Redescription of the acanthodian *Gladiobranchus probaton* Bernacsek & Dineley, 1977, and comments on diplacanthid relationships

Gavin F. HANKE
Royal British Columbia Museum,
675 Belleville Street, Victoria, British Columbia V8W 9W2 (Canada)
ghanke@royalbcmuseum.bc.ca

Samuel P. DAVIS
Stang Korvenn, F-29520 Laz (France)
sam.davis@uclmail.net

ABSTRACT

Gladiobranchus probaton Bernacsek & Dineley, 1977 was described based on poorly preserved specimens, and originally assigned to the Ischnacanthiformes because of its resemblance to *Uraniacanthus spinosus* Miles, 1973. Incomplete fossils of *G. probaton* which were available to Bernacsek and Dineley for the original species description, lacked teeth and/or dentigerous jaw bones and until now, the classification and relationships of *G. probaton* remained unresolved. New, nearly complete specimens show details of the rostrum, jaws, and the complete caudal fin, and correct some errors in the original species description. The toothless jaws, the enlarged anterior and posterior circumorbital plates, elongate, deeply inserted dorsal fin-spines, the structure of the scapulocoracoid, and the prepelvic fin-spine complement all indicate that *G. probaton* is a diplacanthoid, and not closely related to ischnacanthid acanthodians. Re-examination of *U. spinosus* shows that there are no dentigerous jaws with any body fossils, and the striking similarity of *U. spinosus* and *G. probaton* suggest that both should be placed in the same diplacanthoid family, Gladiobranchidae.

KEY WORDS
Gladiobranchus,
Uraniacanthus,
Acanthodii,
taxonomy,
diplacanthids,
systematics.

RÉSUMÉ

Redescription de l'acanthodien Gladiobranchus probaton *Bernacsek & Dineley, 1977, et commentaires sur sa parenté avec les diplacantoïdes.*

Gladiobranchus probaton Bernacsek & Dineley, 1977 fut décrit d'après des spécimens mal conservés et rapportés à des Ischnacanthiformes à cause de leur ressemblance à *Uraniacanthus spinosus* Miles, 1973. Aux spécimens de la description originale de *G. probaton* Bernacsek & Dineley, manquaient des dents et/ou les os de mâchoires dentigères ainsi que, jusqu'à présent, la classification et les relations de parenté de *G. probaton*, restées non résolues. La découverte de nouveaux spécimens plus complets permet de connaître les détails du rostre, des mâchoires et de la nageoire caudale. Ainsi, des erreurs de la description originale peuvent être corrigées. Par leurs mâchoires édentées, par les plaques circomorbitaires antérieures et postérieures plus grandes, par des aiguillons de nageoires dorsales profondément insérées et allongées, par la structure du scapulocoracoïde et par les aiguillons prépelviens, *G. probaton* est un diplacanthide. Le réexamen d'*U. spinosus* permet d'affirmer l'absence de restes corporels associés avec des mâchoires dentigères. La ressemblance frappante d'*U. spinosus* et de *G. probaton* suggère que se sont des Gladiochanchidae, une famille de diplacantoïdes.

INTRODUCTION

Several acanthodian fishes from the MOTH locality, southern Mackenzie Mountains, Northwest Territories, Canada, initially were described from poorly preserved material, but new, better-preserved specimens collected since the 1980s indicate that all but one species, *Cassidiceps vermiculatus* Gagnier & Wilson, 1996, required redescription. *Brochoadmones milesi* Bernacsek & Dineley, 1977 has been re-evaluated (Gagnier & Wilson 1996b; Hanke & Wilson 2006), and revisions of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 and the MOTH locality ischnacanthids currently are underway. *Paucicanthus vanelsti* Hanke, 2002 is a recently described addition to the MOTH fish fauna; its description was based on fairly complete body fossils. *Tetanopsyrus lindoei* Gagnier, Hanke & Wilson, 1999 and *T. breviacanthias* Hanke, Davis & Wilson, 2001 possess some diplacanthoid characters and are known from nearly complete body fossils (Gagnier *et al.* 1999; Hanke *et al.* 2001; Hanke & Wilson 2004). A third diplacanthoid species from MOTH, *Gladiobranchus probaton* Bernacsek &

Dineley, 1977, which was based on a fairly complete type specimen, is the focus of this paper.

We provide a redescription of *Gladiobranchus probaton*, a genus and species known only from the MOTH locality in the Mackenzie Mountains, Northwest Territories, Canada (Bernacsek & Dineley 1977; Wilson *et al.* 2000; Hanke & Wilson 2004). Bernacsek & Dineley (1977: 14-17) based their original description of *G. probaton* on incomplete body-fossils (all housed in the National Museum of Canada, now known as the Canadian Museum of Nature, Ottawa). Specimens of this taxon which were available at that time, lacked rostrum, jaws, and parts of the caudal fin. These incomplete body-fossils prevented researchers from reaching consensus on *Gladiobranchus* interrelationships. Our redescription and reconstruction of *G. probaton* (Fig. 1) is based on our re-examination of the holotype (NMC 22700A) (Fig. 2) and study of new fossils from the MOTH locality.

Published accounts of *G. probaton* have shown that it is nearly identical to *Uraniacanthus spinosus* Miles, 1973 (Long 1986; Hanke *et al.* 2001).

Both *Uraniacanthus* and *Gladiobranchus* species, possess fin-spines, opercular plates, postorbital plates, and other body structures which are similar to those of other diplacanthoid fishes (Hanke *et al.* 2001; Davis 2002) and not ischnacanthiforms as originally suggested by Bernacsek & Dineley (1977). Bernacsek & Dineley (1977: 13) did note that that the pectoral girdle of *G. probaton* was similar to that of "climatiiform fishes", but this was based partly on their description of pinnal plate armour in this taxon, which we show to be incorrect. Our re-examination of *U. spinosus* specimens has allowed us to identify and correct errors in the original description of this taxon (Miles 1973) in addition to *G. probaton*.

MATERIALS AND METHODS

New specimens of *Gladiobranchus probaton* were prepared with repeated immersion in dilute acetic acid (Rixon 1976) with subsequent freshwater rinse; silt-sized siliciclastic residues remaining after each acetic acid treatment were removed while wet using soft paint brushes. After preparation, the slab was dried and stabilized using a 5% solution of Glyptal™ cement. Ammonium-chloride sublimate was used to whiten specimens for photography.

Small groups of scales were removed from specimens where possible, embedded in Luminate 83 HA 4 epoxy, polished to expose histological structure using 600- and 1000-grit wet-dry sandpaper, and given a final polish using moistened alumina powder on a glass plate. High-magnification images were taken using a Nikon Coolpix 990 digital camera attached to a Nikon SMZ 1500 dissecting microscope. Line drawings were made with the same dissecting microscope and its camera lucida attachment.

ABBREVIATIONS
MORS   Middle Old Red Sandstone;
MOTH   Man-on-the-Hill refers to the informal name for UALVP locality 129;
BNMH   Natural History Museum, London;
NMC   National Museum of Canada (now: Canadian Museum of Nature), Ottawa;
UALVP   Laboratory for Vertebrate Palaeontology, University of Alberta.

af.   anal fin;
afs.   anal fin-spine;
ax.r.   axial ridge of scapulocoracoid;
circ.orb.   circumorbital scales;
dfa.   anterior dorsal fin-web;
dfa.sp.   anterior dorsal fin-spine;
dfp.   posterior dorsal fin-web;
dfp.sp.   posterior dorsal fin-spine;
sc.bl.   dorsal scapular blade;
epi.ch.l.   epichordal lobe of the caudal fin;
gz.   growth zone;
hgc.   hyoidean gill cover;
hl.   hypochordal lobe of the caudal fin;
ins.a.   insertion area;
lc.   main lateral line canal trace;
lt.   left;
mk.   Meckel's cartilage;
ot.   otic statoconia;
p.br.l.   postbranchial lamina of scapulocoracoid;
pcf.   pectoral fin-web;
p.f.   posterior flange of scapulocoracoid;
pfs.   pectoral fin-spine;
pls.   pelvic fin-spine;
p.ps.   prepectoral spine;
prim.   scale primordium;
prp.   prepelvic spine;
pv.f.   pelvic fin-web;
rt.   right;
sco.   scapulocoracoid;
sh.f.   Sharpey's fibre traces.

SYSTEMATICS

Class ACANTHODII Owen, 1846
Order CLIMATIIFORMES Berg, 1940
Suborder DIPLACANTHOIDEI Miles, 1966

Family GLADIOBRANCHIDAE
Bernacsek & Dineley, 1977

REMARKS
This family presently contains only two genera, *Uraniacanthus* and *Gladiobranchus*.

Genus *Gladiobranchus*
Bernacsek & Dineley, 1977

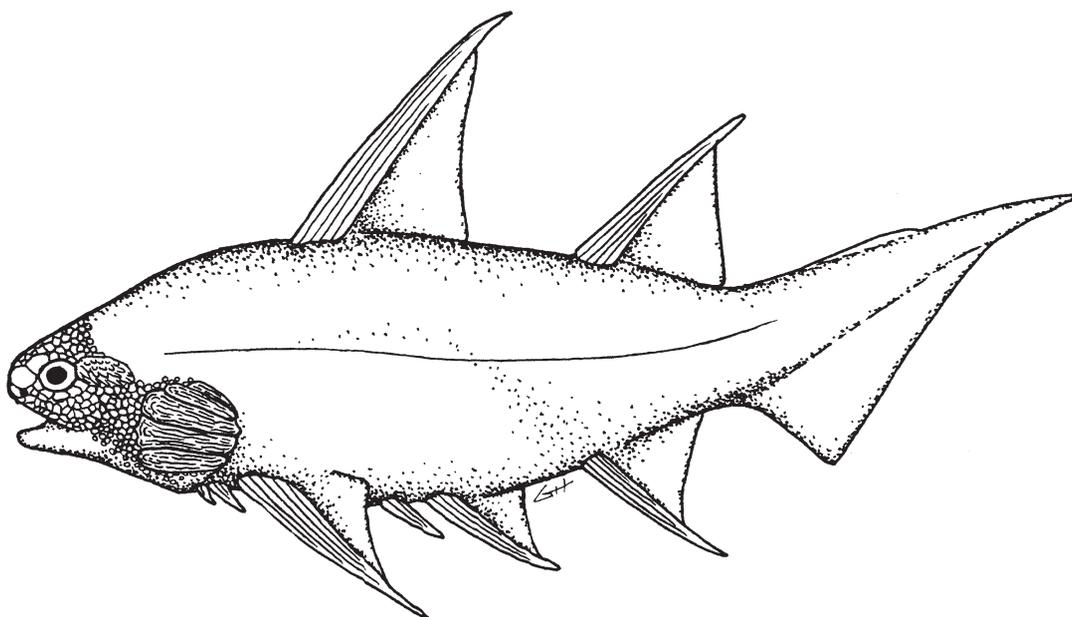REVISED DIAGNOSIS. — As for the only included species, *G. probaton*.

FIG. 1. — *Gladiobranchus probaton* Bernacsek & Dineley, 1977, composite reconstruction based on the holotype (NMC 22700A) and UALVP 41862, 41858, 38679, and 41857.

Gladiobranchus probaton
Bernacsek & Dineley, 1977
(Figs 1-13)

HOLOTYPE. — NMC 22700A.

MATERIAL EXAMINED. — UALVP 19259, 32448, 32469, 38679, 41669, 41857, 41858, 41862, 42095, 44046, scales: 45366-45396.

HORIZON AND AGE. — All known *Gladiobranchus* specimens are from the single UALVP locality 129 in Early Devonian (Lochkovian) dark grey argillaceous limestone of the Delorme Group, Delorme Formation, District of Mackenzie.

TYPE LOCALITY. — In talus below the UALVP locality 129 (62°32"N, 127°45"W), also known as the MOTH fish layer, MOTH section, section 43 (Gabrielse *et al.* 1973), Central Mackenzie Mountains, Northwest Territories, Canada. The descriptive geology of the locality was summarized by Hanke *et al.* (2001), Hanke (2002), Hanke & Wilson (2004), and Zorn *et al.* (2005).

REVISED DIAGNOSIS. — Diplacanthoid acanthodians with rostral plates having enlarged tubercles along posterolateral edges; an enlarged anterior circumorbital plate with radiating rows of tubercles situated posterolateral to the rostrum; single ovate, enlarged postorbital plate ornamented with spiky tubercles associated with the circumorbital plate series; perichondrally ossified Meckel's cartilage with strong symphyseal connection; dorsally-directed process positioned mid-way along Meckel's cartilage; dermal mandibular splint absent; heavily-ornamented, spathiform opercular plates cover the entire gill chamber laterally; pectoral dermal plate armour absent; two pairs of prepectoral spines inserted between scales on the isthmus; axial ridge of scapular blade of scapulocoracoid separating postbranchial and posterior laminae of coracoid region; medial surface of scapulocoracoid flat; paired fin-spines possessing simple reclined nodular ornament on anterior-most ribs; anterior dorsal fin-spine approximately twice the length of posterior dorsal fin-spine; enlarged body scales with fine surface ridges surround base of fin-spines; body scales behind branchial chamber, on fins, and along dorsal and ventral midline posterior as far as caudal peduncle ornamented with fine parallel ridges whereas body scales at mid-flank possess unornamented crowns; body scale histology consisting of few, thick growth zones in crown and flat to slightly tumid mass of basal tissue; body scale neck and basal tissue expanded perpendicular to long-axis of scale crown.
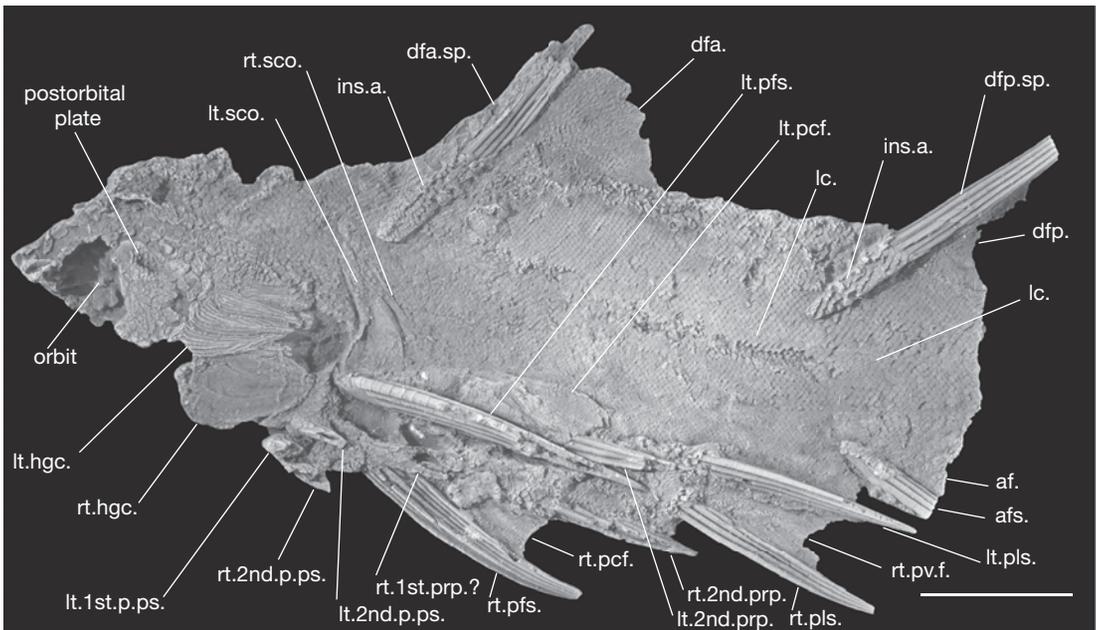
Fig. 2. — Photograph of the holotype of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (NMC 22700A). Scale bar: 1 cm.

DESCRIPTION

GENERAL STRUCTURE

We provide a composite reconstruction of *Gladiobranchus probaton* (Fig. 1) based on several new specimens for comparison to photographs and the description which follows. Collected specimens of *G. probaton* range from 42 mm to over 110 mm in total length (estimated for UALVP 41862, the largest specimen of *G. probaton* known). All specimens are preserved on their left or right side, which suggest that the body of the fish was deep and compressed (Figs 2-5). New specimens indicate that the body of *G. probaton* was deeper than indicated by Bernacsek & Dineley (1977: fig. 12).

A notable feature of *G. probaton* is the steep slope of the predorsal midline (about 20° from horizontal) beginning from the insertion point of the anterior dorsal fin-spine to the rostrum (Figs 3-5). This feature also is characteristic of diplacanthid acanthodians. Dermal cover ranges from aligned body scales which range in size depending on where they are positioned on the body, to tiny, well-aligned fin scales. The head and rostrum are covered by large, tuberculated or ridged polygonal plates (Figs 6; 7). Sensory line traces on the body are obvious due to disruption of scale alignment, however, the course of all cranial sensory lines cannot be determined with the available material.

ROSTRUM

The rostrum of *Gladiobranchus* is unique among diplacanthoids in its overall shape and surface structure (Figs 6B; 7D). The rostral plate is short but laterally expanded and is covered with tubercles. Larger tubercles cover the anterolateral corners of the rostral plate, and at its posterior-most edge, the rostral plate contacts the enlarged anterior circumorbital plate (Fig. 7D). Unfortunately, the arrangement of the dermal plates surrounding the nares of *Gladiobranchus* is difficult to define because of *post mortem* compaction.

CIRCUMORBITAL PLATES

The eyes of *G. probaton* lack sclerotic rings, and the position and size of the orbits are similar to that

of diplacanthids. The posterior edge of the orbit is positioned anterior to the jaw articulation in all specimens for which the information is available (Figs 3; 4; 6). The anterior margin of the orbit is nearly level with that of the dorsal process of Meckel's cartilage (Figs 3; 6B).

The orbit is surrounded by an array of small circumorbital plates punctuated by enlarged anterior and posterior plates (Figs 3; 6B). The upper anterior quarter of the orbit is dominated by the anterior circumorbital plate which has a prominent central tubercle, and from this point, ornamented ridges radiate towards the plate margin (Fig. 7D). Ridge ornamentation consists of low, overlapping rounded tubercles which increase in size toward the plate margin.

The ventral half of the orbit is bordered by a tightly-nested series of small sub-rectangular to polygonal plates which have low, irregularly-shaped crown ridges and longitudinal troughs (best seen on UALVP 42095 and 41862; Figs 3; 6; 7C). The troughs of these small circumorbital plates align with each other and may have housed the suborbital sensory line. The location and structure of this suborbital chain of plates bears a close resemblance to the suborbital plates in Watson's reconstruction of *Diplacanthus striatus* (Agassiz, 1844), now *D. crassissimus* Duff, 1842, (Watson 1937: 91, fig. 15), except that the trough which presumably carried the suborbital sensory canal extends more anteriorly in *Gladiobranchus*. The suborbital circumorbital plates pass posterodorsally and end at the enlarged postorbital plate (seen in basal view in UALVP 41858, 38679, and NMC 22700A; Figs 2-5; 6B; 7E, F). The ornamentation of the smaller plates covering most of the head and adjacent to the circumorbital plates is complex (Figs 6; 7A, B, E-H). The postero-dorsal quarter of the orbital margin is dominated by an enlarged postorbital plate.

TEMPORAL REGION AND CHEEK

A single ovate postorbital plate is located just postero-dorsal to the orbit (Figs 2-5; 6B; 7E, F), which is equivalent to the "postorbital plate" as described by Bernacsek & Dineley (1977: 16). The anterodorsal edge of the postorbital plate contacts the postero-dorsal margin of the orbit (Figs 2; 3; 5; 6B). The postorbital plates may shift relative to each other during decay and compaction of the carcass such

that they commonly do not overlap perfectly, leaving the plate from the opposing-side of the fish visible in basal view through the orbit, or through gaps in the scale cover (Figs 4; 5).

The postorbital plate is covered by contiguous rows of interconnected spiky tubercles (Fig. 7E). The largest of these tubercles straddle the centre of the postorbital plate in horizontal rows. Tubercles are smaller towards the plate perimeter where their external structure more closely resembles that of the parallel ridged surface of the suprabranchial and body scales. Postorbital plate ornamentation does appear to vary as some specimens possess only a single greatly-enlarged tubercle at the centre of the plate (Fig. 7F). In no case is there evidence of lateral line traces on a postorbital plate. In comparison, shallower, rounded and more loosely-aggregated tubercles occur on the equivalent postorbital plate of *Uraniacanthus spinosus* (Miles 1973: pl. 13, fig. 1; Davis 2002: fig. 5.1c). A smooth rectangular dermal plate is found in the same position in *Diplacanthus crassissimus* (*D. striatus* in Watson 1937: 89, text-fig. 14; pl. 10). Enlarged postorbital plates are absent from both Miguasha diplacanthid species (*D. ellsi* Gagnier, 1996, and *D. horridus* Woodward, 1892) based on the original description of these two taxa (Gagnier 1996). Small polygonal plates are present between the operculum and the orbit, dorsal and ventral to the branchial chamber, along the ventral margin of the orbit, and on the isthmus ventral to the branchial chamber (Figs 6; 7A, B, G, H). These small polygonal plates have a flat to slightly concave base, and basal vascular canals are not visible if present. The crowns of these small plates are ornamented with thin, raised ridges which radiate and bifurcate toward the plate margin (Fig. 7A). Some cranial plates are elongate and have an axial ridge from which the other peripheral ridges diverge, although the pattern of ridge branching and distribution varies. The small polygonal plates that are found anterior to the prepectoral spines on the isthmus grade into anterior body scales around the base of the prepectoral spines.

OPERCULUM

Spathiform opercular plates (branchiostegal rays of Bernacsek & Dineley 1977: 16; hyoidean gill
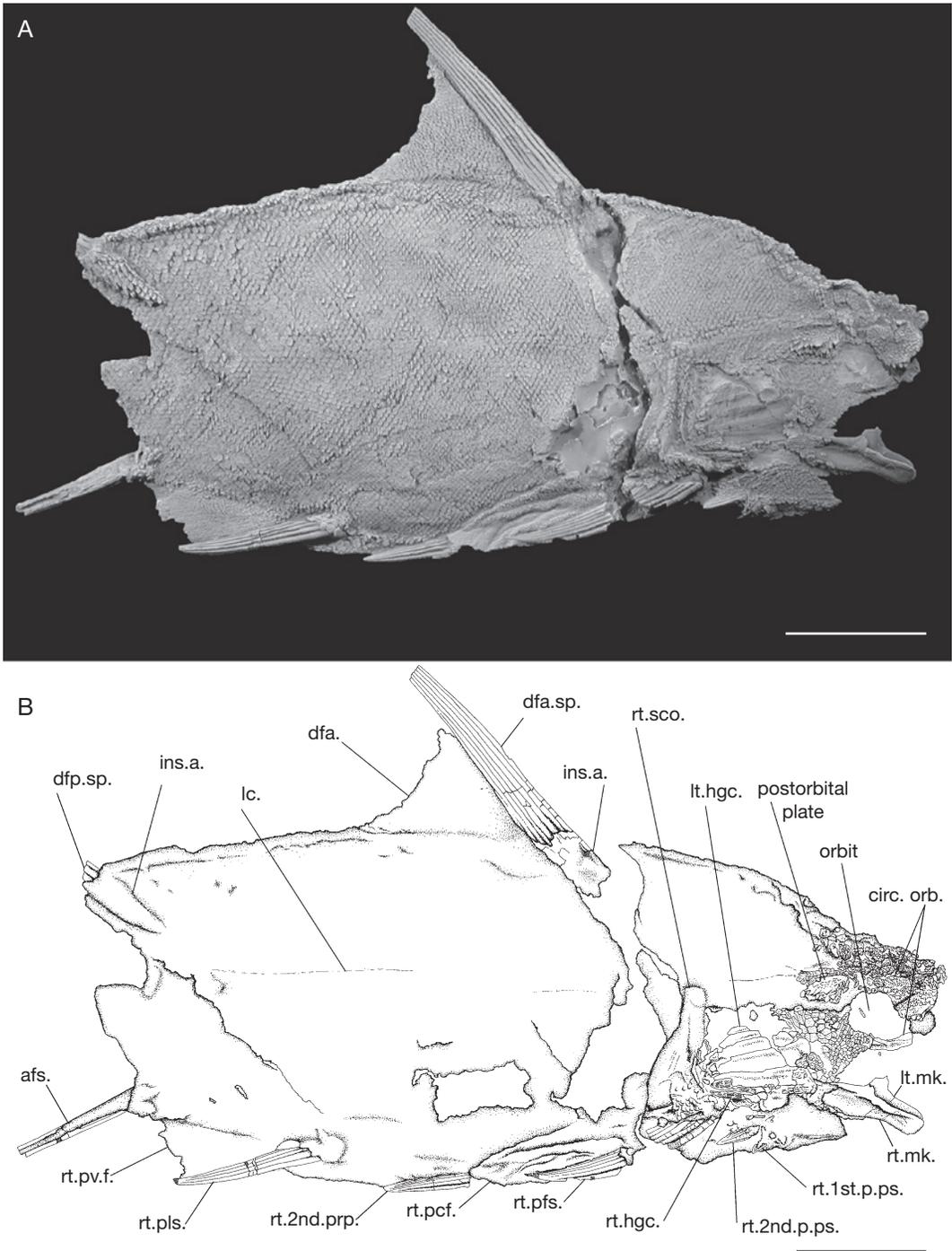
Fig. 3. — Articulated specimen of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (UALVP 41862): **A**, photograph; **B**, camera lucida drawing (1st.prp. pair is between lt. and rt.pfs). Scale bars: 1 cm.
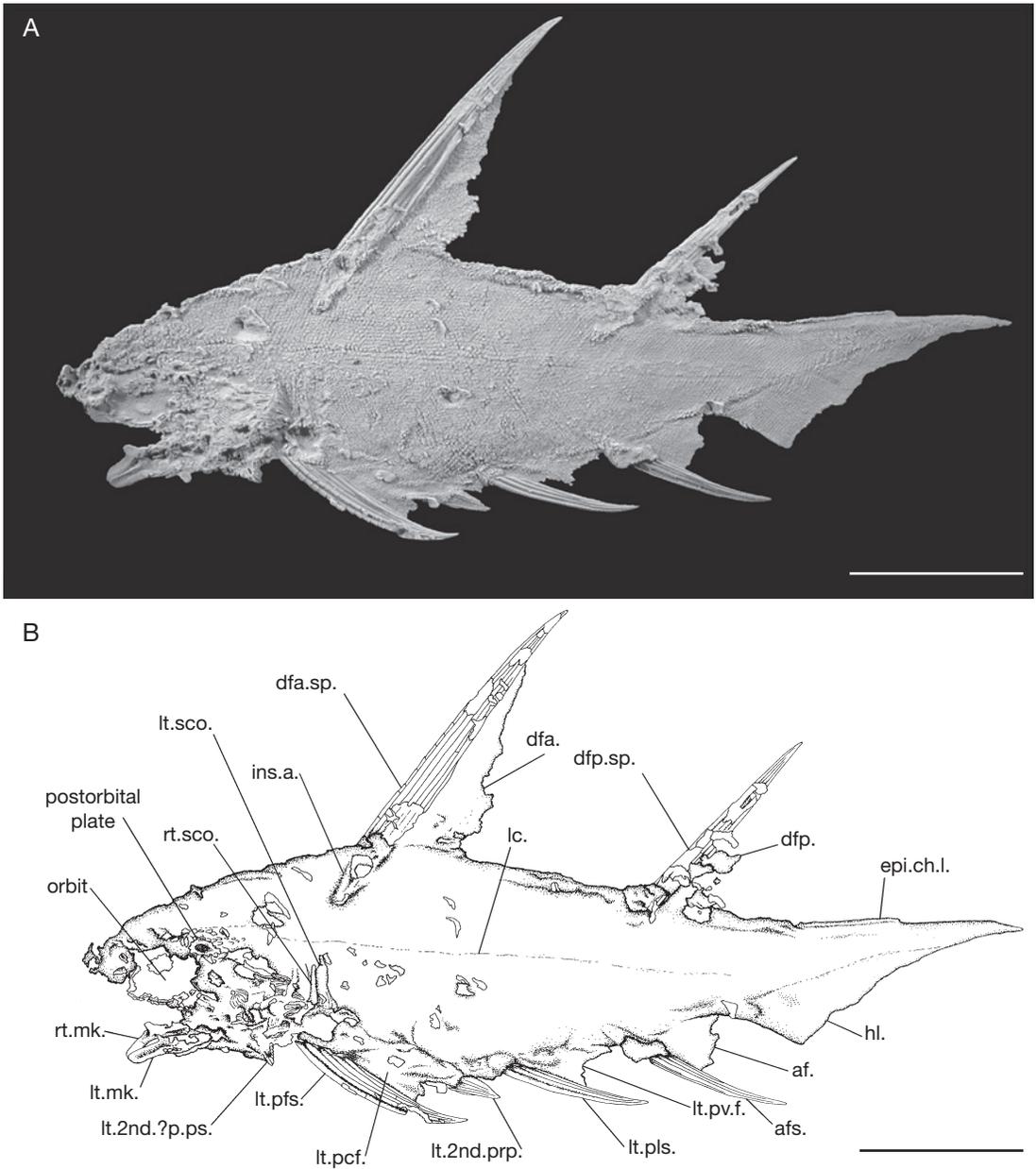
Fig. 4. — Articulated specimen of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (UALVP 41858): **A**, photograph; **B**, camera lucida drawing. Scale bars: 1 cm.

covers as used by others) insert just behind the posterior-most edge of the Meckel's cartilage (Figs 3; 6). Opercular plates from the left and right sides

of the holotype shifted slightly during decay and settling of the carcass, therefore, plates from the left side exhibit external ornament, and those from
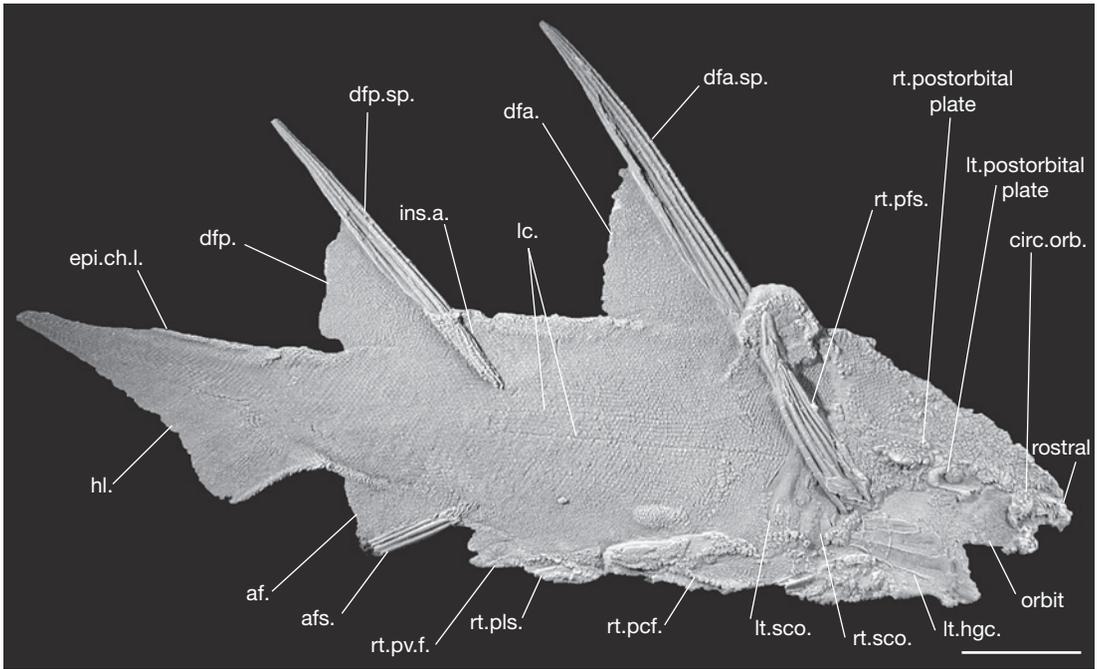
Fig. 5. — Photograph of an articulated specimen of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (UALVP 38679). Scale bar: 1 cm.

the right side display their visceral surface (Fig. 2). There are four to six opercular plates present in the series (Bernacsek & Dineley 1977; see also Fig. 6). The largest opercular plates are situated near the centre of the operculum, flanked by smaller, shorter plates dorsally and ventrally. This plate group forms a compound dermal shield covering the entire branchial chamber, but the plates are not fused and likely had limited flexibility where the individual plates abut each other (Figs 2; 3; 5; 6). The opercular plates terminate just anterior to the postbranchial lamina of the scapulocoracoid (Figs 2; 3; 5; 6B).

The intersecting ridges covering each opercular plate of *G. probaton* (Figs 2; 6A; 7H) are nearly identical to the ornamental ridges of the opercular plates of *Uraniacanthus spinosus* (Fig. 8A; Miles 1973: pl. 13, fig. 1). The basal surface of each opercular plate of *G. probaton* and *U. spinosus* possesses a shallow, longitudinal sulcus (Figs 3; 5; 6B). The opercular shields of both *G. probaton*

and *U. spinosus* are compound structures lacking sensory grooves, and in these two characteristics, differ from the opercular shields of *Culmacanthus stewarti* Long, 1983, *C. antarctica* Young, 1989, and *C. pambulensis* Young, 1989 (Long 1983: figs 2b, 3, 9; Young 1989: figs 2a-d, 3-5).

As described by Bernacsek & Dineley (1977: 16), "high crowned tesserae" are positioned just dorsal to the opercular plates to form the "dorsal portion" of the operculum. The crowns of these suprabranchial scales are similar to the small scales posterior to the branchial chamber (Fig. 9B, C), in that each scale is ornamented with longitudinal ridges which continue over the entire length of the crown and converge towards the posterior tip of the scale. The suprabranchial scales have a low neck and a flat base.

PALATOQUADRATE
The upper jaw of *Gladiobranchus* is not preserved in any of the available specimens. An unossified
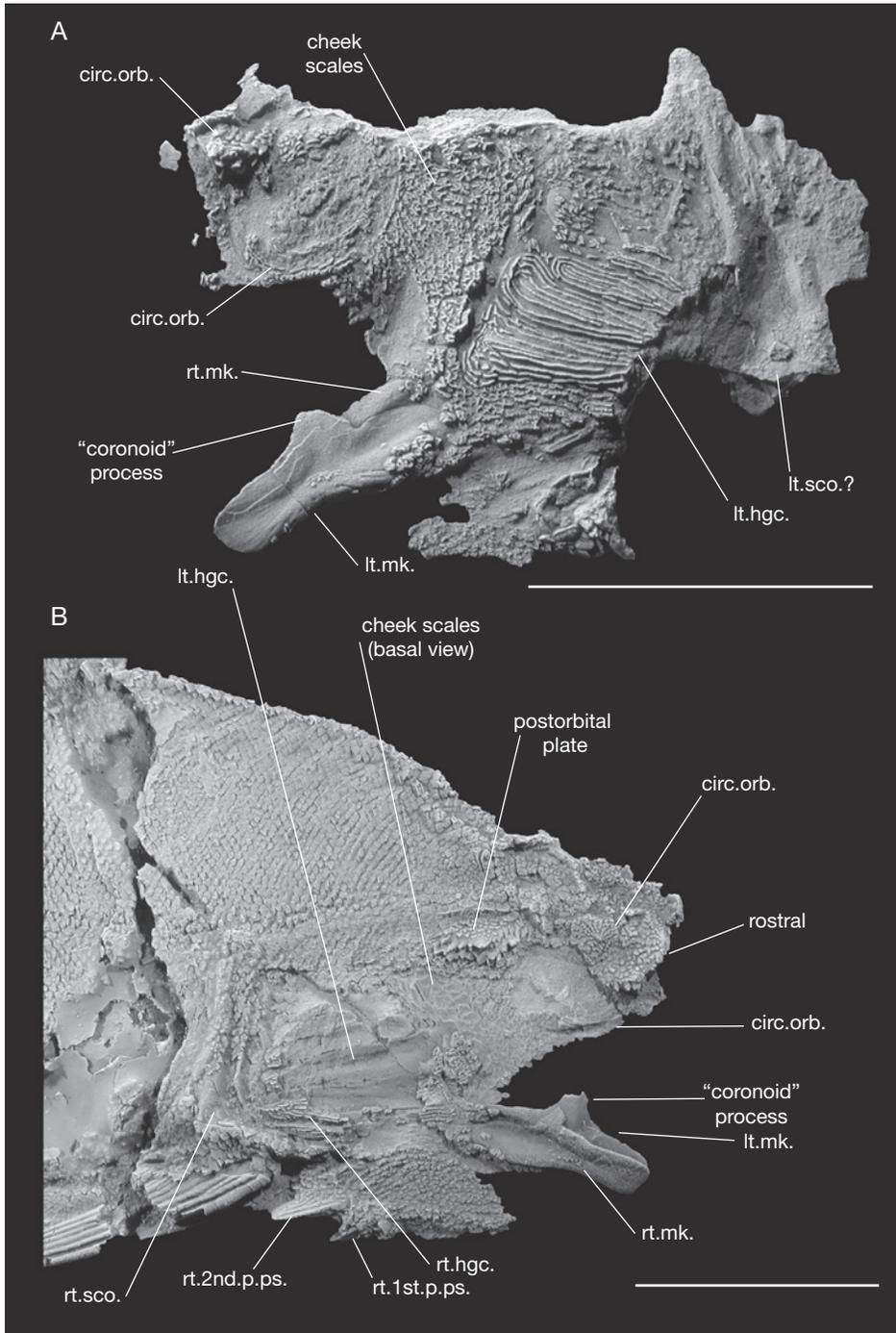
F𝐼G. 6. — Photographs of articulated specimens of *Gladiobranchus probaton* Bernacsek & Dineley, 1977: **A**, portions of the head and branchial chamber (UALVP 42095); **B**, head and pectoral girdle (UALVP 41862). Scale bars: 1 cm.
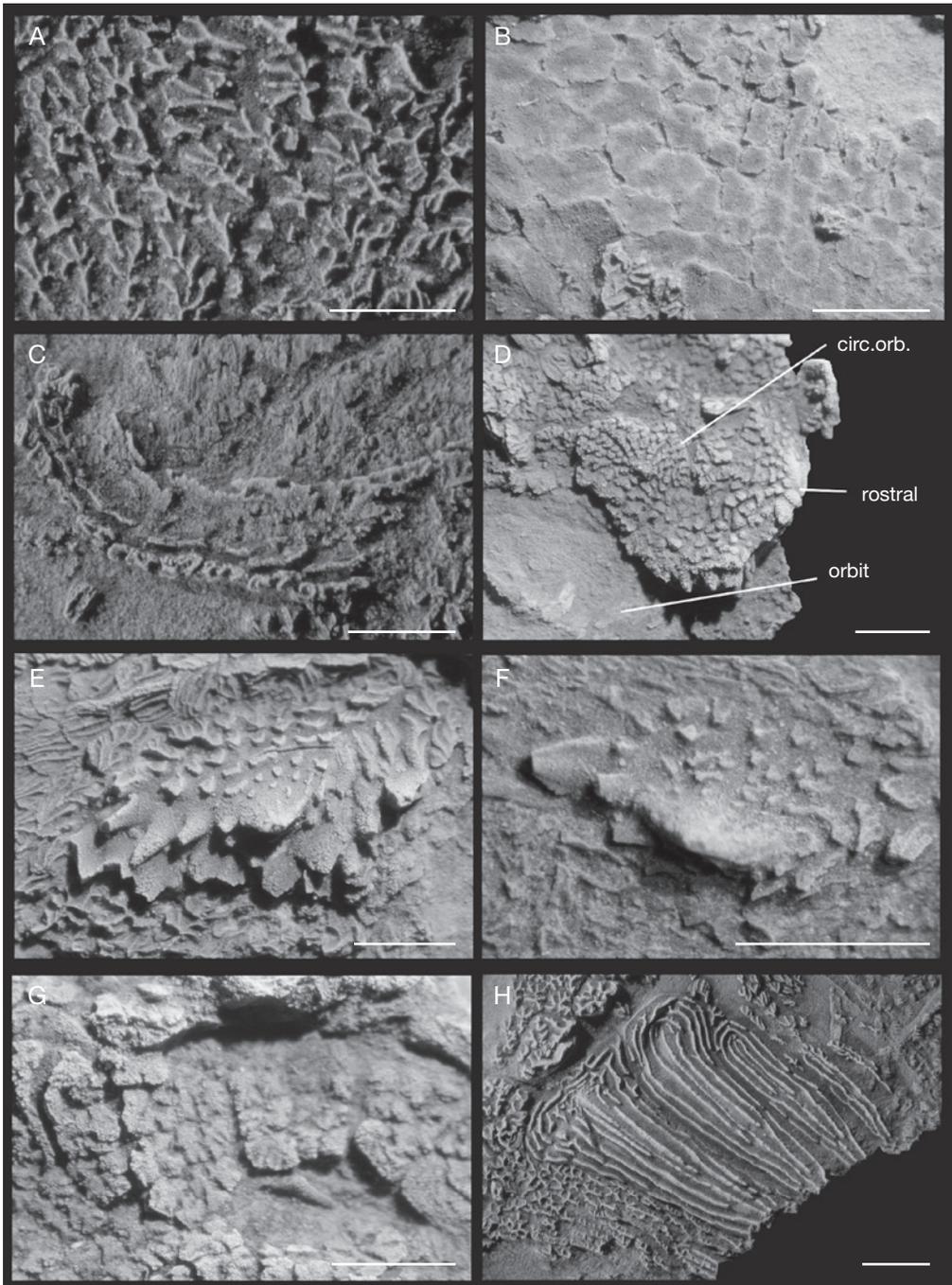
Fig. 7. — Photographs of cranial armour of *Gladiobranchus probaton* Bernacsek & Dineley, 1977: **A**, small, ridged scales from the cheek (UALVP 42095); **B**, same scale type in basal view (UALVP 41862); **C**, small circumorbital scales specialized to support the infraorbital sensory canal (UALVP 42095); **D**, enlarged preorbital scales (UALVP 41862); **E**, postorbital plate (UALVP 41862); **F**, postorbital plate (UALVP 38679); **G**, enlarged tesserate scales over the orbits (UALVP 41862); **H**, external view of the opercular plates (UALVP 42095). Scale bars: 1 mm.

palatoquadrate (i.e. apparent absence) is consistent with previous observations of all other diplacanthoid genera except *Tetanopsyrus lindoei* and *T. breviacanthias* (Gagnier *et al.* 1999; Hanke *et al.* 2001), which have perichondrally-ossified mandibular arch.

MECKEL'S CARTILAGE

The lower jaw is preserved as a single, perichondrally-ossified unit, which articulates anteriorly with its counterpart at the symphysis (Figs 3; 4; 6; 9D). In all specimens of *G. probaton* which retain their jaws, the two halves of the lower jaw meet at the anterior tip suggesting a firm symphyseal connection in life. Viewed laterally, the antero-posterior axis of Meckel's cartilage is slightly convex and a large, sub-triangular anterodorsally-directed process emerges from the dorsal edge midway along the length of the jaw (Figs 6; 9D). Anterior to this process, the jaw is slender and flares slightly laterally at the symphysis.

The posterior end of the jaw forms a deep, spoon-shaped blade with a large shallow depression which may have served for jaw muscle attachment (Fig. 9D). The shallow depression of the posterior half of Meckel's cartilage continues anterior to the dorsally-directed process as a shallow trough. The ventral edge of Meckel's cartilage is thickened and perforated by fine canals which could have housed blood vessels (Fig. 9D). Viewed dorsally, the lower jaw curves medially to the level of the anterodorsally-directed process, and then straightens to meet its antimere at the symphysis, thus forming a narrow scoop. The lower jaw may have been a simple scoop or could have acted as a slicing blade, but none of the *Gladiobranchus* specimens show stomach contents and so we cannot speculate on how the jaws helped procure prey.

The Meckel's cartilage of some diplacanthoid taxa, namely: *Diplacanthus crassissimus*, *Rhadinacanthus longispinus* (Agassiz, 1845), *D. tenustriatus* (Traquair, 1894), *D. ellsi*, *D. horridus*, and *Milesacanthus antarctica* Young & Burrow, 2004, is supported externally by dermal splint bones. However, a dermal splint is absent not only in *Gladiobranchus*, but also *Culmacanthus*, and is unknown in *Uraniacanthus*. Note that the ischnacanthid jaws attributed to
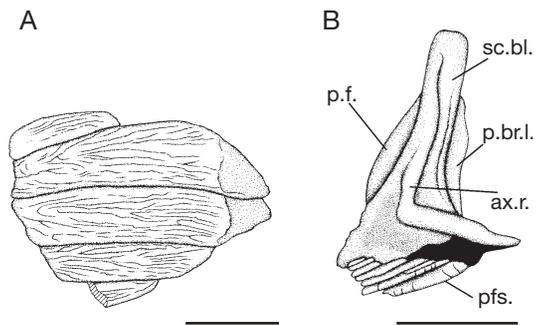

FIG. 8. — Camera lucida drawings: **A**, ornamented surface of the spathiform opercular plates of *Uraniacanthus spinosus* Miles, 1973 (BNMH P.16612); **B**, right scapulocoracoid of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (UALVP 41862) after Davis (2002: figs 2.3.2b, 5.3a). Scale bars: A, 1 cm; B, 0.25 cm.

Uraniacanthus spinosus (Miles 1973: pl. 12, fig. 1, text-fig. 17a) were found in the same outcrop, not in articulation with *U. spinosus* body fossils.

SCAPULOCORACOID

The scapulocoracoid of *G. probaton* is a perichondrally-ossified structure (Figs 2-6; 8B). This bone closely resembles the "sail-like" scapulocoracoids found in the MORS diplacanthids. Young (1989) corrected Bernacsek & Dineley (1977) when he noted that the scapulocoracoid of *Gladiobranchus* is not "a low broad element" but instead has "a higher dorsal termination, with an anterior ridge and expanded posterior ventral part". Young's reassessment correctly steered *Gladiobranchus* towards a diplacanthid taxonomic placement. The tall, straight dorsal scapular blade narrows towards the dorsal tip. The lateral surface of the scapular blade is convex with a prominent axial ridge spanning the length of the blade (Figs 6B; 8B). At the junction between the scapular blade and the coracoid portion of the scapulocoracoid, the axial ridge seems to turn anteriorly, almost perpendicular to the scapular blade (Figs 6B; 8B). This apparent bend in the axial ridge is seen only on UALVP 41862, and may have been caused the basal rim of the left pectoral fin-spine pressing upwards through the scale cover and scapulocoracoid during compression of the carcass.
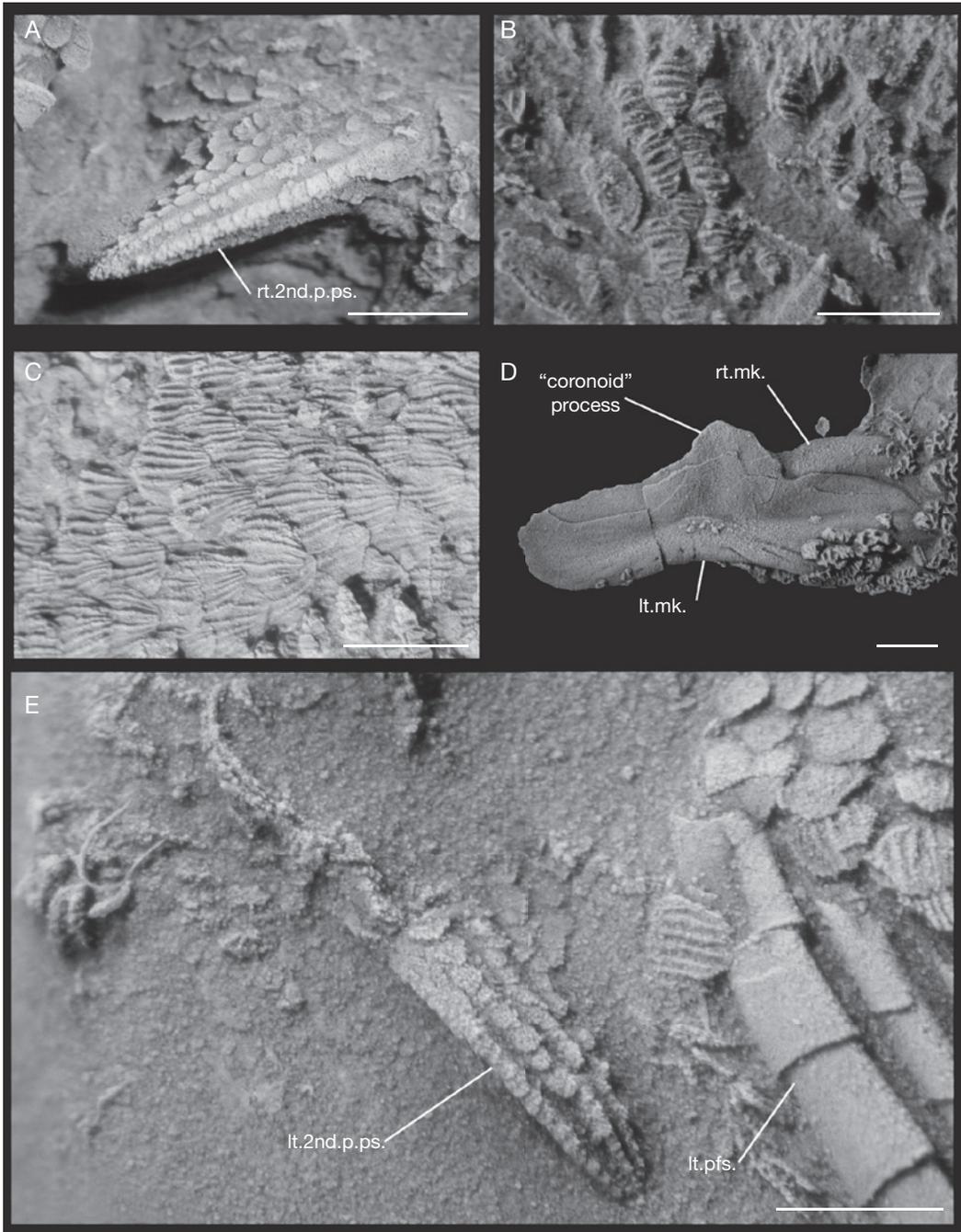
F_{IG}. 9. — Photographs of cranial and pectoral structures of *Gladiobranchus probaton* Bernacsek & Dineley, 1977: **A**, second prepectoral spine and surrounding scales (UALVP 41862); **B**, **C**, ridged suprabranchial scales (UALVP 42095, and UALVP 41862, respectively); **D**, lower jaws (UALVP 42095); **E**, second prepectoral spine, surrounding scales and leading edge of the pectoral fin-spine (UALVP 41857). Scale bars: 1 mm.

A posteriorly-directed scapular flange (*sensu* Miles 1973: text-fig. 40, p.f) is present, forming a convex trailing edge behind the axial ridge on the scapular blade (Figs 2; 3B; 6B; 8B). This feature is absent in *Uraniacanthus*, *Culmacanthus* and *Ischnacanthus gracilis* (Egerton, 1861). Young & Burrow (2004) suggest that a portion of the posterior flange may have been present but was lost during preparation of the type specimen of *Milesacanthus antarctica*.

In addition, an anterior, postbranchial lamina (*sensu* Miles 1973: text-fig. 40, la.pbr) is present anterior to the axial ridge of the scapulocoracoid of *G. probaton* (Figs 6B, 8B).

The scapulocoracoid of *Gladiobranchus* is tilted slightly forward and the dorsal tip of the scapular blade is squared-off, thus this area is wider antero-posteriorly than in MORS diplacanthids. This wide, blunt scapular-blade tip is also seen in non-diplacanthoid taxa. The scapular blade of *G. probaton* is similar to that of the MORS diplacanthids in that it is approximately D-shaped in cross section, whereas the scapular blade in *Uraniacanthus* (BNMH P16612; Miles 1973: pl. 13, fig. 1; Davis 2002: fig. 5.10c) and *Ischnacanthus* (e.g., UALVP 41491) has an axial trough along the medial surface and is U-shaped in cross section. In most specimens of *G. probaton*, the coracoid region is covered by scales and difficult to reconstruct. The coracoid region articulates with the pectoral fin-spine (seen best in UALVP 41862; Figs 6B; 8B). The pectoral fin-spine articulation appears to be located anteriorly on the coracoid, as in *Culmacanthus* and the MORS diplacanthids.

Scapulocoracoids with an anterior postbranchial and posterior laminae separated by a well-defined axial ridge, may be a synapomorphy of *G. probaton*, the Scottish MORS diplacanthids, *Diplacanthus ellsi* and possibly *D. horridus*. Gagnier's (1996) account of *D. horridus* does not permit comment, and the scapulocoracoids of *Milesacanthus antarctica* resemble those of *Culmacanthus* species (Young & Burrow 2004) and *Uraniacanthus* (Davis 2002: fig. 5.10d).

DERMAL PECTORAL ARMOUR

Bernacsek & Dineley (1977: 15, 16) reported that the dermal armour of the pectoral girdle of *Gladiobranchus* consisted of a large "compound" pinnal plate bearing spines. This is incorrect. Examination of NMC 22700A (Fig. 2), coupled with observations on UALVP 41857, 41858 and 41862, reveal that this feature is absent in *G. probaton* (Figs 3; 6B; 9E).

Isolated fragments of perichondral bone with similar surface texture as the scapulocoracoids are found under the scales of the isthmus of several *Gladiobranchus* specimens. These perichondral bones are not attached to the inserted basal rim of the prepectoral spines, and may represent ossified procoracoids. Better-preserved specimens are needed to confirm the existence of procoracoid bones in *G. probaton*.

Bernacsek & Dineley (1977) may have misidentified fragments of perichondral bone as dermal pinnal plates, which as mentioned above, may indicate the presence of ossified procoracoids. However, new specimens from MOTH indicate unequivocally that the isthmus of *G. probaton* is completely devoid of ornamented dermal plate armour, and is covered instead by scales. Prepectoral spines are inserted into the skin between these scales (Figs 6B; 9A, E).

DORSAL FIN-SPINES

The anterior dorsal fin-spine of *G. probaton* is approximately 20-30% longer, and more stout than the posterior dorsal fin-spine, and is inserted above the pectoral fin, along the dorsal midline (Figs 2-5). Enlarged anterior dorsal fin-spines are also found on *Diplacanthus crassissimus*, both Miguasha diplacanthids, *Culmacanthus* species, and *Uraniacanthus spinosus*; the anterior dorsal fin-spine of *Milesacanthus antarctica* is curved throughout its length, more like that of *Ischnacanthus* species and *Cassidiceps vermiculatus*. *Parexus recurvus* Agassiz, 1845, and *P. falcatus* Powrie, 1870, currently assigned to the Climatiiformes, also have large anterior dorsal fin-spines.

The anterior dorsal fin-spine of *Gladiobranchus* has a prominent insertion area that is roughly 16% of the fin-spine length, is convex anteriorly, and has a straight posterior edge (Figs 2-5). The posterior edge of the insertion area forms the rim for the basal opening of the spine. The insertion area is fluted with smooth, closely-spaced canals. Vascular tissue
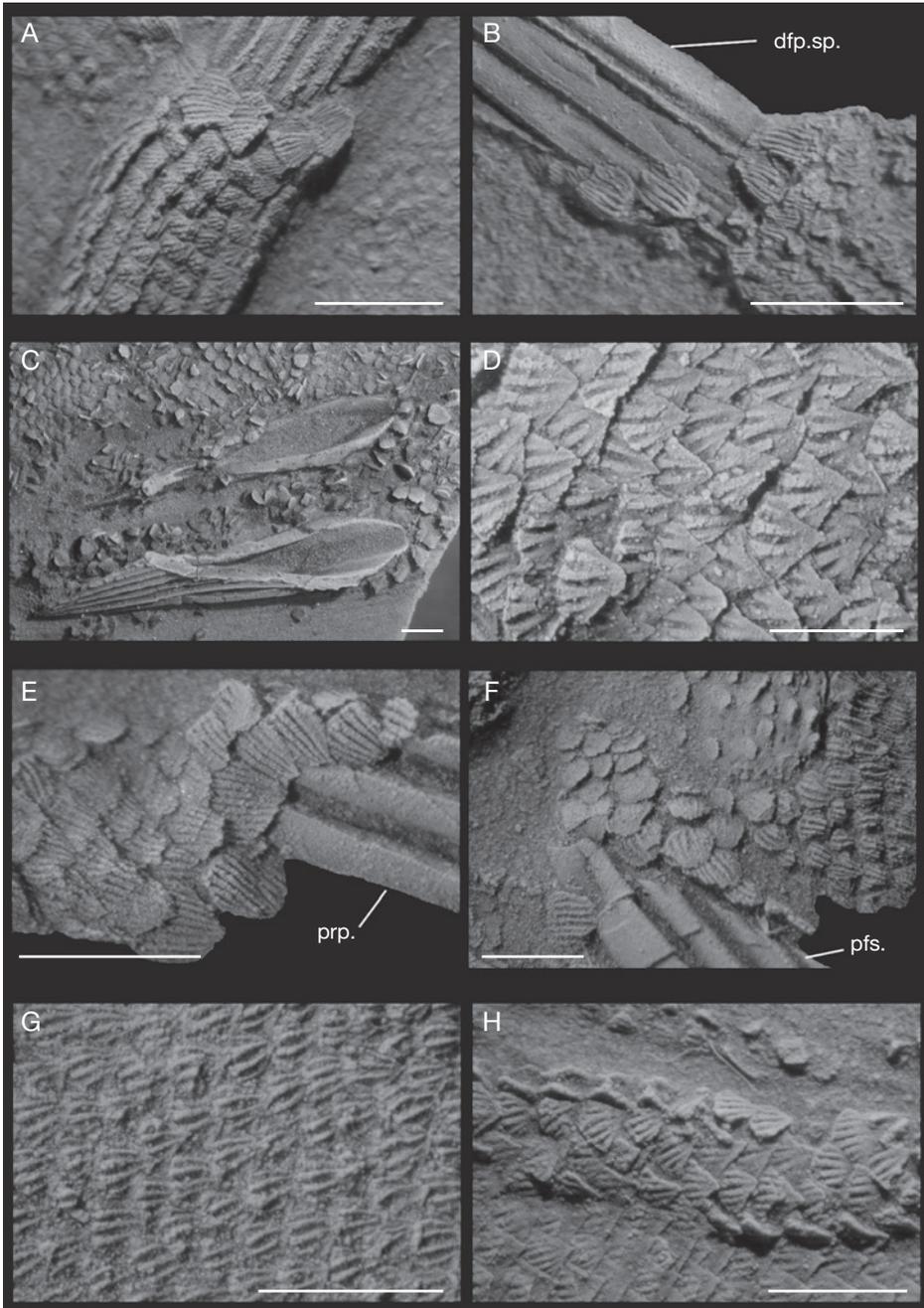
Fig. 10. — Fin-spines and scales of *Gladiobranchus probaton* Bernacsek & Dineley, 1977: **A**, base of the anterior dorsal fin-spine (UALVP 41857); **B**, base of the posterior dorsal fin-spine (UALVP 41669); **C**, second pair of prepelvic spines (UALVP 3????, catalogue number obscured on specimen); **D**, scales from the predorsal midline (UALVP 32448); **E**, enlarged scales from around the posterior prepelvic spine (UALVP 41857); **F**, enlarged scales from around the base of the pectoral fin-spine (UALVP 41857); **G**, postbranchial scales (UALVP 41857); **H**, scales from the dorsal midline, between the two dorsal fins (UALVP 41857). Scale bars: 1 mm.

which supplied the fin-spine probably was housed within the canals; the remaining surface of the insertion area may have attached to muscles and/or ligaments to control fin-spine erection.

Most dorsal fin-spine ribs follow the full length of the spine and only merge near the tip (Figs 3-5). Bernacsek & Dineley (1977: 15) reported that *G. probaton* possessed "eight or nine" ridges (ribs). Our observations indicate that the anterior dorsal fin-spine has six (UALVP 41857 and 41669) or seven (UALVP 38679, 41858, and 41862) ribs per side. The apparent variability of this feature indicates that caution should be applied when using meristic characters as part of a species description (Davis & Martill 1999). The rib count appears to be consistent for all sizes of fish examined (i.e. fin-spine ribs are not added as fish grow).The anteriormost and posterolateral ribs of the dorsal fin-spines bear simple, smooth, reclined nodes towards the base of the spine (cf. the "subquadrate" nodes of the fin-spines of *Tetanopsyrus* species, Gagnier *et al.* 1999; Hanke *et al.* 2001), but spine ribs are smooth distally. The ribs along the side of each spine decrease in thickness posteriorly and towards the spine tip.

The posterior dorsal fin-spine is similar to its anterior neighbour in overall structure with nodular ornament covering the leading few ribs, and an insertion area with similar structure and surface texture (Figs 2-5). The insertion area of the posterior dorsal fin-spine is roughly 25% of the fin-spine length. The posterior dorsal fin-spine has fewer ribs than the anterior dorsal spine, with four ribs in UALVP 41669, and five in UALVP 38679 and 41857. As with the anterior dorsal fin-spine, there is some variability in the number of ribs; Bernacsek & Dineley (1977: 15) only accounted for five ribs. The insertion of the posterior dorsal fin-spine is positioned above the insertion of the anal fin-spine (Figs 4; 5). In contrast, Bernacsek & Dineley (1977: 14) stated that "the posterior dorsal fin-spine is inserted between the pelvic and anal fin-spines". Although the ventral apex of the insertion area is indeed situated just anterior to the insertion of the anal fin-spine, the base of the exserted portion is level with the origin of the anal spine of NMC 22700A (Fig. 2). The relative positions of

dorsal and ventral fin-spines may shift relative to the vertebral axis due to decay, settling, and compression of the carcass.

The bases of the exserted portions of the dorsal fin-spines of *G. probaton* are surrounded by enlarged, finely-ornamented body scales (Fig. 10A, B). The dorsal fin-spines of *G. probaton* lack ossified or calcified endoskeletal basal supports.

ANAL FIN-SPINES
The anal fin-spine is longer and more slender than the pelvic spines. The anal fin-spine also seems to be more laterally compressed in comparison to the other spines of *G. probaton*, and possesses three (UALVP 41857), four (UALVP 38679), and possibly as many as six (UALVP 41858) ribs. The anal fin-spine has smooth ribs which appear similar in size and structure to those of the pelvic fin-spine.

DORSAL AND ANAL FINS
The median fins are homogenous in overall structure and squamation. The dorsal fins are triangular, with straight trailing margins resembling lateen sails, and each is attached to over half of the trailing edge of its respective fin-spine (Figs 3-5). The proximal edge of each median fin (i.e. the foot of the sail) is attached for its entire length to the body wall.

Scales on the median fins (including the caudal fin) are aligned in rows, and are considerably smaller than typical body scales, thus forming an abrupt transition at the body-fin boundary.

CAUDAL FIN
The caudal fin of *G. probaton* is only slightly deflected dorsal to the body axis. The caudal peduncle and the hypochordal lobe of the caudal fin combine to form a large fin (Figs 4; 5). A small epichordal lobe is present dorsal to the caudal fin axis (Figs 4; 5), but may be an artefact of preservation/compaction rather than a feature visible in life, and is present in many acanthodians (e.g., *Brochoadmones milesi*, *Ischnacanthus* spp., *Tetanopsyrus* spp., *Euthacanthus macnicoli* Powrie, 1864, *Mesacanthus mitchelli* (Egerton, 1861), *Triazeugacanthus affinis* (Whiteaves, 1887), and *Lodeacanthus gaujicus* Upeniece, 1996 (Watson 1937; Gagnier 1996; Upeniece 1996; Hanke *et al.* 2001).

PREPECTORAL SPINES

Two posterolaterally-directed pairs of prepectoral spines are present anteromedial to the pectoral fin-spines of *G. probaton* (Figs 2; 3; 6B; 9A, E). The base of each prepectoral spine is attached directly to the body wall rather than a pinnal plate. Minute scales surround the base of each spine where prepectoral spines were pressed into the skin during compaction of the carcass.

The posterior prepectoral spine pair is slightly larger than the anterior pair. Prepectoral spines possess noded longitudinal ribs which surround its circumference and gather at the spine tip. Four ribs are found on each side of the anterior prepectoral spine, and five reinforce each side of the posterior prepectoral spine. Prepectoral spine ribs are smoother towards the spine tip with the leading edge, and the posterolateral ribs exhibiting simple crenulations near the spine base (Fig. 9A, E). Prepectoral spines are present not only in some diplacanthids, but also in *Lupopsyrus* (Bernacsek & Dineley 1977), and climatiiforms such as *Climatius reticulatus* Agassiz, 1845, *Parexus recurvus*, *Vernicomacanthus* Miles, 1973, *Brachyacanthus scutiger* Egerton, 1860, *Sabrinacanthus* Miles, 1973, *Erriwacanthus* Ørvig, 1967, and *Ptomacanthus* Miles, 1973, *Acritolepis ushakovi* Valiukevičius, 2003, and putative chondrichthyans such as *Obtusacanthus corroconis* Hanke & Wilson, 2004, *Lupopsyroides macracanthus* Hanke & Wilson, 2004, *Seretolepis elegans* Karatajute-Talimaa, 1968, and *Kathemacanthus rosulentus* Gagnier & Wilson, 1996. The presence of prepectoral spines likely is an acanthodian symplesiomorphy given their presence in both climatiiform acanthodians and putative chondrichthyans (Hanke & Wilson 2004; Wilson *et al.* 2007).

PECTORAL FIN-SPINES

The pectoral fin-spines of *G. probaton* are dorsoventrally compressed, and curve posteriorly for most of their length (Figs 2; 4; 5). The pectoral spine is the longest of the paired spines but is shorter than both dorsal fin-spines. An insertion area is present, but its structure remains obscured by a cover of scales in all available specimens (Figs 2-5; 6B). However, Bernacsek & Dineley (1977: 23, text-fig. 21) described an isolated pectoral fin-spine

with a prominent insertion area, but unlike dorsal fin-spines, the insertion area of this pectoral spine has irregularly spaced vascular canals.

All pectoral fin-spine ribs are nearly parallel and congregate near the spine tip (Figs 2-5). The leading edge and portions of the posterolateral ribs nearer to the body wall are ornamented with smooth reclined nodes (Fig. 9E). The trailing edge of the pectoral fin-spines lack denticles unlike *Lupopsyrus*, *Vernicomacanthus*, MORS diplacanthids, and both Miguasha *Diplacanthus* species. *Milesacanthus antarctica* and tetanopsyrids also lack denticles on their pectoral spines (Hanke *et al.* 2001; Young & Burrow 2004).

PECTORAL FINS

The pectoral fins in all available *Gladiobranchus* specimens appear lobate, but the precise shape is difficult to determine because of *post mortem* collapse. The fin-base appears to have limited contact with the body wall, but the fin-web extends beyond the tip of the pectoral fin-spine, especially in UALVP 41862 (Fig. 3). The pectoral fin of the holotype is shorter than the pectoral fin-spine (Fig. 2). The anterior margin of each pectoral fin is attached to the trailing edge of the pectoral fin-spine.

PREPELVIC (INTERMEDIATE + ADMEDIAN) SPINES

There are two pairs of posterolaterally directed prepelvic spines (Figs 2-4; 10C). The anterior prepelvic ("admedian") spines are shorter than the posterior ("intermediate") pair and are subcylindrical in cross section with a large, hollow basal cavity. They are positioned medial to the pectoral fin-spine insertion. In most *Gladiobranchus* specimens, the anterior prepelvic spines are obscured by the pectoral spines, however, in UALVP 41862, the anterior prepelvic spines are visible through a break in the pectoral fin-spine. The anterior prepelvic spines are held at a low angle relative to the body wall, and have ribs and ornamentation similar to that of other paired fin-spines. Janvier (1996: 178) stated that diplacanthids had only one pair of prepelvic ("intermediate") spines, and this was possibly the case because "admedian" spines are commonly treated separately from "intermediate" spines. However, in Janvier (1996: fig. 4.61c), the "admedian" spines ventromedial to

the pectoral fin-spines were mistakenly labelled as "intermediate" spines, and the spine pair half-way between the "admedian" spines and the pelvic fin-spines was neither identified nor discussed.

The posterior prepelvic spine pair is inserted at a shallow angle into the ventral wall of the abdomen, just posterior to the insertion area of the anterior dorsal fin-spine. The left and right posterior prepelvic spines are separated from each other by only a narrow gap across the ventral midline (Fig. 10C), and as expected due to the presence of the coelomic cavity, had only a shallow insertion in the body wall. The basal cavity of the posterior prepelvic spines is large and extends for almost two-thirds of the spine's length. The posterior prepelvic spines have a complete cover of fine, smooth ribs which converge only at the spine tip (Fig. 10C).

Pelvic fin-spines and fins

The pelvic fin-spines are situated between both dorsal fin-spines relative to the antero-posterior axis, although slightly nearer to the posterior dorsal fin-spine insertion. The exact position of the pelvic fin-spine insertion varies among specimens, due likely to taphonomic artefacts during decay and compression of the abdominal wall. The pelvic fin-spine angle from the body wall, is approximately parallel to the anal fin-spine (Figs 2-4). Pelvic fin-spines have four (UALVP 41857, 41858, and 41669) to five (UALVP 41862) ribs, which have similar ornamentation and orientation to the long-axis of the spine as for other paired and median fin-spines.

The pelvic fin-web is covered by aligned rows of minute scales, which form an abrupt transition to the larger scales near the ventral midline of the body. The pelvic fin-web has a long basal attachment to the body wall, and almost the entire length of the pelvic fin-spine (Fig. 2). The trailing margin of the pelvic fin-web is poorly preserved in all available specimens.

Scale ornament and variation

The body scales of *G. probaton* show two extremes of ornamentation which intergrade. Scales with distinct ridges are found over the entire anterior third of the body in a tapering band along the dorsal and ventral midline, around the bases of the median and paired fin-spines, and on the dorsal, anal, and paired fin-webs (Figs 9E; 10A, B, D-H). These ornamented scales grade into the flat, smooth-crowned scales along the mid-flank, on the caudal fin axis, and the caudal fin-web (Fig. 11A). The largest body scales are found near the posterior dorsal fin, and scales decrease in size away from this region.

The ridged scales of the body differ slightly from the suprabranchial scales mentioned previously, in that the body scales have wide and flat-topped ridges which cover the entire scale crown (Figs 11A, B; 12A-M); the ridges on the suprabranchial scales are arched in cross section and are narrow relative to the intervening troughs (Fig. 9B, C). The smallest ornamented body scales are found behind the branchial chamber and have fewer longitudinal ridges than the suprabranchial scales (Fig. 10G).

The number of ridges on the ornamented scales is fairly consistent over the body. The scales around the pectoral fin base have up to seven ridges, those around the bases of the pelvic fins have up to eight ridges; scales along the dorsal and ventral midline have as many as eight ridges, and other body scales can have up to six ridges (Figs 10A, B, D-H; 11A, B; 12A-M). The transitional scales, where the ridged scales grade into the flat-crowned flank scales, may have up to nine narrow ridges (Fig. 11A, B).

The scales along the predorsal midline have wide, flat-topped, nearly parallel ridges which continue over the entire crown (Fig. 12A-M). Similar scales are found along the dorsal and ventral midline, although the scales that found posteriorly along the body have narrower ridges.

Scales on fin-webs are similar in shape to typical body scales, although they are much smaller (Fig. 11C). The fin-web scales decrease in size towards the distal edge of the fin, and are aligned in rows. Fin-web scales are ornamented with five to ten ridges which run the full length of the crown, and in some scales, these ridges converge toward the posterior tip of the crown. Fin-web scales have low necks and a small, flat to convex mass of basal tissue.

The transition between the ornamented scales and the flat-crowned scales of the mid-flank and caudal fin is gradual (Fig. 11A, B). The ridges on the crowns of these transitional scales are thin and low.
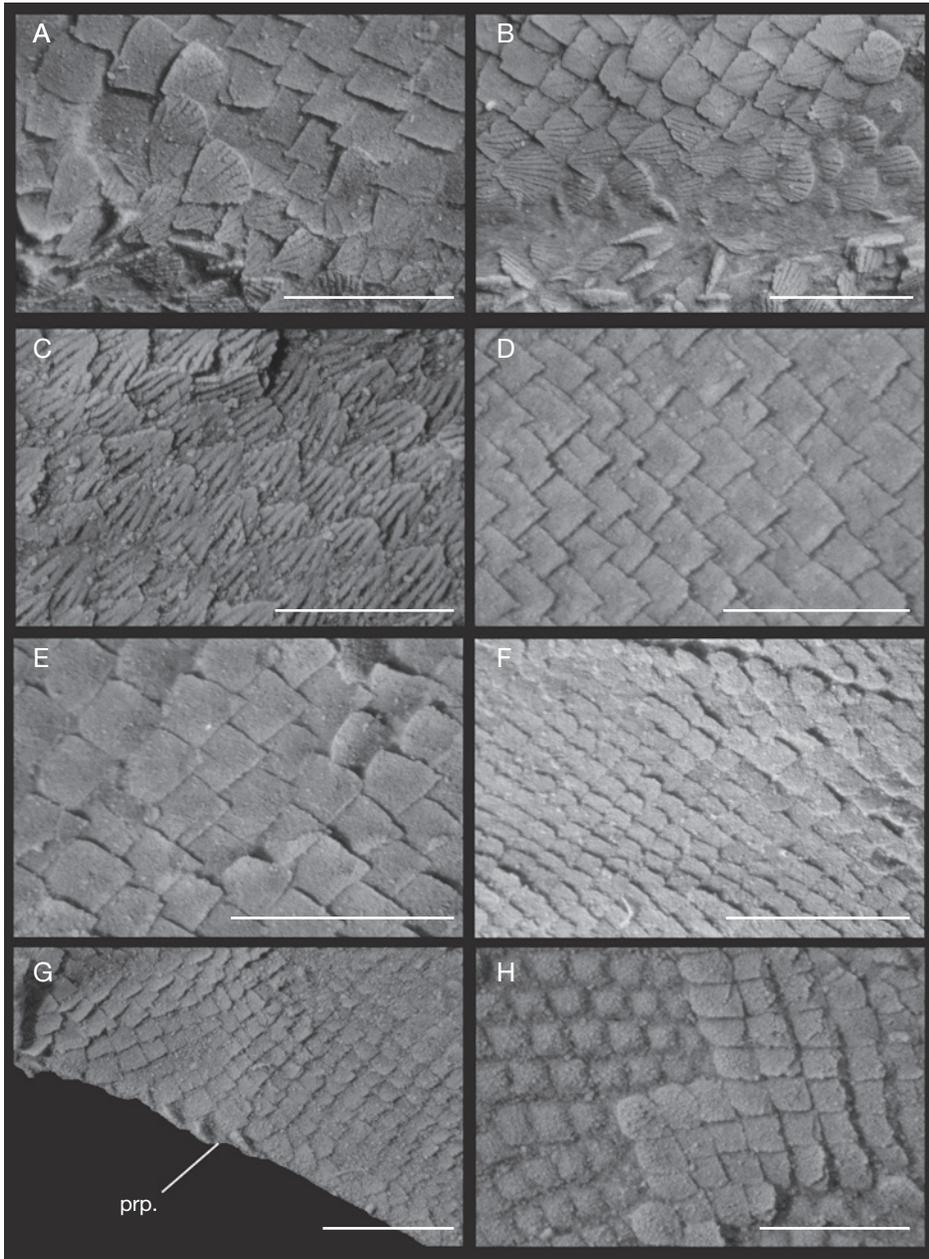
Fɪɢ. 11. — Body and fin scales of *Gladiobranchus probaton* Bernacsek & Dineley, 1977: **A**, transitional scales near the anal fin-web (UALVP 3????, catalogue number obscured on specimen); **B**, transitional scales just anterior to the pelvic spines (UALVP 41862); **C**, scales from the predorsal midline (UALVP 32448); **D**, smooth body scales from mid-flank below the posterior dorsal fin (UALVP 41857); **E**, smooth scales from the caudal peduncle (UALVP 38679); **F**, caudal fin scales (UALVP 38679); **G**, scales along the leading edge of the hypochordal lobe of the caudal fin (UALVP 41858); **H**, narrow scales found in the posterior third of the caudal-fin axis (UALVP 41857). Scale bars: 1 mm.
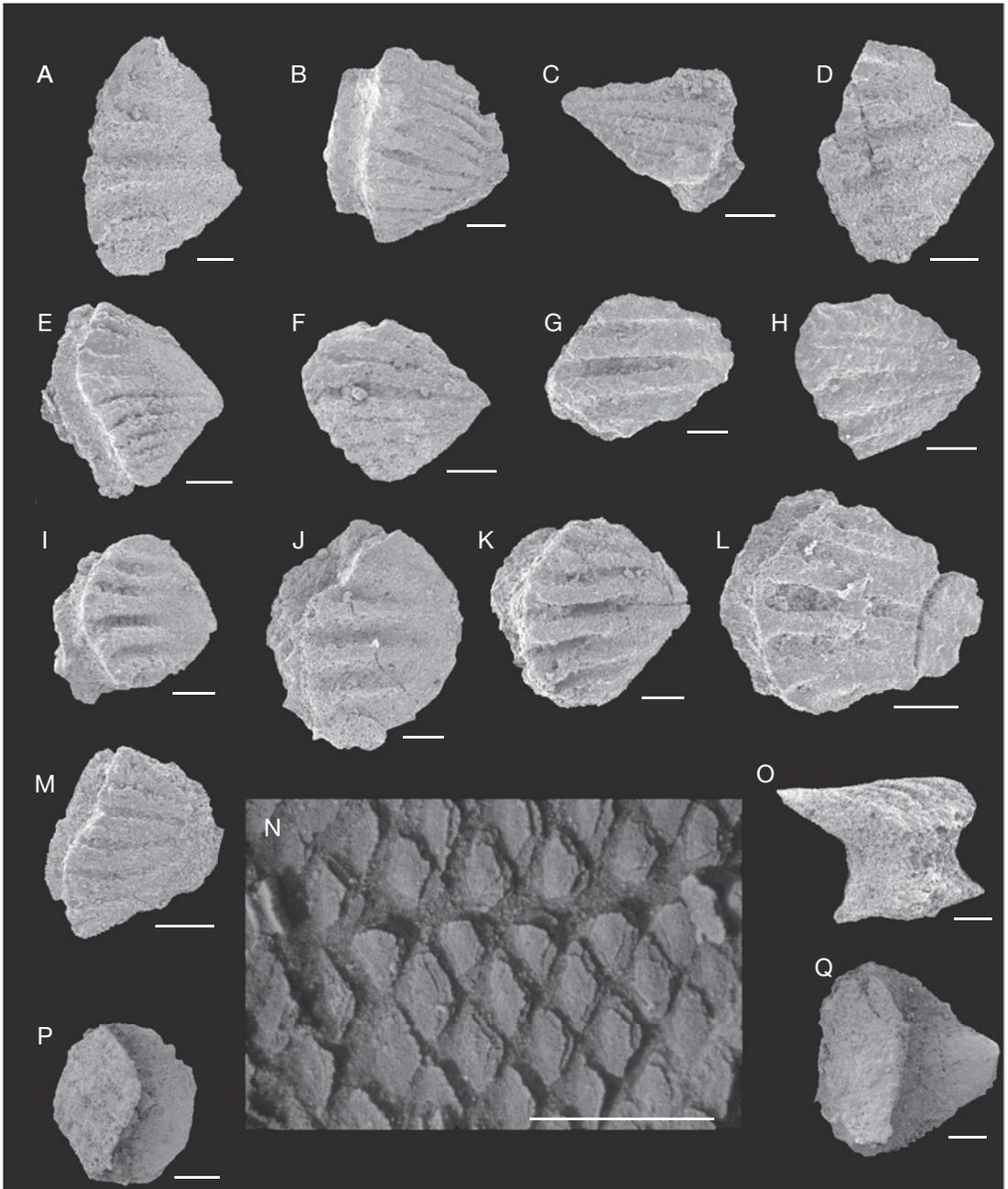
Fɪɢ. 12. — SEM images of isolated scales of *Gladiobranchus probaton* Bernacsek & Dineley, 1977, all scales in crown view taken from UALVP 32448, and all scales in basal views taken from UALVP 3???? (catalogue number obscured on specimen): **A-M**, ridged predorsal and dorsal and ventral midline scales in crown view; **N**, basal view of scales adjacent to the main lateral line below the anterior dorsal fin of UALVP 3???? (catalogue number obscured on specimen); **O**, predorsal scale in side view showing the flat mass of basal tissue and unornamented neck; **P**, **Q**, scales from the mid-flank in basal view, showing the flat, transversely expanded base, and the overhanging posterior end of the crown. Scale bars: A-M, O-Q, 100 μm; N, 1 mm.
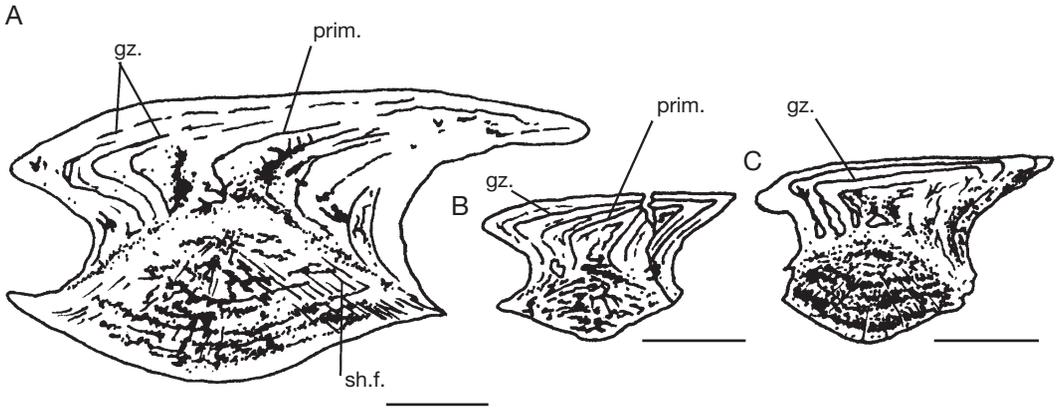
FIG. 13. — Camera lucida drawings of thin sections of body scales of *Gladiobranchus probaton* Bernacsek & Dineley, 1977 (all from UALVP 32448): sagittal sections of typical body scales. Scale bars: 100 μm.

Most scales on the mid-flank and all scales on the caudal-fin axis and caudal fin-web have smooth, flat crowns (Fig. 11D-H). The shape of the crown of most ornamented and smooth body scales is similar. These scales have rounded anterior margins and straight to slightly curved sides which converge to an acutely-pointed trailing tip. Scales with convexly-curved sides and crowns which are convex in transverse section are found around the bases of fin-spines, on the leading edges of the caudal fin, and on the dorsal and ventral midline of the caudal peduncle. The crowns of all body and fin-web scales are larger than their respective bases, and therefore, bases can not be seen in crown view. The trailing tip of both ornamented and smooth scales overlaps the leading edge of adjacent scales, and scales are aligned in oblique rows on the body and fins (Figs 10A, D, G, H; 11).

The basal tissue and the neck rim of scales may be rhombic to round in basal view (Fig. 11H), although most body and fin-web scales have transversely-expanded rhombic bases (Fig. 12N, P, Q). Scales with rounded bases are found towards the dorsal and ventral midline and along the caudal axis, and may have permitted increased flexibility at these positions. Scale bases adjacent to the main lateral line are truncated on the side closest to the lateral line (Fig. 12N).

The neck and basal tissue is attached to the anterior half of the scale crown (Fig. 12O, Q). Minute scales

from the fin-webs and behind the head have shallow necks, whereas those at the bases of the fin-spines and on the flank have elongate necks. The neck canals are not visible in most scales, however, few eroded scales show neck canals; these neck canals align in the superpositioned odontodes to form radial canals. The necks of body scales appear smooth.

There is an abrupt transition from the larger scales on the caudal-fin axis to the small scales on the caudal fin-web (Figs 4A; 5; 11G). The scales on the caudal fin-web are aligned in rows, have narrow, acutely-pointed crowns, and decrease in size towards the margin of the fin-web (Fig. 11F, G). Caudal fin-web scales have small flat-to-convex bases and low necks in comparison to body and caudal axis scales. The neck and basal tissue of each fin-web scale is expanded into a narrow, rhombic structure. Enlarged fin-web scales with convex crowns reinforce the leading edge of the hypochordal lobe of the caudal fin (Fig. 11G).

The caudal-fin axis is covered with elongate, narrow, smooth-crowned scales which decrease in size towards the posterior tip of the caudal axis (Fig. 11H). These caudal-axis scales have round to rhombic bases and a low neck.

FIN-SPINE MICROSTRUCTURE
None of the fin-spines of *G. probaton* have been thin-sectioned, and therefore, it is not possible at present to give a detailed account of spine microstructure.

SCALE MICROSTRUCTURE

The body scales of *G. probaton* have a large primordium relative to the entire scale crown, and few (up to four), thick growth zones (Fig. 13). Each growth zone is supplied by a large diameter ascending canal, and the scale crown is composed of orthodentine. The basal tissue appears to be acellular, but in all of the sections prepared the basal tissue has dark pyrite inclusions, and cell lacunae, if originally present, may be obscured. The basal tissue shows lamellar growth increments and lacks basal vascular canals, however, traces of Sharpey's fibres are abundant (Fig. 13A). None of the prepared thin sections intercepted a neck canal and/or radial canal.

DISCUSSION

Gladiobranchus probaton was described by Bernacsek & Dineley (1977) based on poorly preserved specimens (NMC 22700A, 22701A, 22701B, 22702, and 22703). *Gladiobranchus* originally was assigned to the Ischnacanthiformes (*sensu* Miles 1973) because of a notable resemblance to *Uraniacanthus spinosus*, and that both genera shared a similar dermal shoulder girdle and opercular armour. The incomplete body fossils available to Bernacsek & Dineley lacked teeth and/or dentigerous jaw bones, and until now, the classification and relationships of *G. probaton* have remained unresolved. Furthermore, errors in the original description of *U. spinosus* complicated attempts to accurately classify both *U. spinosus* and *G. probaton*. The anatomy and systematic relationships of *Gladiobranchus* have been discussed to varying degrees by Denison (1979: 32), Long (1983: 52), Young (1989: 19), Hanke *et al.* (2001: 747-752), Young & Burrow (2004: 25), Hanke & Wilson (2004: 206-209, fig. 12), and Wilson *et al.* (2007: 140).

Bernacsek & Dineley (1977) failed to recognize the significance of the postorbital plate on *Gladiobranchus*. Although they mentioned that an enlarged postorbital plate was present in *Diplacanthus* and other climatiiforms, they did not think that this plate had any taxonomic relevance. Denison (1979) recognized that *G. probaton* shared no derived characteristics with ischnacanthiforms, and

used the compact branchial chamber, enlarged circumorbitals, deeply inserted fin-spines, and probable absence of teeth, to support the relationship between *G. probaton* and diplacanthid acanthodians. However, Long (1983: 52) disagreed with Denison, and suggested that *Gladiobranchus* be reclassified with *Uraniacanthus* based on the body shape, the presence of similarly enlarged hyoidean gill covers (opercular plates as used here), the presence of a low scapula, and the fact that *Climatius*, *Brachyacanthus* and *Parexus* have slightly enlarged head scales posterior to the eye. Because Long (1983: 52) realigned *Gladiobranchus* with *Uraniacanthus*, by default, *Gladiobranchus* was reclassified as an ischnacanthiform following Miles' (1973) original errors in the description of *U. spinosus* (see below). Unfortunately, Long (1983) considered that the postorbital plate of *Gladiobranchus* was too much like the enlarged head scales of *Climatius*, *Parexus* and *Brachyacanthus* to warrant its use as a diplacanthid character, even though the enlarged head scales of the latter three taxa are not part of the circumorbital series.

GLADIOBRANCHUS AS AN ISCHNACANTHID

Since Bernacsek & Dineley (1977) associated *Gladiobranchus* with *Uraniacanthus*, and since *Uraniacanthus* was classified as an ischnacanthiform by Miles (1973), it is important to review the characters defining the Ischnacanthiformes. Miles (1966: 166) suggested that ischnacanthiform fishes should have the following features: 1) *Acanthodes*-type body scale microstructure and *Poracanthodes*-type scales along some of the cephalic lateral lines; 2) two dorsal fins; 3) no intermediate (prepelvic) spines; 4) fin-spines deeply inserted into body wall; 5) no ventral shoulder girdle plates; 6) gill covers which shield the entire gill chamber laterally; 7) strong jaw bones (upper and lower) to which teeth are ankylosed; and 8) symphysial tooth whorls in the mouth.

Later, Miles (1973: 150, 151) thought that the tall, deeply inserted dorsal fin-spines, and the presence of two pairs of prepelvic ("intermediate") spines of *Uraniacanthus* were "superficial" because they were also present in the climatiiforms. Therefore Miles instead emphasized dentigerous jaw bones, the lack of ventral dermal armour and prepectoral

spines, and the presence of deep insertions for the dorsal and anal fin-spines in his attempt to classify *Uraniacanthus* as an ischnacanthiform. Unfortunately, Miles assigned a dentigerous jaw to *Uraniacanthus* which was found in the same outcrop, even though the jaws themselves were not found in articulation with any body fossils of *U. spinosus* (P.53032, Miles 1973: 148-150, pl. 12, fig. 1, and text-fig. 17a). The subsequent misinterpretation of the postorbital plate as a dentigerous jaw bone (see Miles 1973: 150, pl. 13, figs 1, 2, dg.b), coupled with the fact that these specimens had not been critically re-examined until recently, meant that *Uraniacanthus* has remained as an ischnacanthid in most classifications. The similarity between *Gladiobranchus* and *Uraniacanthus* and the fact that the earlier known specimens of both, lacked articulated jaws, only perpetuated the uncertainty in the relationships of these two taxa.

To accommodate *Uraniacanthus*, Miles (1973) amended his 1966 definition of the Ischnacanthiformes. To do this, he changed character 3 (above) to read: intermediate (prepelvic) spines present. He also deleted characters 1, 6, and 8 because of uncertainty of how widely distributed these features were within ischnacanthids. Also, the histological character (character 1) is not informative relative to ischnacanthiforms because *Acanthodes*-type scales obviously are found in acanthodiforms and are not unique to a single order. Furthermore, with such loose definitions, characters 6 and 8 are indeed widespread among gnathostomes (Janvier 1996) and not unique to ischnacanthiforms. Miles also eliminated character 4 (deeply inserted fin-spines), although he did not mention this in his revised diagnosis.

Miles' amended diagnosis of the Ischnacanthiformes now included: 1) the presence of dentigerous jaw bones in both upper and lower jaws; 2) intermediate (prepelvic) spines present; 3) two dorsal fins present; and 4) dermal plates and prepectoral spines absent. Essentially, Miles (1973) took features of *Uraniacanthus* and integrated them into a revised Ischnacanthiformes, and this classification was not challenged until Bernacsek & Dineley (1977) published their description of *Gladiobranchus*. As an aside, it is interesting to note

how, even in recent works, characters supporting established classification schemes are modified and truncated to accommodate new taxa rather than acknowledging the anatomical diversity exhibited by new taxa (e.g., Gagnier & Wilson 1996a, b; Long 1983; Young & Burrow 2004). This practice underestimates anatomical diversity and lumps disparate taxa together, often based on features that probably are symplesiomorphies.

Bernacsek & Dineley (1977) thought that *Gladiobranchus* was closely related to *Uraniacanthus*, and following Miles' (1973) amended classification scheme, they argued for the inclusion of their new taxon within the Ischnacanthiformes. Taking Miles' (1973) amended character list as a template, except character 2 (the presence of prepelvic spines, which they ignore in their account), Bernacsek & Dineley (1977) set out to revise characters to support a gladiobranchid/ischnacanthid relationship. However, they mistakenly thought that *Gladiobranchus* had dermal pectoral plate armour with fused prepectoral spines. Dermal pectoral plate armour is simply not present in any ischnacanthid taxa known. Furthermore, Bernacsek & Dineley (1977) could not demonstrate the presence of dentigerous jaws from the partial body fossils they had available. In short, Bernacsek & Dineley failed to convincingly lump *Gladiobranchus* into the Ischnacanthiformes.

Although new specimens reveal that *Gladiobranchus* lacks dermal pectoral plate armour, the absence of such plates is taxonomically uninformative given that given that a wide range of taxa, including *Lupopsyrus*, *Brochoadmones*, *Tetanopsyrus*, *Paucicanthus*, *Cassidiceps*, *Milesacanthus*, ischnacanthiforms, and acanthodiforms also lack this feature. The presence of two dorsal fins (Miles' original character 2) is also primitive for acanthodians.

Bernacsek & Dineley (1977) were left with one character (dentigerous jaw bones in upper and lower jaws), but they dismissed this feature because species of *Nostolepis* Pander, 1856 (presumed to be climatiid acanthodians) were also thought to possess dentigerous jaw bones (a thought that has yet to be demonstrated based on any articulated body fossils). Jaw fragments and scales also were associated in the descriptions of *Acanthospina irregulare* Valiukevičius, 2003, and *Acritolepis ushakovi*

(Valiukevičius 2003: 138, 141, 142, 188, 189, figs 3, 46), and articulated body fossils with jaws have yet to be found. Bernacsek & Dineley (1977) agreed that the presence of dentigerous jaw bones in both climatiiform (i.e. *Nostolepis*) and ischnacanthid taxa prevented an unequivocal assignment of *Gladiobranchus* with ischnacanthids, but they did so anyway (Bernacsek & Dineley 1977: 17). Articulated *Nostolepis* showing dentigerous jaw bones are still lacking and the taxonomic affinities of this genus are still undetermined.

Despite new and better-preserved fossils, character comparisons between *Gladiobranchus* and the Ischnacanthiformes (represented by *Ischnacanthus gracilis* and *Poracanthodes menneri* Valiukevičius, 1992) reveal no synapomorphies. The jaws and all other features of *G. probaton*, now are known to be quite different than comparable features of ischnacanthids.

GLADIOBRANCHUS AND *URANIACANTHUS*
Bernacsek & Dineley (1977) found characters shared by *Gladiobranchus* and *Uraniacanthus*, but Young (1989: 19) rejected their interpretation. However, Bernacsek & Dineley (1977: 16) acknowledged the weaknesses in their taxonomic scheme, and furthermore, mentioned in their generic diagnosis that "this genus [*Gladiobranchus*] may be distinguished from *Uraniacanthus* by the above characters (i.e. dermal shoulder girdle plates and two pairs of prepectoral spines) which are lacking in the latter (i.e. *Uraniacanthus*)".

Although scale and spine features can be discounted as general diplacanthoid characters, the spathiform opercular plates are almost identical in both genera (compare Miles 1973: pl. 13, and Figs 2; 3; 5; 6; 7H; 8A). Furthermore, both genera have an enlarged, tuberculated postorbital plate posterodorsal to the orbit. The postorbital plates of *Gladiobranchus* and *Uraniacanthus* have nearly identical placement on the cheek directly above the opercular plates, behind the orbit, and posterodorsal to the jaws, and the postorbital plates of both genera have similar lateral and medial surface structure (Davis 2002). The postorbital plate of *Gladiobranchus* and *Uraniacanthus* should also not be confused with the postorbital projection of

Climatius (see Miles 1973: 125, 127, text-fig. 5, popr), *Parexus* spp. and *Brachyacanthus scutiger* which is minute by comparison. Bernacsek & Dineley (1977: 16) agreed with Miles that the enlarged postorbital plate of *Gladiobranchus* was the "lowest tessera of the postorbital projection", but the unit Miles (1973) discussed is a small component of a larger dermal grouping on *Climatius reticulatus* composed of multiple tesserae; the larger, ovate element in *Climatius reticulatus* is also separated from the orbit by several smaller tesserae. The postorbital plate as described by Bernacsek & Dineley (1977: text-fig. 13, pl. 7) was misinterpreted as part of the multi-plated structure of *C. reticulatus* due mainly to structural similarity (i.e. the smooth, concave visceral surface of the postorbital plate on NMC 22700A which resembles the illustration of the "lowest tessera" of *Climatius* in Miles [1973: text-fig. 6d]). Young & Burrow (2004: 29) noted that the diplacanthiform *Milesacanthus antarctica* lacks an enlarged postorbital plate, and as a result, they suggested eliminating postorbital plates as a diplacanthid synapomorphy in their re-diagnosis of the family to accommodate *M. antarctica*. In our opinion, the overall similarity between *Uraniacanthus* and *Gladiobranchus* is striking, and *Uraniacanthus*, based on current evidence, should be placed within the Gladiobranchidae. Unique features that can be used in a revised diagnosis of the Gladiobranchidae may be as follows: acanthodians with an enlarged postorbital plate with rounded, to spiky raised tubercles; broad, spathiform opercular covers ornamented with fine ridges in a loose chevron pattern. Other features (e.g., jaws, rostral plates), which are obvious on *G. probaton*, may occur on *U. spinosus*, but confirmation will depend on more complete specimens of the latter taxon.

Diplacanthoid characters
To understand more precisely how *Gladiobranchus* fits inside a diplacanthoid taxonomic framework, we must detail the history of the diplacanthoids, their characters, and the associated problems with these characters when applied to all referred taxa.

Berg (1940: 129) erected the order Diplacanthiformes, and the taxon was largely ignored because the diplacanthids were considered by other

researchers to reside within the Climatiiformes, and ordinal-level ranking for diplacanthids was not considered appropriate. However, Novitskaya & Obruchev (1964) reversed tradition and erected a different order, the Diplacanthida, which combined both Climatiidae and Diplacanthidae. Acanthodians within their Diplacanthida possessed: 1) two dorsal fins; 2) intermediate (prepelvic) spines; 3) pectoral girdle with dermal bones; 4) cartilaginous endocranium; 5) one or two bones developing in each jaw; 6) fin-spines inserted in the skin, or deeply inserted in musculature; and 7) an anterior dorsal fin-spine supported by basals and radials. Characters 1, 2, and 4-6 probably represent plesiomorphies for acanthodians, and the order Diplacanthida did not gain wide acceptance.

Novitskaya & Obruchev (1964) suggested that fishes with: 1) a single pair of intermediate spines on ventral surface; 2) ossified branchial and neural arches; 3) single operculum on branchial opening; 4) two ossification centres on each jaw; 5) extra-mandibular (mandibular splint as used today) present; 6) teeth absent; 7) anterior dorsal fin-spine deeply inserted into musculature with endoskeletal basal supports; 8) pectoral girdle with a pair of accessory spines (possibly "admedian" spines); and 9) scale microstructure of *Acanthodes* type, should be included in the family Diplacanthidae. Novitskaya & Obruchev (1964) did not recognize the shape of the scapulocoracoid, enlarged circumorbital bones, or the enlarged postorbital plates of diplacanthids, but they did note that diplacanthids have two pairs of prepelvic spines, with the anterior-most pair positioned ventromedial to the pectoral girdle. Furthermore, the body scales of *Diplacanthus* (Gross 1973: fig. 8j, k) and also *Gladiobranchus* (Fig. 12) show few growth zones, large vascular canals, and a fairly large primordium, and so do not resemble scales of acanthodiforms (e.g., Gross 1947: figs 13a, 18a; 1973: figs 6d, e, 7b, d, e, 8f). Unfortunately, the large number of diplacanthid characters provided by Denison (1979: 31) did not improve the definition of this taxon.

To include the genus *Culmacanthus* within the diplacanthid ranks, Long (1983: 52) redefined the suborder Diplacanthoidei (modified from Miles 1973: 190) using the following features:

1) the presence of a deep body form; 2) body scales with a low flat crown; 3) high scapulocoracoid (dorsal scapular process as used here); 4) large dermal plates bearing laterosensory canals on cheek; 5) one pair of pinnal plates with anterior median bone (lorical plate) or paired pinnal plates only; 6) deeply inserted fin-spines; and 7) less than three pairs of intermediate (prepelvic) fin-spines. A deep, compressed body appears to have evolved convergently in *Brochoadmones* (Gagnier & Wilson 1996b; Hanke & Wilson 2006), and *Kathemacanthus* (Gagnier & Wilson 1996a), and so is not unique to diplacanthoid fishes. Furthermore, a scapulocoracoid with a long scapular blade appears coincide with a deeply compressed body, and again may be convergently acquired in deep-bodied fishes. Since flat, smooth-crowned scales are found in *Paucicanthus*, *Cassidiceps*, ischnacanthids, mesacanthids, acanthodids, and *Gladiobranchus*, and diplacanthids and gladiobranchids possess ornamented scales, there is no simple scale-based feature to define all diplacanthoid fishes. Furthermore, Long's character 4 is a synapomorphy of *Culmacanthus* species, not an entire suborder. In contrast, character 5 is widespread among climatiids (e.g., *Climatius*, *Brachyacanthus*, *Ptomacanthus*, *Parexus*, and *Vernicomacanthus*), as well as *Culmacanthus* and species of *Diplacanthus*, but not *Gladiobranchus* and *Uraniacanthus*, and is not diagnostic of diplacanthoids to the exclusion of other acanthodian taxa. Long's character 6 is shared with *Brochoadmones* (Hanke & Wilson 2006), mesacanthids, acanthodids (Denison 1979), and the putative chondrichthyan *Kathemacanthus* (Wilson *et al.* 2007: fig. 3.7c), as well as other elasmobranchs and holocephalians (see examples in Zangerl 1981; Stahl 1999). The seventh character (less than three pairs of prepelvic spines) is characteristic of mesacanthids, diplacanthids, and *Milesacanthus*, while *Culmacanthus* species, acanthodids, and ischnacanthids lack prepelvic spines. Perhaps the problem with defining the diplacanthoid fishes stems from too many disparate forms being shoe-horned into one taxon based on deep-bodies and long median fin-spines. The cladistic analysis by Hanke & Wilson (2004: fig. 12) suggests that *Culmacanthus* species do not belong with diplacanthoids, and this would simplify the diagnosis of the group (eliminating

the need for Long's [1983] characters 4 and 5). However, when Hanke & Wilson's analysis is re-run with new taxa, it is very likely that *Milesacanthus antarctica* (Young & Burrow 2004) will join the clade of diplacanthoid fishes without overly complicating the list of diagnostic characters.

GLADIOBRANCHUS AS A DIPLACANTHOID
Young & Burrow (2004) provided an exhaustive list of characteristics for the Diplacanthidae: 1) short mouth and cheek region; 2) mandibular splint present; 3) teeth and ossified toothplates absent; 4) a high cylindrical scapular blade and a triangular posterior flange on the coracoid region; 5) some with procoracoids; 6) circumorbital bones plus a "preopercular" cheek plate present (not to confuse "preopercular plates" with osteichthyan bones); 7) up to five pairs of "opercular" plates; 8) ornamented scales with acellular dentine and wide canals in the crown and acellular scale bases; 9) fin-spines with smooth ribs paralleling the leading edge of the fin-spine; 10) pectoral girdle may have pinnal plates; 11) anterior-most prepelvic (admedian) spines ventromedial to the pectoral girdles, and the posterior pair (intermediate) positioned farther back along the abdomen; and 12) median and pelvic fin-spines deeply inserted into the body musculature.

Interestingly, not all *Diplacanthus* species possess the full complement of features that Burrow & Young listed for the family Diplacanthidae, and so some of the characteristics that they detailed help define groups of taxa within the family, but are not general diplacanthid features. For example, features seen in gladiobranchids and tetanopsyrids include: ossified toothplates, and the presence of enlarged circumorbital and "preopercular" cheek plates. *Milesacanthus* and culmacanthids possess scapulocoracoids with a high scapular blade, while gladiobranchids and culmacanthids have pelvic fin-spines deeply inserted into the body musculature. Gladiobranchids, culmacanthids, and tetanopsyrids have a short mouth and cheek, they lack teeth, and have median fin-spines deeply inserted into the body musculature; note again that *Brochoadmones milesi* (Bernascek & Dineley 1977; Gagnier & Wilson 1996b; Hanke & Wilson 2006) and a variety of chondrichthyan taxa (Zangerl 1981; Stahl 1999)

also have deeply inserted median fin-spines. In contrast, fin-spines with smooth ribs paralleling the leading edge of the fin-spine, also are known in non-diplacanthiforms (e.g., ischnacanthiforms, acanthodiforms, *Brochoadmones milesi*, *Cassidiceps vermiculatus*, and *Paucicanthus vanelsti* (Denison 1979; Gagnier & Wilson 1996a, b; Hanke 2002; Hanke & Wilson 2006), and pectoral girdles with pinnal plates are found also in climatiiforms (Watson 1937; Miles 1973; Denison 1979), and so these two features, while present in diplacanthids, cannot be used to define the family.

From Young & Burrow's original list, *G. probaton* has: a short mouth and cheek region; an ossified lower jaw; lacks teeth; a fairly high scapular blade (although triangular in cross section, not cylindrical) and a triangular posterior flange on the coracoid region; enlarged anterior circumorbital bones and an enlarged postorbital cheek plate; a series of ornamented spathiform opercular plates; ornamented scales with acellular dentine, wide canals in the crown, and acellular scale bases; fin-spines with smooth ribs (although some ribs have reclined, nodular ornament near the spine base) and the ribs parallel the leading edge of the fin-spine to near the tip; the anterior-most prepelvic (admedian) spines are ventromedial to the pectoral girdles; a posterior prepelvic spine pair is positioned farther back along the abdomen; and the median and pelvic fin-spines are deeply inserted into the body musculature. Given that many of the features of *G. probaton* are widespread among diplacanthoids, there is no doubt that *G. probaton*, and the Gladiobranchidae are diplacanthoid taxa, and not ischnacanthiforms.

CONCLUSIONS

Gladiobranchus probaton was originally assigned to the Ischnacanthiformes because of its resemblance to *Uraniacanthus spinosus*. *Uraniacanthus* was misinterpreted as an ischnacanthiform based on errors in the original description of *U. spinosus* by Miles (1973). The taxonomic affinities of these two species have been difficult to resolve because, until recently, all known gladiobranchid acanthodians

lacked heads and articulated jaws. New, nearly-complete specimens of *G. probaton* show details of the rostrum, jaws, the pectoral girdle which lacks pinnal plates, and the complete caudal fin. Re-examination of the holotype of *U. spinosus* has also demonstrated that the assignment of dentigerous jaws, and the identification of dentigerous elements on the holotype, were errors. The presence of toothless jaws, enlarged anterior and posterior circumorbital plates, elongate, deeply-inserted dorsal fin-spines, the structure of the scapulocoracoid, and the prepelvic fin-spine complement indicate that *G. probaton* (and the Gladiobranchidae) are diplacanthoid taxa. The striking similarity between *U. spinosus* and *G. probaton* suggests that both taxa should be placed in the same diplacanthoid family, Gladiobranchidae. Neither genera are closely related to ischnacanthiform acanthodians.

REFERENCES

Berg L. S. 1940. — Classification of fishes, both recent and fossil. *Travaux de l'Institut de Zoologie de l'Académie des Sciences de l'URSS* 5: 1-517.

Bernacsek G. M. & Dineley D. L. 1977. — New acanthodians from the Delorme Formation (Lower Devonian) of N.W.T., Canada. *Palaeontographica*, abteilung A, 159: 1-25.

Davis S. P. 2002. — *Comparative Anatomy and Relationships of the Acanthodian fishes.* Unpublished Ph.D. thesis, University College London, United Kingdom, 293 p.

Davis S. P. & Martill D. M. 1999. — The Gonorhynchiform Fish Dastilbe from the Lower Cretaceous of Brazil. *Palaeontology* 42 (4): 715-740.

Denison R. 1979. — Acanthodii, *in* Schultze H.-P. (ed.), *Handbook of Palaeoichthyology.* Volume 5. Gustav Fischer Verlag, Stuttgart, 62 p.

Gabrielse H., Blusson S. L. & Roddick J. H. 1973. — Geology of the Flat River, Glacier Lake, and Wrigley Lake Map-areas, District of Mackenzie and Yukon Territory. *Geological Survey of Canada, Memoir* 366: 1-153.

Gagnier P.-Y. 1996. — Acanthodii, *in* Schultze H.-P. & Cloutier R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada.* Verlag Dr. Friedrich Pfeil, München: 149-164.

Gagnier P.-Y. & Wilson M. V. H. 1996a. — Early Devonian acanthodians from northern Canada. *Palaeontology* 39 (2): 241-258.

Gagnier P.-Y. & Wilson M. V. H. 1996b. — An unusual acanthodian from northern Canada: revision of *Brochoadmones milesi. Modern Geology* 20: 235-251.

Gagnier P.-Y., Hanke G. F. & Wilson M. V. H. 1999. — *Tetanopsyrus lindoei*, gen. et sp. nov., an Early Devonian acanthodian from the Northwest Territories, Canada. *Acta Geologica Polonica* 49 (2): 81-96.

Gross W. 1947. — Die Agnathen und Acanthodier des Obersilurischen Beyrichienkalks. *Palaeontographica*, abteilung A, 96: 91-161.

GROSS W. 1973. — Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen bonebeds des Devons. *Palaeontographica*, abteilung A, 142: 51-155.

HANKE G. F. 2002. — *Paucicanthus vanelsti* gen. et sp. nov., a Lower Devonian (Lochkovian) acanthodian that lacks paired fin-spines. *Canadian Journal of Earth Sciences* 39: 1071-1083.

HANKE G. F. & WILSON M. V. H. 2004. — New teleostome fishes and acanthodian systematics, *in* ARRATIA G., WILSON M. V. H. & CLOUTIER R. (eds), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag Dr. Freidrich Pfeil, München: 187-214.

HANKE G. F. & WILSON M. V. H. 2006. — Anatomy of the Early Devonian acanthodian *Brochoadmones milesi* based on complete body fossils, with comments on the evolution and development of paired fins. *Journal of Vertebrate Paleontology* 26 (3): 526-537.

HANKE G. F., DAVIS S. P. & WILSON M. V. H. 2001. — New species of the acanthodian genus *Tetanopsyrus* from northern Canada, and comments on related taxa. *Journal of Vertebrate Paleontology* 21: 740-753.

JANVIER P. 1996. — Early Vertebrates. *Oxford Monographs on Geology and Geophysics* 33. Clarendon Press, Oxford, 393 p.

LONG J. A. 1983. — A new diplacanthoid acanthodian from the Late Devonian of Victoria. *Memoirs of the Association of Australasian Palaeontologists* 1: 51-65.

LONG J. A. 1986. — New ischnacanthid acanthodians from the Early Devonian of Australia, with comments on acanthodian interrelationships. *Zoological Journal of the Linnean Society* 87: 321-339.

MILES R. S. 1966. — The acanthodian fishes of the Devonian Plattenkalk of the Paffrath trough in the Rhineland. *Arkiv för Zoologi* 18: 147-194.

MILES R. S. 1973. — Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. *Bulletin of the British Museum of Natural History* 24 (2): 111-213.

NOVITSKAYA L. I. & OBRUCHEV D. V. 1964. — Class Acanthodei, *in* OBRUCHEV D. V. (ed.), *Fundamentals of Paleontology*. Volume 11. Paleontological Institute of the Academy of Sciences of the USSR: 263-291.

RIXON A. E. 1976. — *Fossil Animal Remains: their Preparation and Conservation*. Athlone Press, London, 304 p.

STAHL B. 1999. — Chondrichthyes III, Holocephali, *in* SCHULTZE H.-P. (ed.), *Handbook of Palaeoichthyology*. Volume 4. Verlag Dr. Friedrich Pfeil, München, 164 p.

UPENIECE I. 1996. — *Lodeacanthus gaujicus* n. g. et sp. (Acanthodii: Mesacanthidae) from the Late Devonian of Latvia. *Modern Geology* 20: 383-398.

VALIUKEVIČIUS J. 2003. — Devonian Acanthodians from Severnaya Zemlya Archipelago (Russia). *Geodiversitas* 25 (1): 131-204.

WATSON D. M. S. 1937. — The Acanthodian Fishes. *Philosophical Transactions of the Royal Society of London* 228B: 49-146.

WILSON M. V. H., HANKE G. F. & SOEHN K. L. 2000. — Diversity and age of the Devonian vertebrate assemblage at MOTH, Mackenzie Mountains, Northwest Territories, Canada. *Ichthyolith Issues*, special publication 6: 137-141.

WILSON M. V. H., MÄRSS T. & HANKE G. F. 2007. — Paired fins of jawless vertebrates and their homologies across the "Agnathan"-Gnathostome transition, *in* ANDERSON J. S. & SUES H.-D. (eds), *Major Transitions in Vertebrate Evolution*. Indiana University Press, Bloomington: 122-149.

YOUNG G. C. 1989. — The Aztec fish fauna (Devonian) of southern Victoria Land: ev olutionary and biogeographic significance, *in* CRAME J. A. (ed.), Origins and Evolution of the Antarctic biota. *Geological Society*, special publication 47: 43-62.

YOUNG G. C. & BURROW C. J. 2004. — Diplacanthid acanthodians from the Aztec Siltstone (late Middle Devonian) of Southern Victoria Land, Antarctica. *Fossils and Strata* 50: 23-43.

ZANGERL R. 1981. — Chondrichthyes 1, Paleozoic Elasmobranchii, *in* SCHULTZE H.-P. (ed.), *Handbook of Palaeoichthyology*. Volume 3A. Gustav Fischer Verlag, Stuttgart, 115 p.

ZORN M. E., CALDWELL M. W. & WILSON M. V. H. 2005. — Lithological analysis of the vertebrate-bearing beds at the Lower Devonian MOTH locality, N.W.T., Canada: insights to taphonomy and depositional setting. *Canadian Journal of Earth Sciences* 42: 763-775.