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Acanthodian microremains from the Frasnian Gneudna Formation, Western Australia

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Abstract – The scale variation seen in articulated acanthodian specimens (*Diplacanthus horridus* and *Rhadinacanthus longispinus*) from the Natural History Museum, London is illustrated to determine whether particular body regions on acanthodians display distinctive scale morphologies. This study has shown that, in the specimens observed, the head, shoulder girdle, lateral line, anterior flank, posterior flank, tail and fin spine insertion points are all characterized by different scale types. Isolated acanthodian scales found in residues from the Gneudna Formation, Western Australia, are assigned to different body regions. Scales determined as coming from the same body region were compared, and from these comparisons two species, Acanthodidae gen. *et* sp. indet. and *Cheiracanthus* sp., have been recognized.

The ratio of acanthodian scales to thelodont scales in different stratigraphic levels in the type section was compared to determine if these ratios are a reliable guide to the depositional environment. A traditional environmental interpretation of the microvertebrate ratios is not supported by lithological evidence or conodont abundance. It is concluded that the differences in this ratio do not add significant information for the interpretation on the depositional environment of the Gneudna Formation.

INTRODUCTION

The Acanthodii is a major group of Palaeozoic fishes that occurs on all continents. They occur in rocks ranging from Lower Silurian to Permian age (Denison, 1979). Often acanthodians are known only from disarticulated material, with their scales and fin spines commonly represented in microvertebrate assemblages (for comprehensive reviews see Denison, 1979; Turner, 1991). Due to the rarity of complete specimens, the overall morphology of acanthodians is poorly known. The majority of Devonian articulated material in the United Kingdom comes from the Welsh Borderland, the Caithness region, and Midland Valley of Scotland. Sites include: Turin Hill (Angus, Scotland), Achanarras County (Scotland) and Wayne Herbert Quarry, (south-west Herefordshire, England) (Watson, 1937; Miles, 1973). In Canada articulated material has been obtained from the Delorme Formation, Northwest Territories (Russel, 1951; Bernacsek and Dineley, 1977), and the Escuminac Formation (Gagnier, 1996; Gagnier and Wilson, 1996). Articulated material in Antarctica has been recorded from the Aztec Siltstone, South Victoria Land (Woodward, 1921; White, 1968; Young, 1989). In Australia entire acanthodians have been found near Mt Howitt, Victoria (Long, 1983, 1986) and several articulated, but incomplete acanthodians have been collected from the Bunga Beds of the southern coast of New South Wales (Burrow, 1996).

Through the study of articulated specimens, considerable variation in the shape of scales, and in the pattern of crown ornament, has been observed in many acanthodian species. Young (1995) carried out one of the most comprehensive studies of scale variation in acanthodians. In her study differences in scale morphology were shown to be present in nine taxa of Early and Middle Devonian articulated acanthodian fishes from the British Isles. Other articulated acanthodians in which scale variation has been recorded include: *Machaeracanthus bohemicus* Gross (1973); *Ptomacanthus anglicus* Miles (1973) *Vernicomacanthus waynensis* Miles (1973); *Acanthodes* Zidek (1976, 1985); *Poracanthodes menneri* Valiukevicius (1992); *Diplacanthus ellsi* and *Diplacanthus striatus* (Gagnier 1996); *Kathemacanthus rosulentus* and *Cassidiceps vermiculatus* Gagnier and Wilson (1996). In disarticulated material intra-specific scale variation is harder to determine. Gross (1973) considered isolated scales Wells (1944) had attributed to four species, to represent the scale variation of one species, which he synonymized as *Cheiracanthoides comptus*. Gross (1973) stated that it was possible that different regions of the body could bear special forms of scales. He synonymized two scale types, that Wells (1944) had described as two *Acanthoides* spp., as *Acanthoides ? dublinensis* (Gross, 1973).

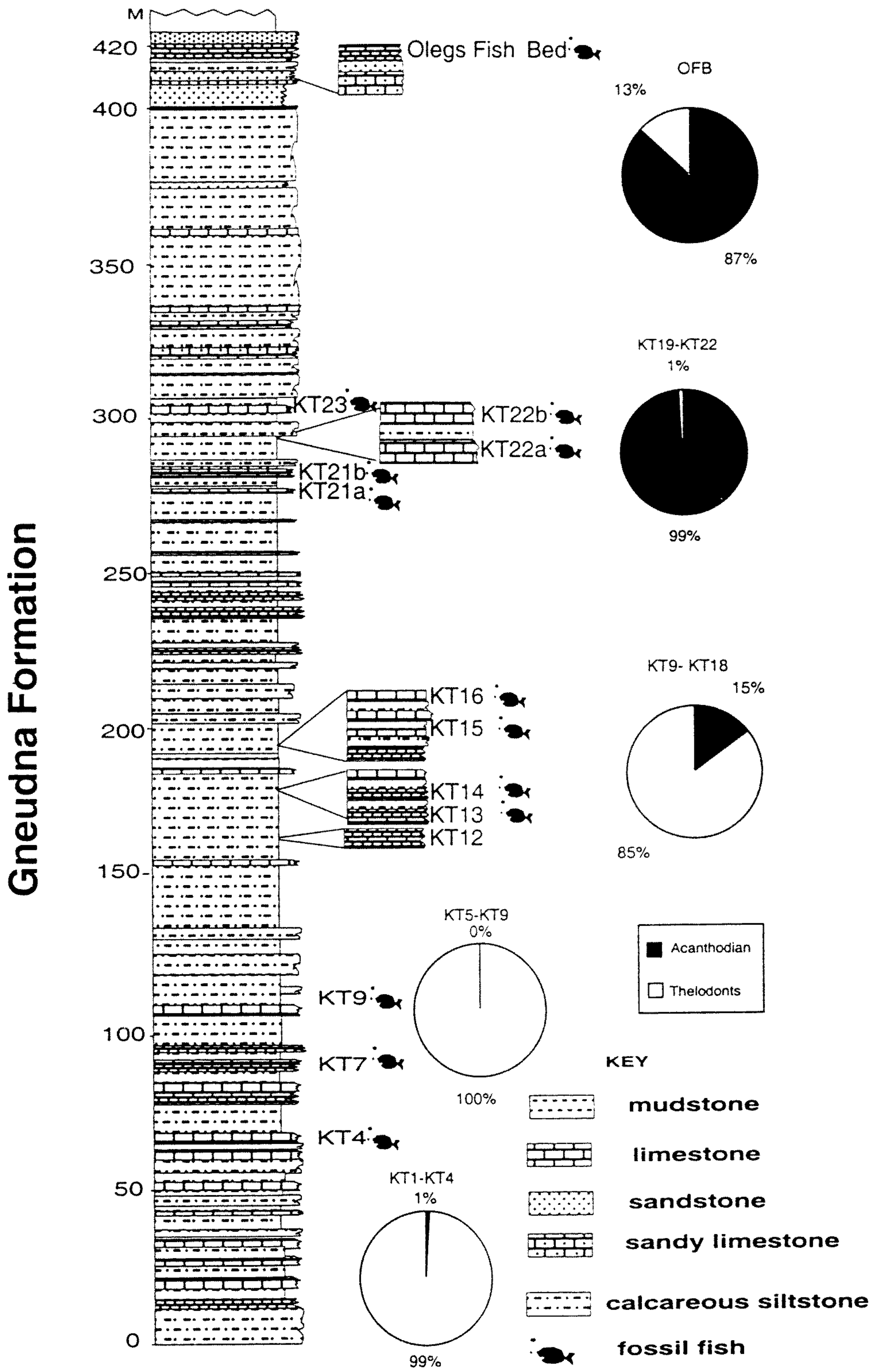

Figure 1 Stratigraphic column showing the lithology of the Gneudna type section and the relative abundance of acanthodians versus thelodonts throughout the section.

Acanthodians are only represented by disarticulated scales in the type section of the Gneudna Formation (Figure 1) in the Carnarvon Basin, Western Australia (Figure 2). This makes identification of the material difficult, especially to the species level. However, by comparing the morphology of isolated scales from the Gneudna Formation with scales from different body regions in described articulated acanthodians, the identification and taxonomic study of isolated scales is shown to be possible.

MATERIALS AND METHODS

To determine variation in scale morphology of different body regions in acanthodians, fully and partially articulated specimens at the Natural History Museum, London were examined. Four acanthodian taxa were studied. The difference in scale morphology of two acanthodians, *Diplacanthus horridus* and *Rhadinocanthus longispinus*, are described. In addition, published descriptions of acanthodian scale variation were used for comparison.

The study is based on isolated scales from the Gneudna Formation, Williambury Station, Western Australia. Scales described in this paper come from the residues of limestone samples digested in 10% acetic acid. The scanning electron micrographs were made on a Philips 505 at the Centre for Microscopy and Microanalysis, The University of Western

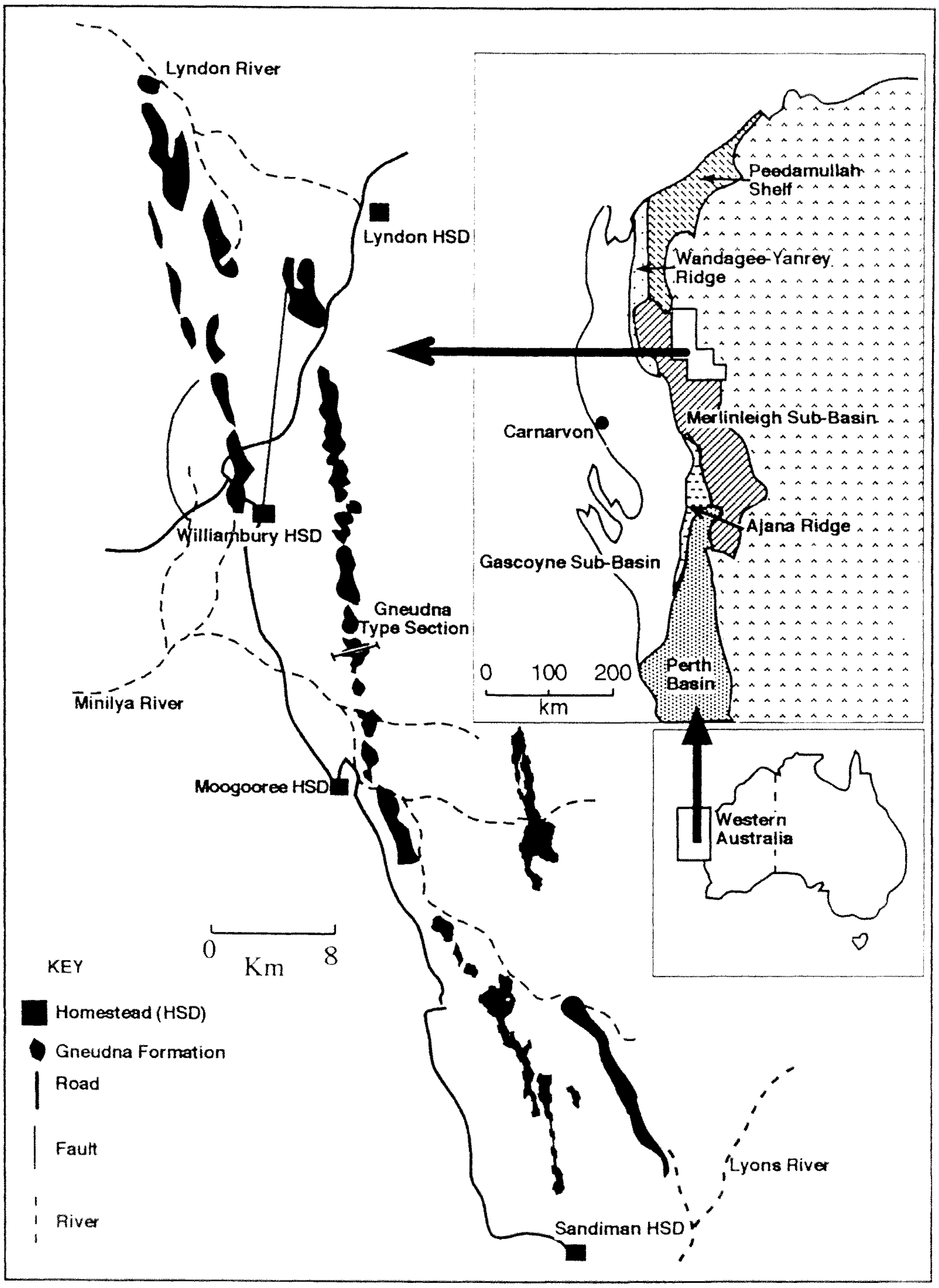

Figure 2 Map of Western Australia showing the locality of the Gneudna Formation and the distribution of its outcrops.

Australia. Sections of scales were ground by hand and examined under confocal and light microscopes. Specimens from the Gneudna Formation have been deposited in the collections of the Western Australian Museum (WAM).

Comparative Material

P61716 *Rhadinacanthus longispinus* Agassiz, 1844 complete articulated specimen.

P6188 *Rhadinacanthus longispinus* Agassiz, 1844 complete articulated specimen.

P6757 *Diplacanthus horridus* Woodward, 1892 complete articulated specimen.

P61859 a, b *Cheiracanthus murchisoni* Agassiz, 1835 incomplete articulated specimen missing the head. In part and counterpart.

DESCRIPTION OF SCALE VARIATION IN ACANTHODIANS

Various trends in scale variation have been reported in acanthodians (Miles, 1973; Young, 1995; Gagnier, 1996). With the exception of Watson (1937) who noted considerable variation of the scale size over the body of acanthodians and Gagnier and Wilson (1996), who noted that scale size decreased posteriorly in fin web scales, most studies (e.g. Miles, 1973; Valiukevicius, 1992) have concentrated on determining scale variation within species. Here, four articulated specimens from three different genera were examined to determine if some variation is consistent at a higher taxonomic level. The scale variation present in two of the species examined, *R. longispinus* and *C. murchisoni*, was illustrated in Young (1995, figures 6, 9) and the variation in the squamation of *P. menneri* was described by Valiukevicius (1992). The scale variation present in *D. horridus* and additional variation noted in *R. longispinus* is described below. By comparing the variation in the squamation of these four genera, morphological scale features that characterise different parts of the fish body have been established. Therefore, description of the unchanging scale features gives an indication of the body position from which an individual scale originated. By comparing scales from the same body region, an indication of the variation within a species, and of the variation between species, can be determined. As a result, more reliable estimates of the numbers of acanthodian species present in microvertebrate assemblages can be realized.

Scale Variation in *Diplacanthus horridus*

Seven distinct scale morphologies are identified from different body regions of *D. horridus*, Upper Devonian, Scaumenec Bay, Canada. In addition there are large dermal tesserae on the cranial roof and part of the narrow ring around the orbit. The size of the flank scales is, on the whole very similar, but they do decrease in size a little towards the dorsal and ventral surfaces and toward the tail. The scales on the fin webs are extremely small, and become smaller as they are traced down toward the margin of the fin. The scales bordering the lateral line are enlarged but have the same shape as those above and below them. The scales located below the lateral line and anterior to the pectoral fin spine (pfs) are high with a tumid base and well-defined neck (Figure 3). The crown is rounded anteriorly and overhangs the base posteriorly. There is an ornament of posteriorly converging ridges on the crown surface. Scales above the lateral line and in front of the anterior dorsal fin (dfa) have an identical crown shape and surface ornament; the base, however is not as high as in scales below the lateral line (Figure 3A). Mid-flank scales at the level of the anterior dorsal fin have a tumid base with a well-defined neck, and the crown overhangs the base posteriorly. The ridges on the crown surface, however, extend only to the middle of the scale (Figure 3B). Scales anterior to the pelvic fin spine (pls) are very high with the crown separated from the base by a well defined, constricted neck. At the junction of the base with the neck, the base flares laterally, extending beyond the width of the crown (Figure 3C). Scales anterior and posterior to the posterior dorsal fin spine (dfp) are also high with a well defined, constricted neck and lateral flaring at the neck-base junction (Figure 3D-E). These scales however, are not as high and the lateral basal flaring is not as extensive as in scales anterior to the pelvic fin spine. Ventral scales from around the anal fin spine (af) (Figure 3E) are higher than dorsal scales from around the dorsal fin spine (Figure 3D). In contrast to anterior body scales the caudal body scales are relatively flat with a poorly defined neck. They are rounded anteriorly and posteriorly and the crown does not overhang the base. The regional variation present on the caudal fin can be compared to that of *Acanthodes*, in which four zones have been described (Miles 1973).

Scale Variation in *Rhadinacanthus longispinis*

The scale morphologies evident in *D. horridus* are also present in *R. longispinis* (Middle Devonian, Old Red Sandstone, Cruaday, Orkney). However, the head is covered by irregular scales and there is a transitional area between the head and body, which is covered by large, irregularly arranged scales. The scales on the flank of the fish are similar in size. There is a reduction in the scale size towards the dorsal and ventral surfaces and toward the tail. The fin web is covered with a mosaic of very small rhombic scales. The lateral line is bordered by enlarged scales similar in shape to the scales above and below them. The scales located below the lateral line and anterior to the pectoral fin spine (pfs) are high with a

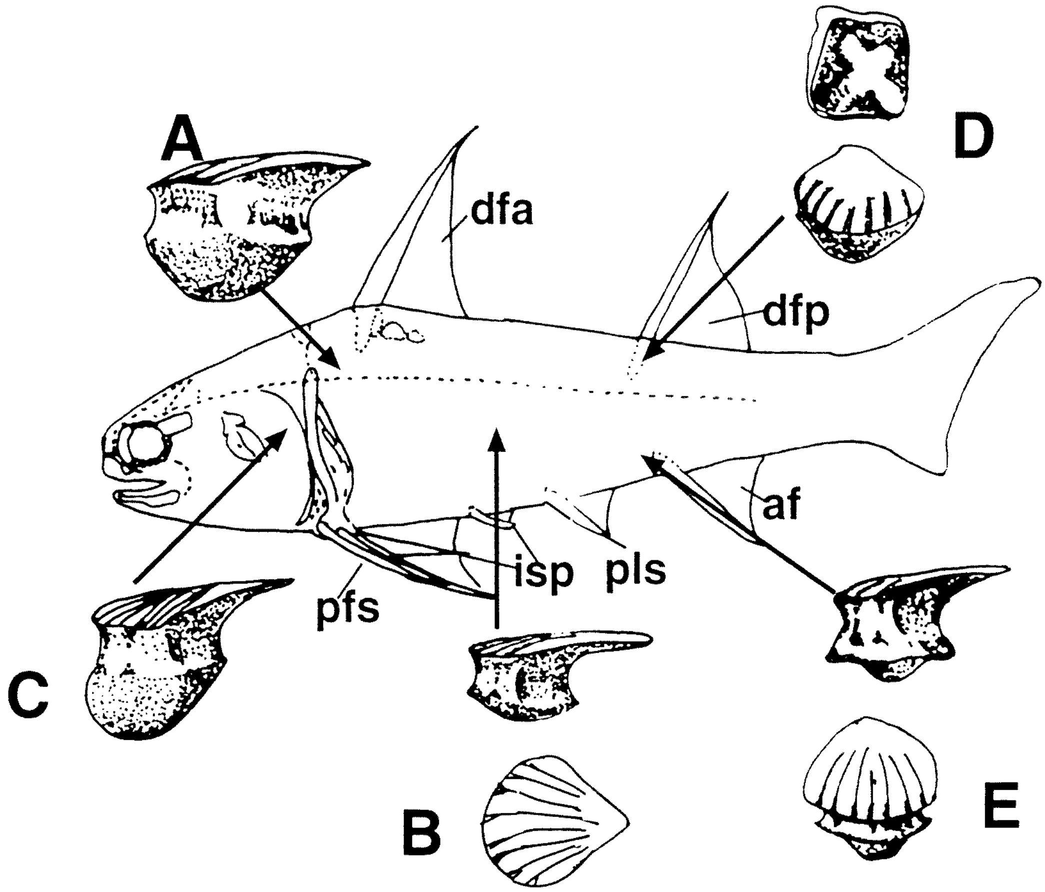

Figure 3 Diplacanthid acanthodian showing the variation and position of scale types found on *Diplacanthus horridus* (after Denison, 1979).

tumid base and well-defined neck. The crown is rounded anteriorly and overhangs the base posteriorly. There is an ornament of posteriorly diverging ridges on the crown surface. There is a small button on the centre of the scale base. Scales above the lateral line and in front of the anterior dorsal fin (dfa) have an identical crown shape and surface ornament; but the base is not as high as in scales below the lateral line, and the button is absent. Mid-flank scales at the level of the anterior dorsal fin have a tumid base with a well-defined neck, and the crown overhangs the base posteriorly. Scales anterior to the pelvic fin spine (pls) are very high with the crown separated from the base by a well defined, constricted neck. At the junction of the base with the neck, the base flares laterally, extending beyond the width of the crown. Scales anterior and posterior to the posterior dorsal fin spine (dfp) are also high with a well defined, constricted neck and lateral flaring at the neck-base junction. These scales however, are not as high and the lateral basal flaring is not as extensive as in scales anterior to the pelvic fin spine. Ventral scales from around the fin spine are higher than dorsal scales from around the fin spine. In contrast to anterior body scales the caudal body scales are relatively flat with a poorly defined neck. They are rounded anteriorly and posteriorly and the crown does not overhang the base.

Discussion

Several morphological body scale features were found to remain constant between these genera, and these allow the allocation of individual scales to a particular body region. The scale morphology changes gradually from the anterior region to the caudal region in acanthodians, and from the lateral line to the dorsal and ventral margins. Because the morphological changes are gradual, several trends common to different genera of acanthodians, have been identified. The anterior flank scales of acanthodians have a high profile, and are rhombic in shape. The shape of the scales progressively changes from rhombic to elongate along the flank, but they continue to have a high profile. Towards the caudal region the scales revert to being short and rhombic again, though they differ from scales from the anterior region in having a very low profile. In addition to the change in scale shape, there is a corresponding reduction in the crown ornament (when present) from the anterior region to the caudal region (e.g. *Diplacanthus striatus* Agassiz, 1844; *Cheiracanthus* *latus* Egerton, 1861; *Euthacanthus macnicoli*, Powrie, 1864; *Parexus falcatus*, Powrie, 1870; *R. longispinus*; and *D. horridus*). Acanthodians also have a number of specialised scales, particularly around the lateral line (Watson, 1937), the shoulder girdle (Miles, 1973) and the tail (Miles, 1970). In addition there are specialised scales around the bases of the fin spines, but these scales vary between genera. In *Diplacanthus*, *Rhadinacanthus* and *Ptomacanthus* these scales have a very high profile in comparison to other body region scales. The scales from around the bases of the dorsal fin spines have a higher profile than scales from around the base of the ventral fin spines. The crown ornament on the scales from around the base of the dorsal fin spines does not differ from the flank scales around them but; these scales have anteriorly flared bases with well constricted necks (*R. longispinus* and *D. horridus*, Figure 3). In *Culmacanthus* and *Mesacanthus* the base of the fin spine is surrounded by enlarged, flat scales (Watson, 1937; Long, 1983).

SYSTEMATICS OF THE GNEUDNA ACANTHODIAN SCALES

Order Acanthodida Berg, 1940

Acanthodida gen. et sp. indet.

Material Examined

WAM 98.4.1; WAM 98.4.2 and 500 other complete scales (WAM 99.8.69–74)

Horizons

KT Beds 4, 12, 20, 21A, 22, OFB (Figure 1)

Description of Morphotype 1 (Figure 4A–C)

This scale is pale orange in colour with a thin translucent crown. The outline of the scale is rhombic. The anterior edge does not overhang the base (Figure 4A–B), but the posterior edge overhangs the base slightly. The tumid and relatively high base is separated from the crown by a well defined neck. There are concentric growth rings visible on the base.

Description of Morphotype 2 (Figure 4D–E)

The outline of the scale is rhombic (Figure 4D). It is longer than scales of morphotype 1 (Figure 4A–B). The posterior edge of the unornamented crown overhangs the base. The constricted neck is well defined. Sharpey's fibre bundles are visible on the moderately high tumid base (Figure 4E).

Description of Morphotype 3 (Figure 4F–G)

The scale shape is rhomboid; the crown is thin and flat; the anterior edge is rounded and does not overhang the base (Figure 4F). There is no ornament on the crown surface. The neck is well defined and separates the crown from a low base. The base is shaped like a cross and there are visible Sharpey's fibre bundles (Figure 4G).

Description of Morphotype 4 (Figure 4H–J)

These scales are typically elongated in shape, the crowns being longer than wide (Figure 4I). The crown is thin with a shallow, mid scale depression. There are numerous pores opening onto the crown surface. Anteriorly, the crown is rounded and level with the base (Figure 4H). The posterior edge of the crown forms an acute angle and overhangs the base (Figure 4I). There is a narrow, well-formed neck separating the crown from the convex base (Figure 4H–J). The neck is deeper posteriorly than anteriorly, and there is no ornamentation visible. At the contact between the base and neck, the base flares to form a narrow ridge (Figure 4H–I). The base is higher than wide with clear Sharpey's fibre bundles visible (Figure 4H).

Histology

There appear to be microscopic dentine tubercles on the crown surface, similar to those described by Derycke and Chancogne-Weber (1995) (Figure 4C). There is a thick dentine layer on the crown (Figure 4K) with straight dentine tubules directed centripetally on the crown growth zones (Figure 4L). In longitudinal section, long tubules of dentine can be seen extending up the neck towards the centre of each growth zone (Figure 4K). The ascending canals are narrow, not much wider than the dentine tubules. The base is of acellular bone penetrated by numerous fine canals. Sharpey's Fibres are arranged in pyramidal layers in the base.

Allocation of Scales to Body Region

Although some acanthodians have scales with no crown ornament, considerable variation in scale morphology from different body regions is still apparent. The shapes of scales from *Ischnacanthus gracilis* Egerton, 1861 were described by Young (1995) as rhombic, sub-rhombic or polygonal, being relatively flat to gently convex and smooth. This same variation in shape and height is seen in the scales referred here to Acanthodidae gen. *et* sp. indet. above. Comparisons with articulated acanthodians (Young, 1995) suggest that the short, deep scales (morphotype 1) collected from the Gneudna Formation are from the anterior regions of the fish; the elongated, deep scales are from the flank regions (morphotype 2); the rhombic low scales with the cross-shaped base are from caudal regions (morphotype 3); and the scales with the lateral extensions to the base are from around the insertion points of fin spines (morphotype 4). As

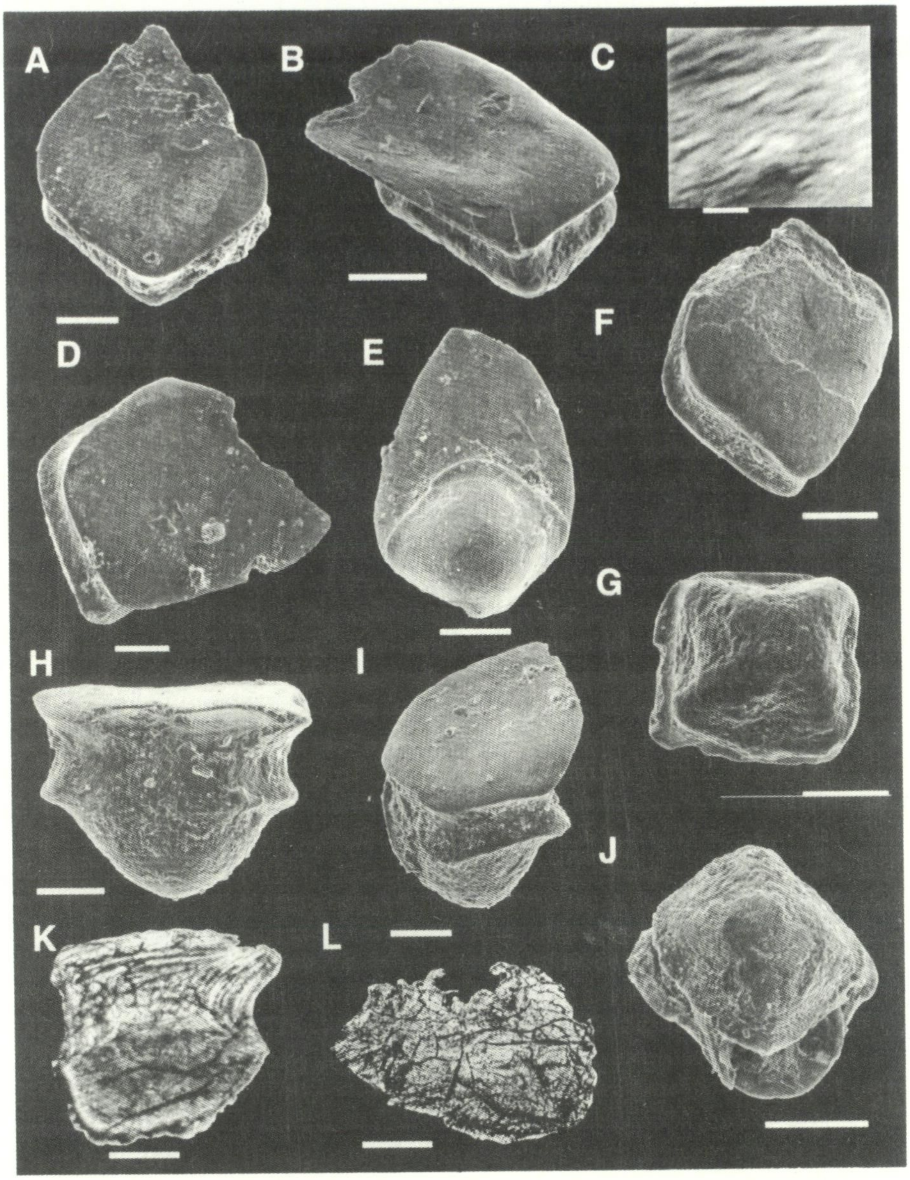

Figure 4 Scales identified as Acanthodidae gen. *et* sp. indet. A–B, morphotype 1 – anterior body scales; C, microornament on crown surface; D–E, morphotype 2 – flank scales; F–G, morphotype 3 – caudal scales; H–J, morphotype 4 scales from around the base of the fin spine insertion points; K, saggital section of a morphotype 1 scale; L crown section of a morphotype 1 scale. Scale bars = 1.0 mm.

the different smooth-crowned morphotypes in the Gneudna Formation samples correspond to variants found on an individual fish, they are assigned here to a single species. However, this will remain conjecture until a complete articulated specimen is found.

Taxonomic Assignment

The scales are referred to the Family Acanthodidae but are not assigned to any known genus or species. The assignment of isolated unornamented scales to a genus or species is difficult, due to a lack of diagnostic features. The Acanthodidae gen. *et* sp. indet. scales described here, evoke the description of *Acanthodes guizhouensis* Wang and Turner, 1985, in having an elongated posterior crown ending in an acute point, a slightly curved anterior margin and a depression near the centre of the crown. This species is recorded from the upper Famennian of Morocco (Derycke-Khatir, 1994) and China (C. Derycke personal communication 1998) and the Lower Carboniferous of China (Wang and Turner, 1985).

There are several other genera erected for articulated fish within the family Acanthodidae, including *Mesacanthus* Traquair, 1888, *Protogonacanthus* Miles, 1966 and *Traquairichthys* Whitley, 1933, which have unornamented scales and cannot be distinguished from each other, based on only scale morphology. In addition to these is the genus

Acanthodes Agassiz, 1833 to which many isolated unornamented scales have been referred in the past. Zidek (1976) considered *Acanthodes* as a *nomen dubium* and Denison (1979) considered that many Devonian scales attributed to *Acanthodes* are not from that genus. Gross (1973) stated that scales characteristized by unornamented crowns are found repeatedly among members of the acanthodian radiation. Wang (1984) also considered that true *Acanthodes* only occur in lower Carboniferous – Permian strata.

To date, the only articulated acanthodian known from the Lower Frasnian of Australia is *Howittacanthus kentoni* Long, 1986, recently placed in its own family Howittacanthidae by Zajic (1995). This family is considered to be closely related to the Acanthodidae because of comparable features in the jaw (Zajic, 1995). Like members of the Family Acanthodidae the Howittacanthidae and Mesacanthidae possess unornamented scales. This Howittacanthidae is represented by a single species, *H. kentoni*, and is only recorded from eastern Australia.

Family Cheiracanthidae Berg, 1940

Genus *Cheiracanthus* Agasssiz, 1835

Cheiracanthus sp. indet.

Material Examined

46 complete scales (WAM 99.8.75–80)

Horizons

KT Beds 4, 9, 14, 21, 22 and OFB (Figure 1)

Description of Morphotype 5 (Figure 5A–B)

The crown is elongate, being longer than wide. An ornament of between 10–12 raised parallel ribs extends from the anterior edge to the posterior third of the scale (Figure 5A–B). There is a narrow unornamented rim around the margin of the scale (Figure 5A). The anterior edge of each rib bifurcates (Figure 5A). The anterior edge of the scale is rounded and slightly overhangs the base. There is a shallow mid-scale depression which is characteristic for *Cheiracanthus*. The posterior edge of the crown is pointed and overhangs the base. A well defined neck separates the crown and deep, tumid base. There are four openings visible in the neck (Figure 5B). Sharpey's fibre bundles are visible on the base.

Description of Morphotype 6 (Figure 5C–D)

This scale type is rhomboid. The anterior margin is rounded and the posterior margin is broken (Figure 5D). The anterior and posterior edges of the crown overhang the base. The crown surface ornament consists of 6–8 parallel ribs, which bifurcate anteriorly (Figure 5C–D). The ribs extend to the middle of the scale, disappearing towards the back. There is a constricted neck and a deep tumid base.

Description of Morphotype 7 (Figure 5E–F)

Morphotype 7 (Figure 5E–F) is very similar to morphotype 6. The anterior and posterior crown margins overhang the base (Figure 5H). The crown ornament consists of eight parallel ribs, which bifurcate anteriorly (Figures 5F–G). The ribs extend to the middle of the scale. The posterior margin of the scale is scalloped. There is a constricted neck and a deep tumid base.

Description of Morphotype 8 (Figure 5I–J)

The scale type is rhomboid in shape with a low profile (Figure 5I–J). The crown surface is very abraded with only traces of the ribbed ornament remaining (Figure 5I). As with the other scales described, there is an unornamented rim around the anterior edge of the scale. The crown does not overhang the base. There are four canals in the neck, which separates the crown from the flattened base. The base is shaped like a cross.

Description of Morphotype 9 (Figure 5G–H)

The specimens representing this scale type are abraded. They have a rhombic to elongate shape (Figure 5G–H). The posterior edge of the crown is scalloped and overhangs the base (Figure 5G). The ornament consists of 4–8 parallel ribs that bifurcate anteriorly. There is an unornamented rim around the margin of the scale. A well defined and constricted neck separates the crown and deep tumid base. The neck contains four canals. At the junction of the base and neck, the base flares laterally, approaching the width of the crown (Figure 5H).

Histology

The crown is composed of orthodentine. In sagittal section it can be seen that the main dentine tubules do not possess many side branches (Figure 5K). This is characteristic of *Cheiracanthus*. A series of growth zones can be seen along the anterior edge in sagittal section and along the dorsal and lateral edges in sagittal section. In the centre of the neck three ascending canals are present. One of these extends to the crown; the other two extend to the neck. The base is acellular.

Allocation of scales to body region

A greater degree of variation is present in acanthodian scales with crown surface ornament than in acanthodian scales that are unornamented. This is because the type of crown ornament may vary in addition to the shape of scales, depending

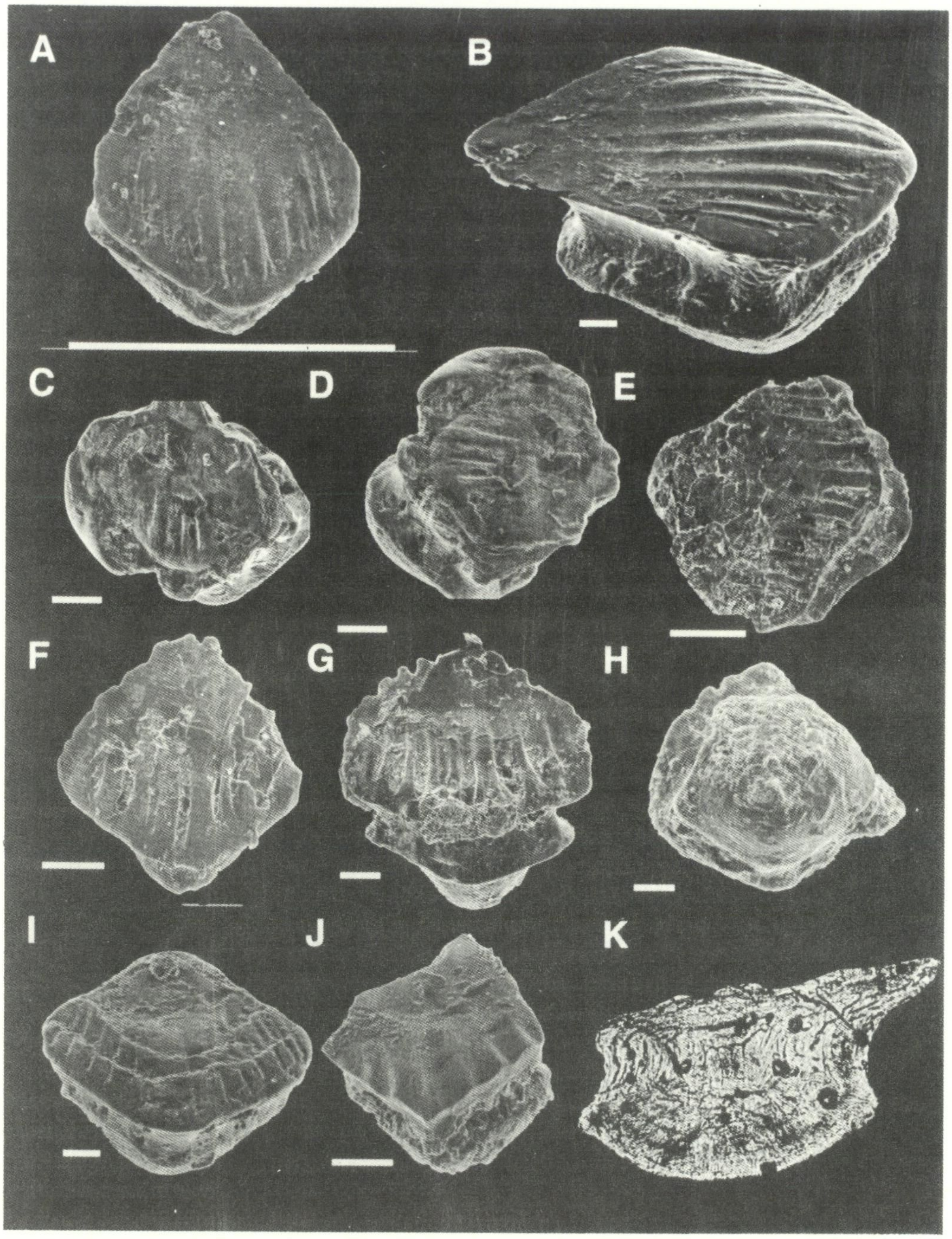

Figure 5 Scales identified as *Cheiracanthus* sp. A–B morphotype 5 – anterior body scales; C–D, morphotype 6 – flank scale; E–F, morphotype 7 – flank scales; I–J, morphotype 8 – caudal scales; G –H, morphotype 9 – scales from around the base of the fin spine insertion points; K, sagittal section of morphotype 1 scale. Scale bars = 0.1 mm.

on the region of the body that the scales are located. The crown ornament in *Euthacanthus macnicoli* shows considerable variation in the number of ridges and the distance each ridge extends posteriorly along the crown surface (Young, 1995). A reduction in the length of the ridges on the crown surface from the anterior region to the caudal region of the fish is also observed in *Diplacanthus horridus* (Figure 3). There is also variation in the base of ornamented acanthodian scales. Gross (1973) observed that the height of the base increases towards the anterior of the fish in *Machaeracanthus bohemicus*. Relatively high scales with tumid bases occur in the anterior region of the fish, and scales with low bases occur in the caudal region of the fish (pers. observation). A greater variation in the shape and height of scale bases is apparent in *D. horridus* (Figure 3).

In *Cheiracanthus* sp., variation in the crown surface ornament and in the height and shape of the base can also be observed. Scales with a high profile and deep tumid base also have the most numerous and longest ridges on the crown surface, suggesting that these scales came from the anterior region of the fish's body (morphotype 5). Scales in which the ridge number and length are less, but which still retain a high profile and tumid base (morphotypes 6 and 7), are considered to have come from the flank region of the fish. Scales that are relatively flat and have ridges only in the anterior third of the scale (morphotype 8), are interpreted as having come from the caudal region of the fish. Scales with a lateral extension above the tumid base (morphotype 9) are considered to have come from around the fin spine insertion points. These scales have correspondingly shorter and fewer ridges on the crown surface.

There are two characters that remain consistent in the crown surface ornament of *Cheiracanthus* sp. that suggest that all scales are from the same species. These characters are: the bifurcation at the anterior end of each ridge and the presence of a narrow, raised lip around the anterior edge of each scale. As with the Acanthodidae gen. *et* sp. indet. scales described above, all scale types from the different body regions present on acanthodians are represented in the samples from the Gneudna Formation. Accordingly, it is concluded that all *Cheiracanthus sp.* scales are from a single species.

STRATIGRAPHIC DISTRIBUTION AND DEPOSITIONAL ENVIRONMENTS

Thelodont scales have been used to indicate bathymetry in Early Devonian sediments. A higher proportion of thelodont scales compared to acanthodian scales is considered to represent nearshore, or shallow water conditions (Märss and Einasto, 1978; Turner, 1984, 1999; Burrow, 1997). The microvertebrate assemblages from the type section of the Gneudna Formation do not support these findings.

Thelodont scales are proportionally most abundant in the beds KT1-5, KT6-9 and KT10-18 (Figure 1). These beds, which consist of crinoidal/ brachiopodal packstone, have been interpreted as representing a shallow nearshore environment. In the beds KT6-9 ptyctodont remains (Long and Trinajstic in press) are well preserved and in some cases partially articulated, indicating lower energy, offshore depositional conditions. Here thelodont scales are more abundant than acanthodian scales. In the upper part of the type section, from KT19 to 22 and OFB, thelodont scales are rare and acanthodian scales are most abundant (Figure 1). According to Märss and Einasto (1978) these proportions should indicate an offshore environment. However, these beds are interpreted as having been laid down in extremely shallow water, with sediments mainly consisting of a well-sorted shell hash having a high quartz content.

There are three possible reasons why thelodonts/ acanthodian scale number ratios do not provide here a reliable environmental indicator in the Gneudna Formation. During the Givetian and Frasnian, the thelodonts declined in number and diversity, with no thelodonts known after the Frasnian. Thus the ratios of acanthodian to thelodont remains may only be an effective environmental indicator for the Early and Middle Devonian, when thelodonts were diverse and abundant, and not hold for the Frasnian. Evidence to support this comes from the study of conodont ratios, in particular the ratios of *Icriodus* to *Polygnathus*, in the section. Like thelodonts, the ratios of certain conodonts have been successfully used as environmental indicators. In the Gneudna Formation the conodont ratios (R. Nicholl personal communication 1997) are consistent with the lithological interpretations of the depositional environments for each interval.

Secondly, many beds within the Gneudna Formation have been extensively affected by post-depositional dolomitization. Thin sections of these beds show many fossil ghosts and the micro-remains recovered from residue are poorly preserved. The actual fossil ratios of the dolomitized beds may be skewed due to preservation bias as a result of diagenic changes.

Thirdly, it is considered that the microvertebrate remains in the area where the type section of the Gneudna Formation was deposited, with the exception of those in bed KT7, have been transported before deposition. Microvertebrate remains are disarticulated and predominantly occur in packstone, due to post-depositional concentration. The Gneudna Formation is also unusual in that there is a complete absence of acanthodian fin spines in the section. The fish-bearing units in the Gneudna Formation are generally well sorted and the absence of acanthodian fin spines could be explained through winnowing.

The difference in the proportion of acanthodian scales to thelodont scales does not provide any bathymetirc information that would indicate the depositional environment of the Gneudna Formation.

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