the ventral edge. The dorsal and the posterior edge connect smoothly as a curvature, and the dorsal-posterior vertex of the rhomboid scale may be poorly defined, forming a broad peg. From the basal view, the socket, keel and posterior ridge are well-developed as those of the lateral flank scales. 2/5 of the scale is occupied by the depressed field. The free field has fine grooves over half of the surface or just at the anterodorsal margins.

The length of the scales ranges from as long as Type 1 lateral flank scales to as short as Type 2 lateral flank scales. The similarity of the articulated relation implies that these scales sit beside the lateral flank scales with a gradual transition. Therefore, they are expected to be just dorsal to the main flank scales.

*Type 6 – dorsal fulcral scales* (Fig. 3G, 4F, 5)

The scales are elongated rhomboid with well-developed peg and socket. The axis is orientated and the dorsal margin turns anterior leaning anteroventral – posterodorsally, with the anterior and posterior margin lying horizontally. The furrows on the free field which indicate the direction of the current from anterior to posterior, sculpture at the dorsal margin, not at the anterior margin as other types of scale. The keel directs to the rostral point of the scale. The posterior ridge is absent.

Such a scale along seems unconformable with other scale types. But when it fuses with its inverted image (Fig. 4F), they appear as the precursor of the bilaterally symmetrical fulcra or basal scute of most Devonian actinopterygians. The oblique dorsal margins of the contralateral scales would form the depressed field along the anterior invaginated margin of the unpaired fulcral scales. Hence, Type 6 scales may act as the paired fulcra preceding or
behind the base of dorsal fin. In *Cheirolepis*, the caudal fulcra are paired and the basal scutes in front of them are usually unpaired, but paired basal scutes have been found in small specimen (Arratia & Cloutier 1996). The new ontogenetic observations on living and fossil Acipenseriformes raised the possibility that unpaired dorsal fulcra were developed from paired elements (Hilton 2004). The paired stage in the development of the dorsal-caudal fulcra in juvenile Acipenseriformes is potentially the recapitulation of the primitive state represented by *Andreolepis*.

**Type 7 – caudal fulcral scales** (Fig. 3H, 4G, 5)
The scales are generally in rod-like shape, more precisely, extremely elongated rhomboid with a concave down ventral margin. They are distinct from the other scale types mainly because they are so slender, but they are variable in detail themselves. The dorsal-posterior vertex is either high up or poorly defined, so that the dorsal-posterior edge is either concave at the part just before the dorsal-posterior vertex or gently convex. The socket, if any, is long but too narrow to be observed. The peg, or the dorsal depressed field, extend caudally, regardless of whether it is well- or weakly- developed. The anterior depressed field is evident, but never reaches the posterior part of the scale. The free field has fine furrows over the whole surface or just at the dorsal and anterior margins.

Several scales of this type have been collected and addressed as the ‘pseudofulcral’ scales by Janvier (1978, Plate II, Fig. 2-10). I agree that these are the paired epaxial fulcra on the caudal lobe.

**Type 8 – ventral flank scales** (Fig. 3I, 4H, 5)
The scales are generally elongated, thin and warped, but vary in detail. The anterior-lateral process is rather long or high, and directs anteriorly or dorsally. In some scales, the anterior-ventral vertex of the rhomboid scale is well defined and the ventral margin is straight. In the others, the connection of the anterior and the ventral margins is a curvature and the ventral margin is concave down. The high anterodorsal process and the high dorsal-posterior vertex make the dorsal edge concave up. The keel is short and the posterior ridge is less visible. The keel and the posterior ridge are either straight or convex outward. The peg can be very high or broad-based and the socket is rather deep or long. The depressed field is as wide as 1/2 of the scale. The free field possesses fine grooves over the whole surface or just at the dorsal and anterior margins or is smooth.
With an extended anterior corner, these skewed scales may be assigned to the abdominal region. Their variability in shape and orientation reflects the influence by the insertion of the paired fins and scale rows. This is the second largest group of scale, if it is from the belly, it could be inferred that *Andreolepis* has a thick body.

*Type 9 – medioventral scales* (Fig. 3J, 4I, 5)
The scales are oval or almond-shaped, even the anterodorsal process is blunt. It is difficult to tell dorsal and ventral, because they are almost bilateral symmetry. All the scales are small, and the crown surrounded by the depressed field, which extends to the caudal point, is so tiny that this type of scale would be neglected on articulated specimens. The slender free field in the middle of the scale is slightly sculptured by furrows at the anterior and dorsal margins. The keel directing to the rostral point of the scale is too weak to be seen.

These minute scales were regarded as a ventral scale (Janvier 1978, Plate II, Fig. 1). They were further considered as the scales on the ventral midline adjoining the Type 8 ventral scales from both flanks. Despite the lack of description from the early osteichthysans, a similar median single element can be found articulating with lateral scales by a couple of symmetrical peg in living *Polypterus* (Pearson 1981, Fig. 2).

*Type 10 – cranial scales* (Fig. 3K, 5)
The scales are ear-shaped. It appears that the anterodorsal process and the anteroventral corner of a standard rhomboid scale are truncated, as a result, the anterior margin and the keel parallel to it are much shorter than the posterior ridge. The groove between the keel and posterior ridge is so deep that a corresponding protuberance can be visible from the crown view. The shortened dorsal margin merges with the posterior margin into a smooth curve. The dorsal margin of the free field which remains in the “original” direction, outlines a huge triangular “peg” with the dorsal margin and the anterior “truncated margin” of the base. The socket extending to the end of the primary keel and the anterior margin of the base is fairly long. Besides the furrows at the antero-dorsal margins, the free field bears a few pores on the surface which are hardly seen in other scale types.

These scales are scarce. A similar auriform scale (P 6432) has been reported by Gross (1968, Fig. 3A) as an “aberrant type” of body scale. But I deemed that its ventral direction was
reverse in his interpretation, by my personal examination. In my opinion, the large peg implies that this scale type is tightly locked in an inflexible area. But the peg can not match the socket, just as the anterior margin can not match the posterior margin. The scale is consequently unable to articulate with a similar scale, but presumably highly articulate with the skull bone.

**Specialized scales**

Some scales show specialized shapes or structures that dissociate them from the major groups of scales in the geometric morphometric analysis. Nevertheless, they may possess some typical features implying that they are from one of the scale types above. They may come from some specialized position of the body, where the squamation is unclear. It is valuable to explore the functional morphology of these scales.

First row scales (Fig. 3L)
The rhombic scale is reliable to be interpreted as a Type 1 scale, but it has no anterior depressed field. It suggests that it was not overlapped by scales anterior to it, but only articulated with scales from the same and the next row. In another words, it is likely from the first row of scale behind the shoulder girdle.

Inversion line scales (Fig. 3M, 4J)
The triangular scale seems as if it was truncated from a Type 2 scale that its posterior margin is much shorter than the anterior one. I inferred that it was around the inversion line causing the oblique reorientation of the scales on the dorsal lobe of the caudal fin. Scales shaped in triangles from the inversion line were clearly observed in Devonian actinopterygian Stegotrachelus (Swartz 2009).

Fin insertion scales (Fig. 3N)
The elongated oval scale has a peg-and-socket articulation, but no depressed field and posterior ridge. In most scales, the keel is narrow and rises from the platform of the base. But in this case, the whole base thickens and rises as a robust keel. So there are no structures for the scale to be overlapped by the previous scale row and to overlap the next one, but a wide area to attach the stratum compactum and to be deeply rooted in the integument. Such a characteristic base may indicate that the scale is embedded at the base of a fin, though scales around different fins may be in different shape.
DISCUSSION AND CONCLUSIONS

Ontogenetic and interspecific differences
As a result of employing geometric morphometrics to compare scales by shape regardless of size, almost each scale type covers a certain size range. Moreover, since no landmark was defined for the pattern of ganoine ridges, scales that carry different forms of sculpture but share the same shape were grouped into the same scale type. Especially for the Type 1 scales (Fig. 3A, B, L), the style of sculpture varies from parallel ridges ending with spikes, sets of complex ridges uniting at the main free field, to one predominant ridges branching several generations of ridgelets on both sides. It implied that our sample may contain different age groups and even species.

On one hand, significant ontogenetic differences have been reported in many studies of scales. The growth of scale was divided into three stages, juvenile, subadult and adult, according to the developmental degree of sculpture, articulation devices and so forth (Esin 1995). Some Moythomasia scales were identified as juvenile or subadult by marked ganoine ridges and faint peg and socket (Trinajstic 1999b). On the other hand, a new species Andreolepis petri was erected mainly by the sculptures (Märss 2001). It put forth a question that weather the types of sculpture observed in the sample came from more than two species. However it requires articulated material and histological studies to differentiate the ontogenetic and interspecific differences of Andreolepis scales.

Early evolution of rhombic scales
Andreolepis scales possess a peg as shallow as those of the Silurian osteichthians Naxilepis (Fig. 6A) and an anterior depressed field no narrower than that of Moythomasia (Fig. 6E) from the Late Devonian. Actually, among early osteichthians flank scales, the articulation devices exhibit a diverse combination. Guiyu, Ligulalepis and Psarolepis (Fig. 6F-I), recently assigned into the stem sarcopterygians (Zhu et al. 2009), all display a narrow anterior depressed field with a wide overhang of the free field in their extremely deep scales. The pegs of Guiyu and Psarolepis are quite weak, but rather pronounced in Ligulalepis, especially in L. toombsi the peg is prominently distinct from the anterodorsal process. L. yunnanensis and Psarolepis have the anterodorsal process direct dorsally integrating with the peg, while Guiyu and L. toombsi have a projecting anterodorsal process in common. Youngolepis, Styloichthys, Powichthys, Arquaticthys (Fig. 6J-M) and some early sarcopterygians even develop another
anteroventral process (Lu & Zhu 2008). The scales of Andreolepis and the Devonian actinopterygians, such as Dialipina, Orvikuina, Howqualepis, Donnrosenia, Gogosardina and Moythomasia (Fig. 6B-E), show a relative wide anterior depressed and a straight anterior margin combining with the anterodorsal process. Consequently, the anterodorsal process appears not to project from the anterodorsal corner, but probably aim upward as that in L. yunnanensis. Although the typical Devonian actinopterygian scales are characterized by the pointed peg that definitely distinguishable from the dorsal margin of the scale, the peg of Orvikuina, as in Andreolepis, is only slightly protuberant from the dorsal margin.

Fig. 6 Flank scales comparison between (A-E) early actinopterygians and (F-K) early sarcopterygians. (A) Naxilapis gracilis, (B) Dialipina salgueiroensis, (C) Orvikuina vardiaensis, (D) Howqualepis rostridens, (E) Moythomasia durgaringa, (F) Guiyu oneiros, (G) Ligulalepis yunnanensis, (H) Ligulalepis toombsi, (I) Psarolepis romeri, (J) Youngolepis praecursor, (K) Styloichthys changae, (L) Powichthys spitsbergensis, (M) Arquatichthys porosus. Age: Late Silurian (A, F, G); Early Devonian (B, H, I, J, K, L, M); Middle Devonian (C); Late Devonian (D, E). Adapted from (A, G) Wang & Dong 1989; (B, C) Schultze 1968; (D) Long 1988; (E) Gardiner 1984; (F) Zhu et al. 2009; (H) Burrow 1994; (J, K, M) Lu & Zhu 2008; (L) Clément & Janvier 2004.
Anterodorsal process and slender peg-and-socket articulation, as well as ganoid and basal fulcra, were considered as synapomorphy characters of actinopterygians (Patterson 1982, Janvier 1996, Schultz & Märs 2004). But the anterodorsal process is also notable in the basal members of sarcopterygians and the peg can be broad based in some actinopterygians. Similarly, Meemannia who bears a ganoine-like dermal surface and Ligulalepis who possesses ganoid scales were both placed as basal sarcopterygians (Zhu et al. 2006, Zhu et al. 2009). Potential paired fulcral scales were discovered in Psarolepis (Q. Qu unpublished observations). These criterions are no longer unique to actinopterygians and the demarcation between actinopterygians and sarcopterygians becomes obscure, when we broaden our knowledge of basal osteichthyans. The mosaic combination of these features may just reflect a parallel evolution of rhombic scales that from an independent tendency of enhancing different articulation devices in primitive osteichthyans to a transition into round scales by secondarily losing these devices in derived actinopterygians and sarcopterygians respectively. Andreolepis scales mark the incipient state in the early evolution of rhombic scales that the articulation apparatus are still underdeveloped. But it is not sensible to assert the systematic affinity of Andreolepis only by its scales morphology or histology.

**Functional interpretations**

Early osteichthyans were heavily armored by a bony scale-jacket. It has been held for a long time that the anterodorsal process and the peg-and-socket articulation restricted the lateral and dorsal-ventral flexibility during undulatory locomotion. In this case, Andreolepis appeared to experience a more active mode of life with a more flexible body than its Devonian descendents. That was to say, the development of interlocking devices was a burden in the rhombic scale evolution. In direct contradiction to this view, the recent studies on Polypterus and Lepisosteus showed no evidence that body bending was more constrained by a ganoid than by an elasmoid squamation. It was argued that the limit of body flexion were never reached during steady swimming, but the extreme of body curvatures during twisting and darting was facilitated by the architecture of the rhombic integument (Gemballa & Bartsch 2002).

The keel is the position attaching the stratum compactum fibers which resists the torsional strain. The anterior depressed field permits the changes in scale overlap under the guidance of the anterodorsal process. The peg-and-socket articulation prevents the slippage between adjoining scales of a true scale row during the sliding movement of the intersecting scale rows.
These integumentary structures are most definite in the anterior flank scales, assisting the enormous body twist. It disproves the former perspective (e.g. Burrow 1994) that the anterior region of the trunk is stiffened. The lateral line scales are most lateral to the neutral midline and suggest to extreme lateral strain, therefore their interlocking apparatus are more developed than the scales dorsal or ventral to them. The attachment of the stratum compactum fibers is limited to a narrow strip in anterior scales, allowing more scale overlap. As the trunk tapers posteriorly, less lateral strain occurs to the same body curvature, and less developed are the articulation devices in the less overlapped posterior scales. The keel becomes boarder and poorly defined in posterior scales, providing a wider attachment area of the stratum compactum (Gemballa & Bartsch 2002).

The same regularity in scale morphological variations along the body is observed in *Andreolepis*. No matter how strong or weak the interlocking devices are, the mechanical function of the rhombic squamation is likely to have been conserved throughout osteichthyan evolution. Compared to the squamation of *Andreolepis*, the architecture of rhombic integument was improved during the divergent evolution of osteichthyan fishes, adapting to vigorous movements in prey-capture and mating actives.

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**REFERENCE**


