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Scales of palaeoniscoid fishes (Osteichthyes: Actinopterygii) from the Late Devonian of Western Australia

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Abstract – The squamation of an articulated specimen of the palaeoniscoid *Mimia toombsi* from the Frasnian Gogo Formation is described following the descriptive terminology of Esin (1990). Scales of various forms are attributed to specific regions of the body in accordance with Esin (1990) and Burrow (1994). Varieties of isolated scales from the Givetian-Frasnian Gneudna Formation are referred to *Mimia toombsi* on the basis of comparisons with the described articulated specimen.

Additional scales from the Gneudna Formation are attributed to *Moythomasia durgaringa* based on ornament, scale shape, the articulation device and the tubercle shape on the ganoine surface. These scales characterize different stages in the development of *M. durgaringa* (*sensu* Esin 1995). Scales representing both the juvenile and subadult stages of development are identified.

INTRODUCTION

Articulated specimens of palaeoniscoids are rare in the Devonian of Australia. The only well-preserved lacustrine specimens are from the Frasnian, Mount Howitt locality in central Victoria (Long 1988). Articulated specimens representing only two marine species, *Moythomasia durgaringa* Gardiner and Bartram, 1977 and *Mimia toombsi* Gardiner and Bartram, 1977, are known from the Frasnian Gogo Formation. To date, the Gogo Formation is the only marine deposit where articulated palaeoniscoids are found in the world. However, isolated scales are far more common, occurring in both marine and freshwater facies.

This paper describes the scales of an articulated Devonian palaeoniscoid, *Mimia toombsi* from the Gogo Formation, in accordance with the terminology of Esin (1990). After describing the squamation of *M. toombsi* and, using earlier descriptions of the squamation of *Moythomasia durgaringa* (Trinajstic in press), the reliable identification and taxonomic study of isolated palaeoniscoid scales from the Gneudna Formation, Western Australia (Figure 1) is shown to be possible.

MATERIALS AND METHODS

The usefulness of palaeoniscoid scales in biocorrelation has so far been limited. This has primarily been the result of difficulties in identifying taxa from isolated scales. To overcome this difficulty Esin (1990) described a pattern of squamation based on nine distinct morphological areas (Figure 2), providing a uniform reference for the identification of isolated scales. Esin's method was successfully used by Burrow (1994) to attribute scales of various forms from *Ligulalepis toombsi* Schultze, 1968 to particular body areas, and by Trinajstic (1997) to refer isolated scales from the Gneudna formation to *M. durgaringa*.

The study is based on complete specimens of *Mimia toombsi* and *Moythomasia durgaringa* from the Gogo Formation, Western Australia, and isolated scales of both species from the Gneudna Formation, Williambury Station, Western Australia. Scales described in this paper come from the residue of limestone samples treated with 10% acetic acid as per Rixon (1979). The scanning electron micrographs were made on a Philips 505 at the Centre for Microscopy and Microanalysis, University of Western Australia. Specimens have been deposited in the collections of the Western Australian Museum, Perth (WAM).

SYSTEMATIC PALAEONTOLOGY

Family Mimiidae Gardiner, 1993

Genus *Mimia* Gardiner and Bartram, 1977

Species *Mimia toombsi* Gardiner and Bartram, 1977

Figure 3

Material Examined

Holotype

WAM 70.4.245. Incomplete specimen consisting of

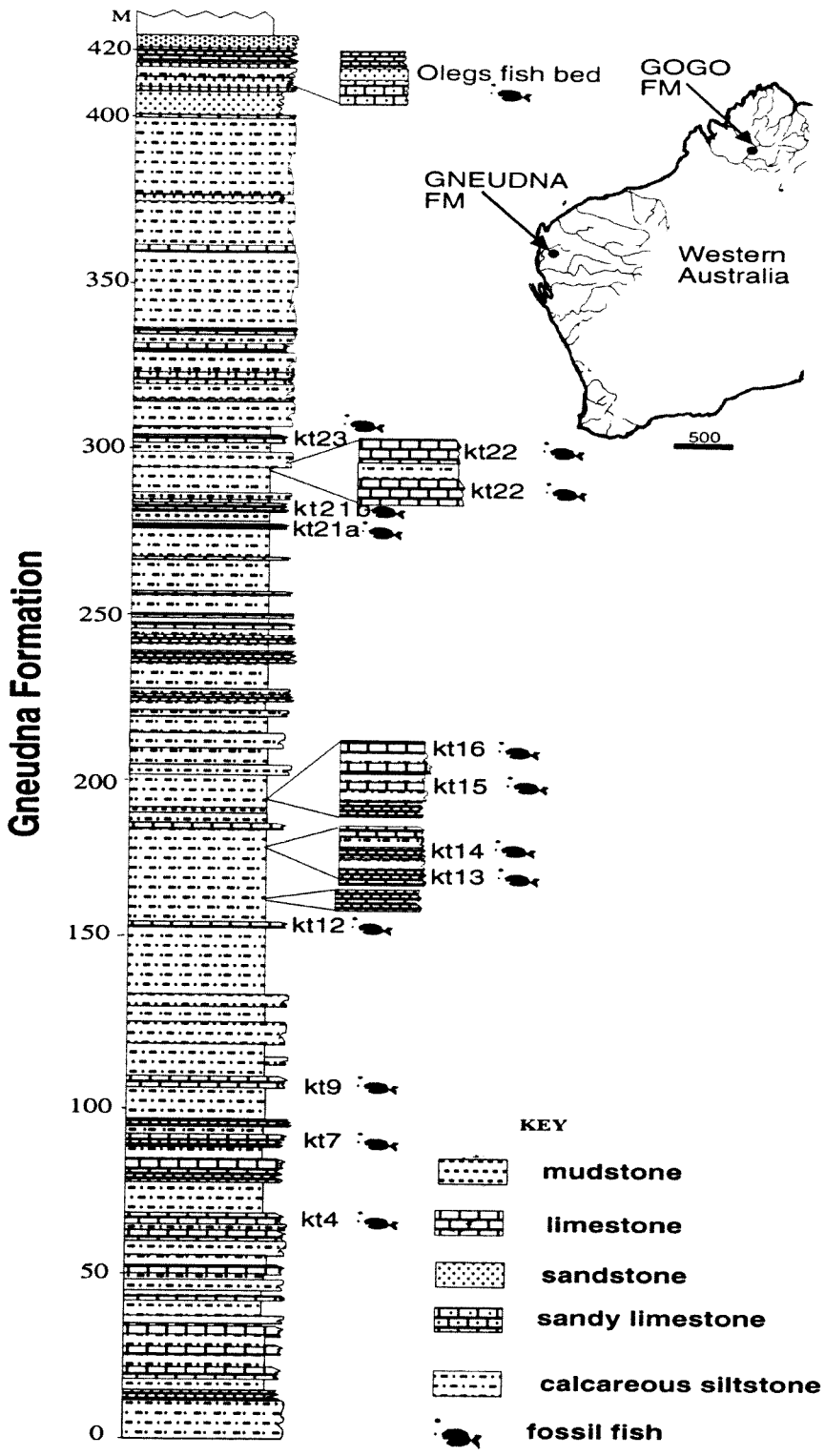

Figure 1 Gneudna Formation stratigraphic diagram and locality map.

a head and body in part and counterpart from the Frasnian, Gogo Formation, Gogo Station, Canning Basin, Western Australia.

Other Material

WAM 97.4.245. Complete specimen which has been fully prepared by acid digestion.

Diagnosis

The diagnosis remains unchanged from that given by Gardiner and Bartram (1977).

Description of the Squamation

In describing the squamation of *M. toombsi* WAM 70.4.245, the lateral surface of the specimen's body

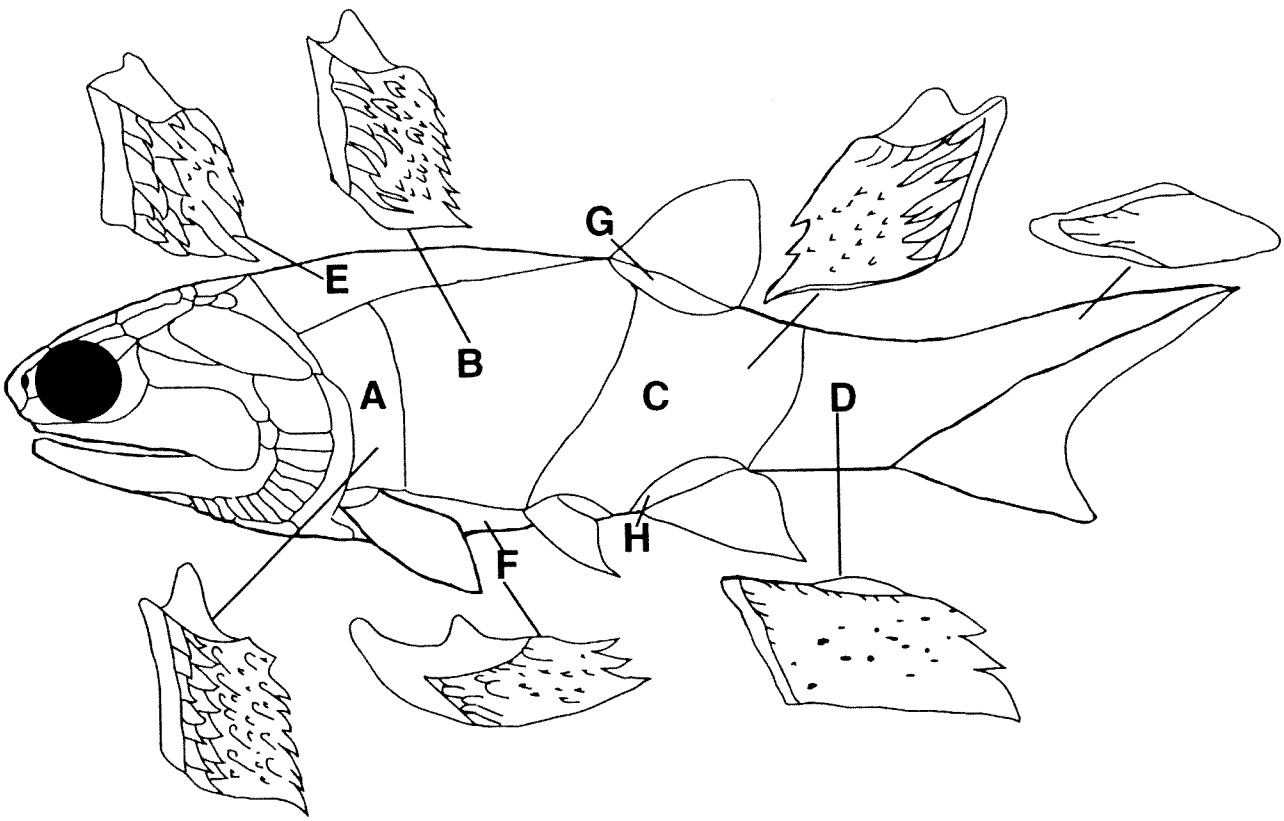

Figure 2 Diagrammatic outline of a fusiform palaeoniscoid fish, showing distribution of major areas with morphologically distinct scale types (after Esin 1990).

was divided into the nine areas designated by Esin (1990) (Figure 2). The ridge scales are described separately.

Area A

Scales in area A are rectangular, with the height to length ratio (h/l ratio) exceeding 3:1. The anterior margin is straight with the rostro-dorsal process high and directed vertically upward. The ventral margin has a 30° slope. The peg is high with a rounded apex and the peg base is 1/5 the width of the scale. Growth increments are present on the peg (Figure 3B; Gardiner 1984, plate 2c). The keel is well-developed and the socket is deep and long. The depressed field is 3/8 the length of the scale. There is an opening for the lateral line canal at the junction of the free field and depressed field on the anterior dorsal margin of the scale.

The anterior margin of the free field consists of posterior anastomosing narrow ridges of ganoine which terminate in up to 10 denticles that overhang the posterior margin (Figure 3A). The ridges slope in a dorsal to ventral-caudal direction at approximately 45°. The ganoine ridges are ornamented with raised striae and have finer striations along the dorsal and ventral margins of the ridges. The striae are more clearly defined in the anterior dorsal area of the free field. There is a decrease in the depth and ornament of scales, and in the number of terminal denticles from area A to area B, and from the median line of area A to the dorsal and ventral margins. Thus the scales closest to areas B and F (Gardiner 1984, plate 2b) are smoother with fewer serrations (4–6) than those scales located in the central region of area A (Figure 3A).

Area B

Scales in area B are rectangular to almost square in shape with the h/l ratio varying between 2:1 for midline anterior scales (Figure 3C) and 1.2:1 for scales nearer to area C and to the dorsal and ventral margins. The keel, peg and socket are well developed and growth lines are evident on the peg. The free field makes up 2/3 of the scale body and the depressed field 1/3. The ornament consists of primarily separated ganoine ridges that terminate in acutely pointed denticles beyond the body of the scale. The ventral three ganoine ridges anastomose posteriorly to form a single terminal point (Figure 3C). As with the area A scales, the main ridges are ornamented with fine central striae and slope in a dorsal to ventral-caudal direction at approximately 45°.

Area C

Scales in area C are twice as long as high (h/l ratio 1:2). The rostro-dorsal process is high with an

acute apex. The anterior margin is straight, the ventral margin is gently convex. The peg and socket are weakly developed in scales close to area B and further reduced in scales close to area D. Where the peg is present it has a wide base, extending across the dorsal margin of the free field (Figure 3D). The keel is well developed in all scales from area C.

The free field ornament remains similar to area B scales, the main difference being a reduction of the number of ridges. Area C scales have two or three ridges. The figured scale (Figure 3D) has three ridges, the dorsal and ventral ridges extending beyond the body of the scale whereas the central ridge fuses with the ventral ridge in the posterior third of the scale. The depressed field is 1/5 the length of the scale.

As with scales in areas A and B there is a decrease in the number of ridges and denticles, ornament, and peg and socket development from area C to more caudal areas and towards the dorsal and ventral margins.

Area D

Scales in area D are rhombic in form (Figure 3E) and become more elongate (Figure 3F) towards the caudal fin. The ridges are reduced to two in scales near area C (Figure 3E) and one in scales close to the caudal fin (Figure 3F). The ridges terminate in acute denticles that extend beyond the body of the scale. The ornament on the ridges remains the same as on scales in other areas, but the ridges do not anastomose. These scales have very poorly-defined pegs, sockets and keels.

The pegs in scales closest to area C are rounded and do not extend above the anterior dorsal margin of the scale. The pegs are located in the posterior halves of the scales whereas in other body areas the pegs are located in the anterior portions of the scales, at the junction of the free field and depressed field. In scales located close to area C (Figure 3E) the depressed field is narrow, but scales closer to the caudal fin (Figure 3F) have a large depressed field that extends along the dorsal and ventral margins of the scale.

Area E

The scales in area E have a h/l ratio of 2:1 with a wide depressed field (Figure 3J). The free field ornament consists of posteriorly anastomosing ridges that terminate in two to three acute points which do not extend beyond the body of the scale. Anteriorly, the sculpture of the scale surface consists of small triangular crests overlapping each other. The rostro-dorsal process is high, approximately the same height as the scale body. There is a well-developed keel, peg and socket. The peg approximates the size of the free field, being almost as high as the rostro-dorsal process and extending the length of the free field.

Area F

Scales in area F are elongated; their h/l ratio ranging from 1:2 to 1:3. The peg is low and extends along the dorsal margin of the scale with the corresponding socket being shallow (Figure 3H–I). The keel is reduced. The rostro-dorsal process is, however, high with a rounded apex in scales closest to the fin margins (Figure 3I) and high with an acutely pointed apex in scales closer to areas B and C (Figure 3H). The anterior, dorsal and ventral margins of the ridged ornament are dissected by thin, shallow furrows running slightly downward in the direction of the rear corner of the scale. Posteriorly the ridges anastomose and overlap. The posterior margin of the free field has one to three denticles which extend beyond the body of the scale.

Areas G and H

The scales in areas G and H are almond-shaped. The h/l ratio is 2:5. The free field is slightly raised above the depressed field. Scales from area G (Figure 3K) have an ornament of separate ridges with fine striae on the dorsal and ventral margins of each ridge. Scales from area H (Figure 3L) possess four small ridges anteriorly, which divide and anastomose towards the middle of the scale, forming a smooth surface along the caudal margin. The margins where the free field meets the depressed field have fine serrations similar to the serrations on the other scales described above. No peg or socket is visible in either scale type, but there is a small anterior notch.

Ridge scales

The ridge scales are bilaterally symmetrical about the midline (Figure 3G). Anteriorly there is a large depressed field, occupying approximately half the scale body. The free field is slightly raised above the depressed field and has an ornament of parallel ridges. The outer ridges have an ornament of five shallow furrows. The ridge scales decrease in width caudally. Striae are present on the anterior scales but absent from the caudal scales.

DISCUSSION

The scale types described for *M. toombsi* (WAM 70.4.245 and WAM 97.4.345) conform to the specific body areas designated by Esin (1990). The variation in scale morphology is consistent with that described for other palaeoniscoids (Long 1988; Esin 1990; Burrow 1994; Trinajstic in press). Esin (1990) stated that there are certain characteristics of scale morphology that remain consistent on

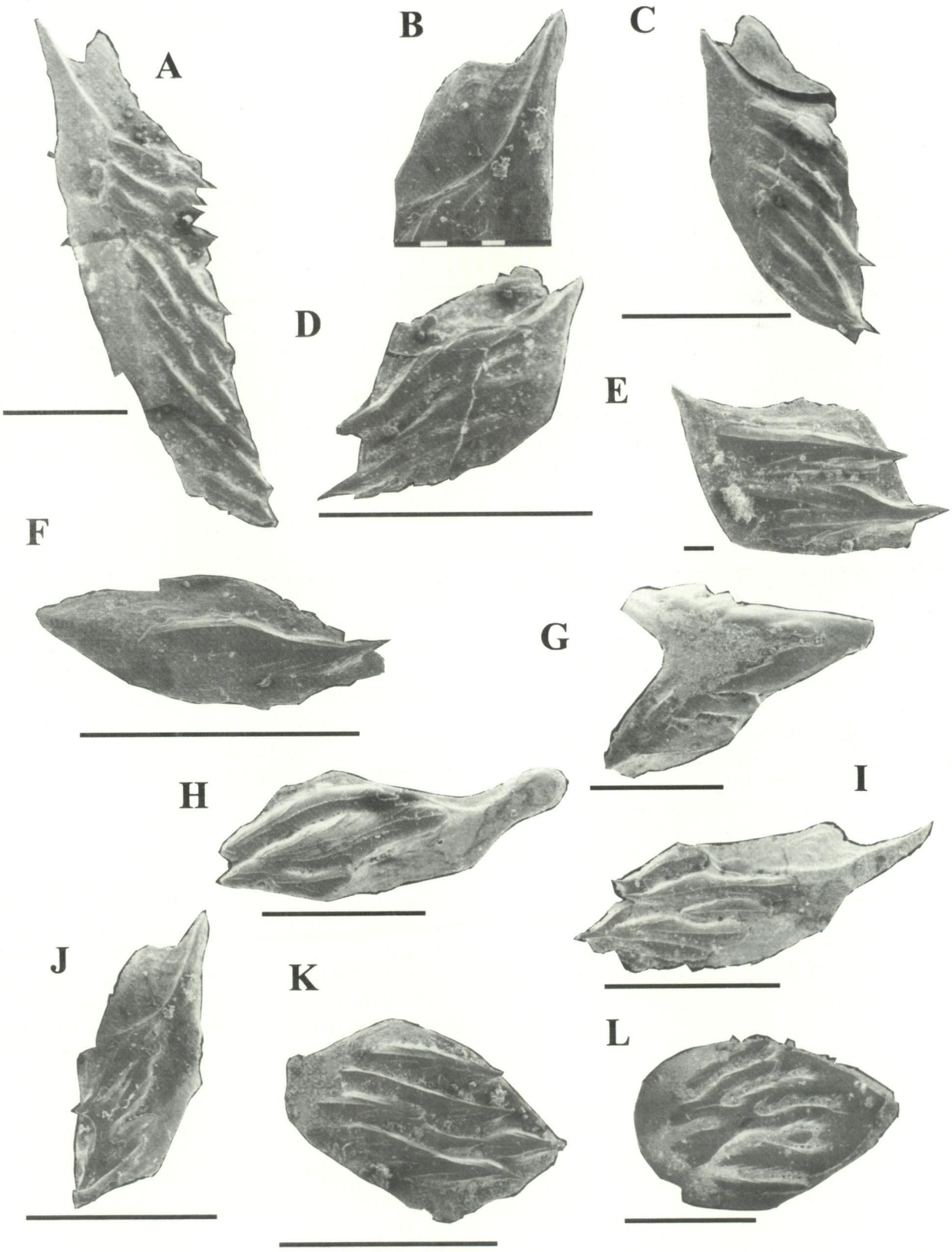

Figure 3 Scales prepared from the articulated specimen of *Mimia toombsi* WAM 97.4.245 from the Gogo Formation. Scale bars for all figures except B and E = 1.0 mm; scale bars for B and E = 0.1 mm. A, scale from anterior region of area A; B, peg on scale from an area A scale, showing growth increments; C, scale from anterior region of area B; D, scale from caudal region of area C; E, scale from central region of area D; F, scale from caudal region of area D; G, ridge scale; H, scale located close to the fin insertion point in area F; I, scale from area F; J, scale from area E; K, scale from area G; L, scale from area H.

scales from different parts of the fish body. In *M. toombsi* the features that remain constant are: the separation of the ganoine ridges in the anterior portion of the scale; the ornament on the ganoine ridges and the extension of the terminal denticles beyond the main body of the scale and, where present, a very wide-based peg. All other morphological features present on the squamation show consistent variation in relation to the position of the scale.

This study, along with similar work done by Gross (1953), Schultze (1968), Jessen (1972), Esin (1990, 1995), Burrow (1994) and Trinajstic (1997) has shown that it is possible to identify isolated scales from Devonian palaeoniscoids to species using the morphological areas designated by Esin (1990). The availability of complete specimens of *M. toombsi* has enabled the comparative study of scales in relation to their position on the body. It is now possible to determine the taxonomic significance of isolated scales from the Gneudna Formation.

DESCRIPTION AND DISCUSSION OF *MIMIA TOOMBSI* SCALES FROM THE GNEUDNA FORMATION

Seven types of scales from the Frasnian Gneudna Formation are attributed to *M. toombsi* (Figure 4). Not all scales types known to be present on *M. toombsi* have been recovered from the Gneudna Formation. Both the extremely fragile nature of *M. toombsi* scales and a disproportionate number of scales on the different body areas have probably biassed the proportions of the different types preserved.

As the morphology of scales has been shown to vary in a consistent manner within *M. toombsi*, it is now possible to assign the isolated scales recovered from the Gneudna Formation to specific areas of the body, based on the criteria of Esin (1990) and Burrow (1994). Descriptive terminology (Figure 2) follows Esin (1990) and Burrow (1994).

Type 1

Material Examined

8 complete scales (WAM 97.11.2; Figure 4A).

Horizons

kt14 and kt21A (Figure 1).

Description

These rectangular scales have a h/l ratio of 2:1. The ornament consists of raised ganoine ridges with fine striations along the dorsal and ventral margins of each ridge. The terminal denticles are not preserved, but the point where they extended beyond the main body of the scale can be determined (Figure 4A). The free field makes up 3/4 of the scale body. The rostro-dorsal process is strongly developed. The peg is broken, but there is a strongly developed keel and socket. The anterior margin of the scale lies at a 30° angle to the long axis of the fish. The ventral margin is gently curved.

Remarks

Scales of type 1 are determined as coming from the central region of area B. They are highly articulated with well-developed interlocking devices suggesting that they originate from a fairly inflexible part of the fish's body. The figured scale (Figure 4A) closely resembles scales (Figure 3C) determined as being from area B in the articulated specimen (WAM 70.4.245) of *M. toombsi*. Scales from area B of *M. toombsi* differ from *M. durgaringa* scales from the same area in having separated ganoine ridges that extend the length of the free field (Figures 3C, 4A), whereas *M. durgaringa* scales (Figure 5D) have no visible ridges, and an ornament of small triangular crests overlapping each other.

Type 2

Material Examined

5 complete scales (WAM 97.11.3, WAM 97.11.4; Figure 4B–C).

Horizons

kt9, kt14 and kt21A (Figure 1).

Description

These scales are longer than high, having a h/l ratio of 2:3. The anterior margin is straight and the ventral margin is gently convex. The peg and socket are moderately developed, but the keel remains strongly developed. The peg extends along the dorsal margin of the free field. In scale WAM 97.11.3 (Figure 4B) the peg is raised above the small, rounded rostro-dorsal process; however, in scale WAM 97.11.4 (Figure 4C) the peg and rostro-dorsal process are not preserved. The free field has four ganoine ridges, each of which has a central crest and fine striae along the dorsal and ventral margins. The ganoine ridges terminate in sharp points which extend off the main body of the scale.

Remarks

Because of the moderately-developed peg and socket, and the strongly-developed keel, scales of type 2 are attributed to area C. This area is considered to be moderately flexible in articulated palaeoniscoids (Burrow 1994). The shape and ornament of the figured scales (Figure

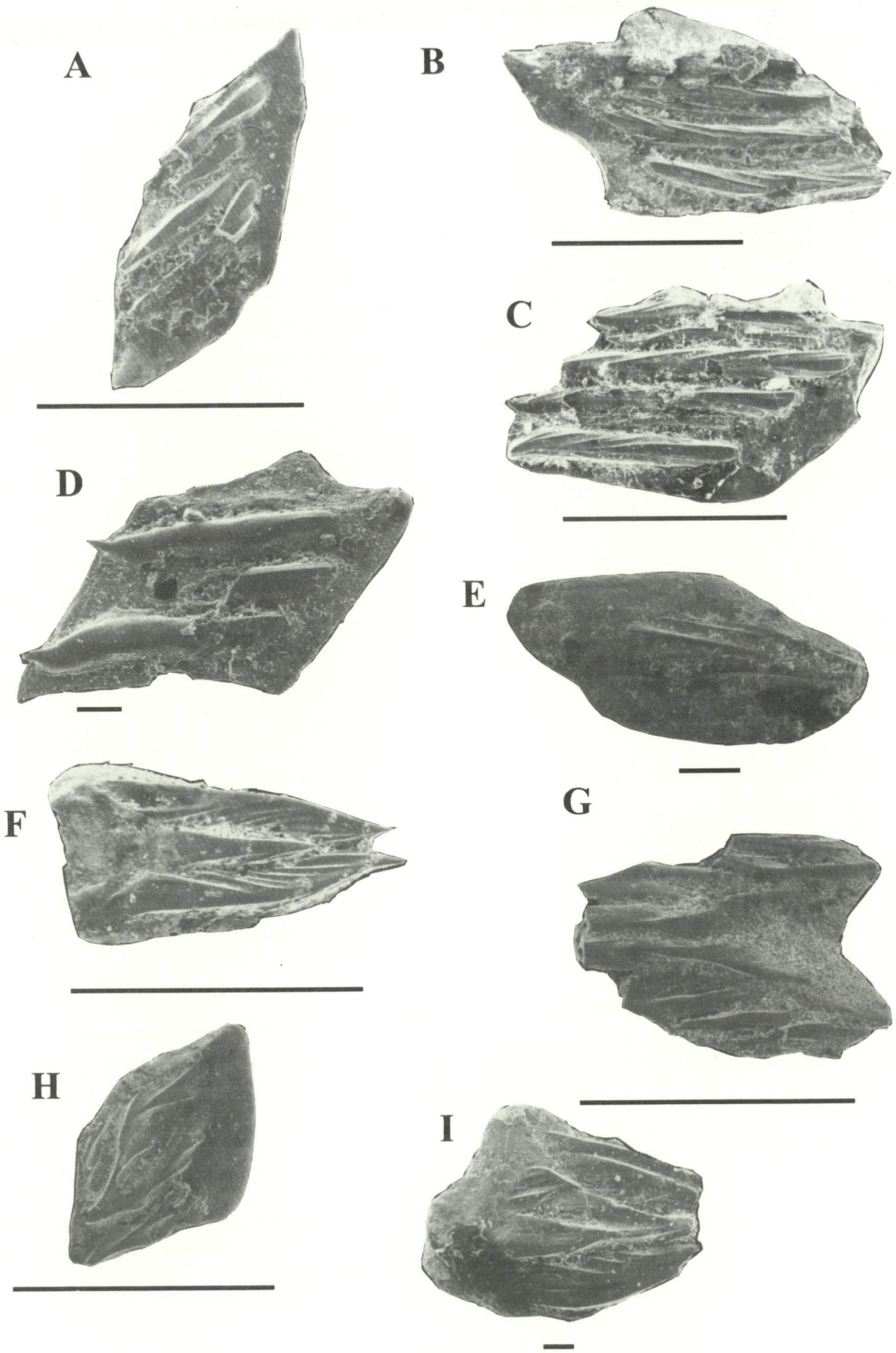

Figure 4 Isolated scales of *Mimia toombsi* from the Gneudna Formation. Scale bars for all figures except D, E and I = 1.0 mm; scale bars for D, E and I = 0.1 mm. A, scale from area B, WAM 97.11.2; B, scale from the central region of area C, WAM 97.11.3; C, incomplete scale from the central region of area C, WAM 97.11.4; D, scale from the central region of area D, WAM 97.11.5; E, scale from the caudal region of area D, WAM 97.11.6; F, caudal ridge scale, WAM 97.11.7; G, anterior ridge scale, WAM 97.11.8; H, scale from area E, WAM 97.11.9; I, scale from area G, WAM 97.11.10.

4B–C) suggest that they came from the lower part of the fish's body close to area D. The ridge ornament closely resembles that present on area D scales (Figure 3E) from the articulated specimen of *M. toombsi*. Scales from the same region in *M. durgaringa* have a smooth ganoine surface on the free field (Trinajstic in press, figure 3E).

Type 3

Material Examined
10 incomplete scales (WAM 97.11.5; Figure 4D).

Horizons
kt13, kt14, kt15 and kt21A (Figure 1).

Description
The scales are almost square in shape with a h/l ratio of 1.5:2. The peg is small, although wide-based, and the socket and keel, when present, are weakly developed. The ornament on the scale consists of ganoine ridges that do not anastomose but terminate in sharp points that extend beyond the main body of the scale. The depressed field is narrow and the free field makes up 4/5 of the scale.

Remarks
Refer to Remarks under scale type 4.

Type 4

Material Examined
1 complete scale (WAM 97.11.6; Figure 4E).

Horizon
kt14 (Figure 1).

Description
The scale is narrow and elongated with a h/l ratio of 2:5. There is no peg, keel or socket developed. There is, however, a narrow depressed field along the anterior and dorsal margins. The free field is ornamented with two ridges that anastomose to form a single posterior point which extends beyond the main body of the scale.

Remarks
Scales in area D are non-imbricating; therefore, when present, the peg, keel and socket are weakly developed. For these reasons scales of types 3 and 4 have been assigned to area D. Scales of type 3 (Figure 4D) occur near area C (Figure 2) and show evidence of a peg and socket. The interlocking devices permit greater articulation between scales than would be present on type 4 scales (Figure 4E), which are interpreted as occurring closer to the caudal fin. The lack of articulation between these scales permitted greater flexibility (Burrow 1994). These scales differ from *M. durgaringa* scales from the same region in having an ornament of ridges on the free field. The free fields of *M. durgaringa* scales from area D are almost smooth with only shallow striae occurring on the anterior and dorsal margins (Figure 5J).

Type 5

Material Examined
1 complete scale and 1 incomplete scale (WAM 97.11.7, WAM 97.11.8; Figure 4F–G).

Horizon
kt14 (Figure 1).

Description
These scales are approximately triangular in shape, with a concave indentation in the anterior face. Anteriorly there is a wide depressed field which extends into the central region of both scales. The ornament consists of numerous separate ganoine ridges with shallow furrowing on the outer edges of the ridges. The furrows are deeper and closer together in WAM 97.11.7 (Figure 4F). There is a single central ridge that does not extend the whole length of the scale body and two marginal ridges which extend off the scale body (Figure 4F). The ornament is more extensive in WAM 97.11.8 (Figure 4G) consisting of four central ridges, the two anterior ridges overlapping two posterior ridges. The posterior region of both scales is raised above the anterior region.

Remarks
These scales are interpreted as being dorsal ridge scales. The large anterior depressed field acts as the overlap area for the scale in front. The larger and wider scale WAM 97.11.8 (Figure 4G) is an anterior dorsal ridge scale while the smaller narrower scale WAM 97.11.7 (Figure 4F) is a posterior dorsal ridge scale. Gardiner (1984) noted that the ridge scales in *M. toombsi* were median structures and were found along the dorsal margin and between the anal fin and tip of the tail along the ventral margin.

Type 6

Material Examined
2 complete scales (WAM 97.11.9; Figure 4H).

Horizon
kt21A (Figure 1).

Description

These scales have a h/l ratio approaching 1:1. The peg is not preserved and the rostro-dorsal process is rounded. There is a poorly-developed keel. The free field ornament consists of three well-spaced ridges. The dorsal and central ridges anastomose in the posterior third of the scale. All three ridges have an ornament of deep striae and are oriented in a ventro-caudal direction.

Remarks

Type 6 scales are from area E. They are comparable to scales from area E of the articulated specimen of *M. toombsi* (Figure 3J). These scales differ from area E scales from *M. durgaringa* in having an ornament of ridges instead of numerous small overlapping triangular crests (Gardiner 1984, plate 3d).

Type 7

Material Examined

1 complete scale (WAM 97.11.10; Figure 4I).

Horizon

kt21A (Figure 1).

Description

The scale is ovoid with a low dorsal notch. The depressed field is wide, approximately 1/3 of the scale, and the free field is raised above the depressed field. The ornament consists of four ridges with striae on the dorsal and ventral margins of each ridge. The two central ridges are raised above the two lateral ridges and anastomose to form a single posterior terminal projection.

Remarks

This scale is from area G and is comparable to area G scales from the articulated *M. toombsi* (Figure 3K). The large depressed field of area G scales allows articulation with the dorsal ridge scales.

Histology

The histology of the scales of *Mimia toombsi* was described by Gardiner (1984, figures 141, 144). Several scales attributed to *M. toombsi* from the Gneudna Formation were thin-sectioned. They show the characteristic large cell spaces lacking dentine tubules. The bony bases are reduced and contain horizontal cell spaces, canals of Williamson and spaces for Sharpey's fibres. Richter and Smith (1995) reported the presence of very fine dentine tubules around large pulp cavities, but these were not found in the thin sections of the Gneudna material.

DESCRIPTION AND DISCUSSION OF ONTOGENTICALLY YOUNG SCALES FROM *MOYTHOMASIA DURGARINGA*

Family Stegotrachelidae Gardiner, 1963

Genus *Moythomasia* Gross, 1950

[= *Aldingeria* Gross, 1942: 431]

Species *Moythomasia durgaringa* Gardiner and Bartram, 1977

Figure 5

Type Species

Moythomasia durgaringa Gardiner and Bartram, 1977, Early Frasnian of Western Australia.

The adult morphology and pattern of squamation in *M. durgaringa* were described by Trinajstic (in press). Since that description was accepted for publication, additional material has been recovered from the type section of the Gneudna Formation that represents ontogenetically younger scales (*sensu* Esin 1995). These are described here.

Type 8

Material Examined

6 complete scales (WAM 97.11.11, WAM 97.11.12; Figure 5B–C).

Horizons

kt14 and kt21A (Figure 1).

Description

The scales are small, 1 mm in length, and higher than long with a h/l ratio of 2:1. The ornament consists of well-separated ganoine ridges that do not anastomose. The triangular ornament of the ridges in the anterior portion of the scale appears to overlap the posterior portion of the same ridge. The peg and socket are not developed in WAM 97.11.12 (Figure 5C) but are moderately developed in WAM 97.11.11 (Figure 5B). The rostro-dorsal process is rounded and does not extend significantly above the dorsal scale margin. The depressed field is large, accounting for 1/3 of the width of the scale (Figure 5B). The anterior margins of the scales are straight and the ventral margins gently curved.

Remarks

These scales show the basic shape of adult scales from area A (Figure 5A), being higher than long, but they retain the ontogenetically young characteristics of a small size (adult scales are 2–2.5 mm in width), separation of the ganoine ridges and absence (Figure 5C) or under-development (Figure 5B) of the articular elements. According to Esin

(1995), the peg, keel and socket are usually present at the subadult stage and so WAM 97.11.11 (Figure 5B) is interpreted as being at that stage of development. As the articular elements are absent from WAM 97.11.12 (Figure 5C), this scale is interpreted as being in the transitional stage from juvenile to subadult.

Type 9

Material Examined
10 complete scales (WAM 97.11.13; Figure 5F).

Horizons
kt4, kt7, kt13, kt14, kt15 and kt21A (Figure 1).

Description
These scales are rhomboid, being only slightly higher than long. The ornament consists of separate ganoine ridges, the anterior dorsal ridges extending only to the central region of the scale. The rostro-dorsal process is poorly developed as are the peg, socket and keel. The anterior depressed field is small, approximately 1/4 of the scale body. The posterior margin of the scale terminates in more than three denticles, the exact number cannot be ascertained as the denticles are broken.

Remarks
This scale type is interpreted as being a subadult scale from area B, probably located towards the central posterior region of area B. The lack of development of the articular process suggests that this scale (Figure 5F) had just entered the subadult stage of development. The separation of the ganoine ridges also indicates an early developmental stage, as adult scales from area B are smoother (Figure 5D).

Type 10

Material Examined
13 complete scales (WAM 97.11.14; Figure 5E).

Horizons
kt4, kt7, kt13, kt14, kt15 and kt21A (Figure 1).

Description
These scales are longer than high and have adult proportions. The pegs, sockets and rostro-dorsal processes are all well developed. The ganoine surface consists of anastomosed ridges in the anterior and dorsal regions of the scales, but in the posterior-ventral region of the scale separate ridges are visible. The anterior margins are straight and the ventral margins are concave. There are five terminal denticles.

Remarks
These scales are from area B and are considered to be in the transitional stage of development, from subadult to adult. The articular processes have all reached adult dimensions and the ornament is approaching that seen in the adult scale from area B (Figure 5D).

Type 11

Material Examined
1 complete scale (WAM 97.11.15; Figure 5L).

Horizon
kt14 (Figure 1).

Description
The scale is elongated, being longer than high. The ornament consists of closely separated ganoine ridges. The ridges are dissected by thin furrows anteriorly and dorsally. The triangular peg is moderately developed, as is the keel and socket. The rostro-dorsal process is anterodorsally directed. The anterior depressed field is narrow. The scale ornament terminates in a series of sharply pointed denticles.

Remarks
This subadult scale type is interpreted as being from the central region of area C. The peg retains a triangular shape rather than the more rounded condition seen in adult scales from area C, and the rostro-dorsal process has not developed the height characteristic of adult scales. It is not until the subadult stage that there is development of the rostro-dorsal process (Esin 1995). Gardiner (1984, plate 3a) figured a similar scale which he identified as a mid flank scale from *M. durgaringa*.

Type 12

Material Examined
15 complete scales (WAM 97.11.16; Figure 5G).

Horizons
kt4, kt7, kt13, kt14, kt15 and kt21A (Figure 1).

Description
These rectangular scales are longer than high. The ornament is almost smooth, with only two depressions indicating the position of underlying ridges. The anterior and dorsal margins of the free field are dissected by fine, shallow furrows. There are well-defined pore canals in the central region of the scales. The peg is small and rounded, and the keel and socket poorly developed in these scales. The rostro-dorsal process is moderately developed, extending dorsally to the level of the peg.

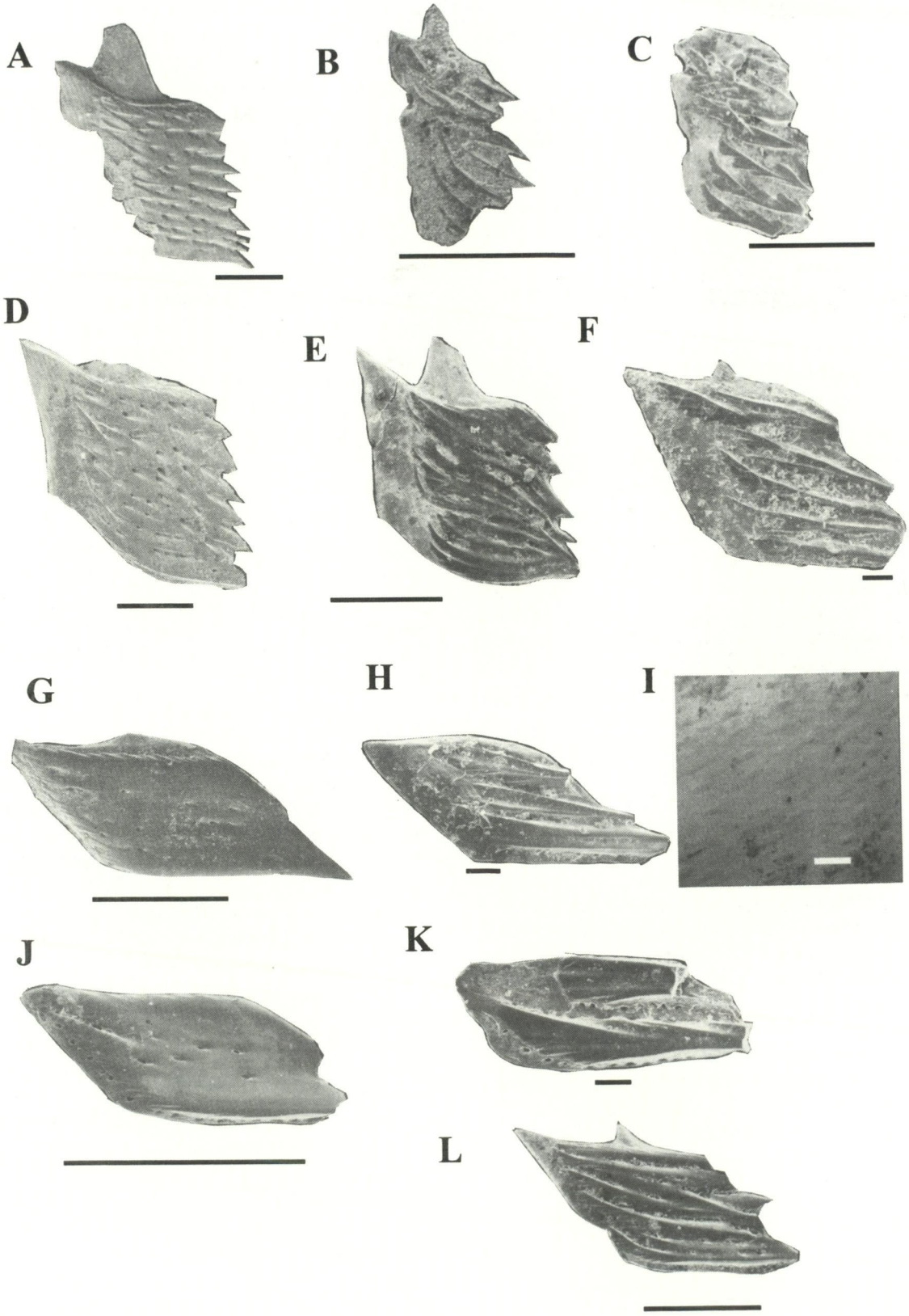

Figure 5 *Moythomasia durgaringa* scales from the Gogo and Gneudna Formations. Scale bars for figures A, B, D, E, G, J, L = 1.0 mm; scale bars for figures C, F, H, K = 0.1 mm; scale bar for figure I = 0.001 mm. A, adult scale from the central region of area A on articulated specimen WAM 97.1.1; B, subadult scale from area A, WAM 97.11.11; C, juvenile scale fom area A, WAM 97.11.12; D, adult scale from area B on articulated specimen WAM 97.1.1; E, transistional scale from area B, WAM 97.11.13; F, subadult scale from area B, WAM 97.11.14; G, transitional scale from the posterior region of area C, WAM 97.11.16; H, subadult scale from the posterior region of area C, WAM 97.11.17; I, microsculpture of elliptical tubercles on the ganoine surface of a scale from area C, WAM 97.11.17; J, adult scale from area D, WAM 97.1.7; K, subadult scale from area D, WAM 97.11.18; L, subadult scale from the central region of area C, WAM 97.11.15.

Remarks

These scales originate from the ventral region of area C. The level of development of the articular process and smoothing of the ornament are characteristic of scales in the transitional period between the subadult and adult stages of ontogeny.

Type 13

Material Examined

4 complete scales (WAM 97.11.17; Figure 5H–I).

Horizons

kt14 and kt21A (Figure 1).

Description

The scales are slightly longer than high, having a h/l ratio of 1.5:2 (Figure 5H). The depressed field is relatively wide, approximately 1/3 the width of the scale. The ornament consists of three, well-separated ganoine ridges. The dorsal and central ridges originate towards the centre of the scale whereas the ventral ridge originates further towards the anterior margin. Posteriorly the central and ventral ridges touch. The anterior and central ridges have an ornament of fine, deep furrows. There is a micro-ornament of elliptical tubercles on the ganoine ridges (Figure 5I). The anterior margin is sloped and the ventral margin is straight. There is no development of the peg or socket, but the keel is present.

Remarks

These scales come from the caudal part of area C, close to area D. The elongated tubercles on the ganoine surface are both characteristic of juvenile and subadult scales. The presence of elongated tubules on the entire surface of the free field is evidence for a juvenile stage (Esin 1995). Esin (1995) also noted that scales in areas of more intensive growth retain the tubular microsculpture into the subadult stage. In adult scales the microsculpture is absent or consists of rounded tubercles (Esin 1995, figure 1G).

Type 14

Material Examined

6 complete scales (WAM 97.11.18; Figure 5K).

Horizons

kt14 and kt21A (Figure 1).

Description

The scales are elongate, having a h/l ratio of 1:3. The depressed field is large, occupying approximately 1/3 of the scale area. The free field is ornamented with two well-separated ganoine ridges. The ridges have deep furrowing along the anterior, dorsal and ventral margins. There is no development of the rostro-dorsal process or of the peg, keel or socket. There are well-defined pore canals between the two ridges and along the anterior and ventral scale margins.

Remarks

These scales are interpreted as being at the subadult level of development from area D of the fish. The subadult scales differ from adult area D scales (Figure 5J) of *M. durgaringa* in having an ornament of separated ridges instead of having a smooth ganoine crown. All the scales have well-defined pore canals and furrowing around the free field margins indicating that they are of the same form.

DISCUSSION

Esin (1995) recognized three developmental stages in the growth of palaeoniscoid scales. These are juvenile, subadult and adult, with a transitional period occurring between each of the stages. The Gneudna scales can be identified as juvenile (Figure 5C, K) or subadult (Figure 5B, F, H, L) by the weak development of the peg and socket articulation, elongated shape of the tubercles and marked boundaries between the ganoine ridges. Transitional scales are also recognized (Figure 5E, G).

These scales can be confidently attributed to *M. durgaringa* on two counts. Firstly, according to Esin (1995) family level taxonomic characteristics are present by the end of the juvenile stage of development, permitting the identification of juvenile scales to this level. Species level taxonomic characteristics develop toward the end of the subadult stage (Esin 1995), and so are recognized in the scales described above. The isolated scales from the Gneudna Formation show a gradation from one stage to the next and so each stage of development plus transitional stages have been identified (Figure 5A–L). Secondly, comparison with scales illustrated by Gardiner (1984 plate 3a, c, g) supports the identification of these scales as *M. durgaringa*.

It can be seen that not only is there considerable variation in the squamation between different body regions of palaeoniscoids (Gross 1953; Schultze 1968; Jessen 1972; Esin 1990; Burrow 1994; and Trinajstic 1997) but that there are also significant ontogenetic differences (Schultze and Bardack 1987; Esin 1990). Therefore, the ontogenetic development of scales needs to be considered carefully before erecting new species.

A more active mode of life is suggested for juvenile individuals of *M. durgaringa* by the absence of articulation devices (Burrow 1994). Juvenile fishes

possibly occupied a very different ecological niche than adult members of the species, a situation that is common amongst modern teleosts.

BIOSTRATIGRAPHIC INTERPRETATION

The occurrence of *M. toombsi* in the Gneudna Formation is significant because two dipnoan taxa, three placoderm taxa and two palaeoniscoid taxa are now recorded from both the Gneudna Formation and the Gogo Formation. The dipnoan genera, *Chirodipterus* and *Adololopas*, as well as the placoderm genera *Bothriolepis*, *Groenlandaspis* and *Holonema*, are found in the top of the Gneudna type section which lies in the *asymmetricus* Conodont Zone and has been dated as lower Frasnian. The genus *Holonema* is represented in both the Gneudna Formation and the Gogo Formation by the species *Holonema westolli* Miles, 1971. The palaeoniscoid species present in both the Gneudna and Gogo Formations are *M. durgaringa* (Trinajstic 1997) and *M. toombsi*, both species occurring throughout the section along with the thelodont *Australolepis seddoni* Turner and Dring, 1981. In addition *A.* sp. cf. *A. seddoni* has been found in the lower Frasnian of Iran (Turner 1997). This further supports the suggestion of Turner and Dring (1981) that the Gneudna Formation is lower Frasnian.

Before the full biostratigraphic potential for palaeoniscoids can be realized, type specimens and other described articulated specimens need to be re-examined. In addition, isolated scales that have already been recovered need to be reanalysed using Esin's methods.

CONCLUSION

At least two species of palaeoniscoid are recognized in the Gneudna Formation. These are *Moythomasia durgaringa* and *Mimia toombsi*. Even when only isolated scales are preserved these species are distinguishable by different ornamentation of the ganoine surface, different formation of the peg and socket and different histological features. Isolated juvenile scales can also be distinguished from adult scales on the basis of shape, ornamentation and tubercle shape on the ganoine surface. It can therefore be concluded that both juvenile and adult individuals inhabited the same geographic area.

The presence of these palaeoniscoids in the Gneudna Formation, along with other fishes, supports a Frasnian age for the Gneudna Formation.

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