University of Alberta

Description of Devonian tessellate heterostracans from the Northwest Territories, Canada and the growth of Lepidaspis

by

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CHAPTER 1: INTRODUCTION

OVERVIEW OF PRIMITIVE VERTEBRATE AND HETEROSTRACAN DIVERSITY

Heterostraci are a group of early vertebrates that are characterized as having a dermal skeleton, composed of either small tuberculate tesserae or large plate-like shields, and one pair of branchial openings. The bone structure of the dermal skeleton tends to show a honeycomb or reticulate-like pattern made of aspidine and dentine. Heterostracans range from the Lower Silurian to the Upper Devonian, making them among the earliest known vertebrates aside from the Arandaspida and the Astraspida.

Arandaspidids range from the Lower to Upper Ordovician and are similar to many tessellate heterostracans such as *Lepidaspis* (Dineley and Loeffler, 1976) in that they have oak-leaf-shaped tubercles on both their dorsal and ventral shields. The arandaspidids also lack paired fins and have a trunk composed of smaller, scale-like units. The main difference between these animals and the heterostracans is that the arandaspidids have a row of branchial plates separating the dorsal and ventral shields, each branchial plate (in arandaspidids) forming part of a branchial opening (Janvier, 1996). This means some may have had up to twenty pairs of branchial openings.

Astraspidids, ranging from the Upper Ordovician to the Lower Silurian, share with the presumed primitive heterostracans the oak-leaf-shaped tubercles on small tesserae. The tubercles, however, have a small enameloid cap (Smith et al., 1995; Janvier, 1996). These tesserae form the dorsal and ventral shields of the animal. *Astraspis* has eight pairs of external branchial openings and, prior to this discovery, was thought to be a heterostracan (Elliott, 1989). These are larger than in arandaspidids, and show that the astraspidids a distinct group of vertebrates (Janvier, 1996).

The Astraspida, Arandaspida, and Heterostraci group together into the taxon Pteraspidomorphi (sharing oak-leaf-shaped tubercles on dermal bone, and large median discs in dorsal or ventral shields) (Janvier, 1996, Donoghue et al., 2000). The Astraspida and Heterostraci group together into the Heterostracomorphi, which have dorso-lateral gill openings according to Janvier (1996), though Donoghue et al. (2000) suggest that heterostracans and arandaspidids are sister groups.

There is a trend towards a reduction of the number of pairs of branchial openings from the (hypothesized) more primitive arandaspidids to the more derived heterostracans. This is an assumption that paleontologists have applied to tessellate heterostracans. Since the branchial openings have not been identified on some forms such as *Lepidaspis serrata*, it is assumed that these animals had only one pair of openings, thus allowing for their inclusion in the Heterostraci. *Lepidaspis* is also considered a tessellate heterostracan, as its cephalothorax, at least early in life, is composed of many small tesserae to make up the armour (Dineley and Loeffler, 1976).

Also from the Man on the Hill (MOTH) locality, *Aserotaspis* is another tessellate heterostracan. It is very similar to *Aporemaspis* described by Elliot and Loeffler (1989) and also found in Northern Canada. *Aserotaspis* and *Lepidaspis* are the most complete of the known tessellate heterostracans. For both, the cephalothorax is composed of small interlocking tesserae; however, for *Lepidaspis* each tessera is topped by a single tubercle while for *Aserotaspis* there is a covering of dentine ridges reminiscent of those of cyathaspidids. By sharing many of the hypothesized primitive conditions with the arandaspidids and astraspidids, the tessellate heterostracans can enlighten our knowledge of early vertebrates, as these three taxa are considered the sister group to all other vertebrates (Janvier, 1996:fig. 5.1; Donoghue et al., 2000:fig.. 17).

It should be noted that both *Lepidaspis* and *Aserotaspis* have been recovered from the MOTH Locality in the Northwest Territories of Canada. This site is renowned for the exceptional preservation of vertebrate fossils both because of the completeness of these fossils and because of the fine detail preserved on the specimens. Fossils recovered from the site include juvenile cyathaspidids (Greeniaus and Wilson, 2003) and cephalaspidids (George et al., 2003), thelodonts with stomach casts preserved (Wilson and Caldwell, 1993), and more than 59 vertebrate species most recently listed in Wilson et al., 2000. With recent work by Gavin Hanke, Chelsea Smith and myself as included in this thesis, this total now likely approaches more than 70 species.

If some of the heterostracans found at MOTH, such as *Lepidaspis serrata* or *Aserotaspis canadensis,* do indeed represent the condition of primitive heterostracans, the discussion of the growth of its dermal armour will help us explain how the fused shield of later heterostracans emerged. Also important is the description of several new species of heterostracans, all sharing a very similar structure of their tubercles and all showing various degrees of the tessellate condition. The first group, including three new species, shows similarities to traquairaspidids, as they all have a central dorsal plate on the cephalothorax that has a crest running down the midline. These also show a cyclomoriform pattern of the tubercle arrangements, with larger tubercles surrounded by varying patterns of smaller tubercles. These plates, unlike those of the second group, appear to be well fused in all examples, and the new species are thoroughly discussed in Chapter Two of this thesis. The second group of organisms includes the two species of *Lepidaspis* at the site, including *Lepidaspis serrata* and *L. loefflerae*, a new species. The abundance of specimens of this second group has allowed me to discuss a hypothesis of the sequence of growth for these animals, and help support a previous hypothesis proposed by several researchers that fusion of many small units of dermal armour into larger plates may be primitive for heterostracans. The new species of *Lepidaspis*, and the description and discussion of bone growth within that genus, is covered in Chapter Three of this thesis.

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CHAPTER 2

THREE NEW TESSELLATED HETEROSTRACAN SPECIES FROM THE LOWER DEVONIAN MOTH LOCALITY, NORTHWEST TERRITORIES, CANADA

ABSTRACT

Three new species, *Grandipiscis exscopulus*, *Quasimodaspis mackenziensis*, and *Q. canadensis*, and two taxa referred to *G. exscopulus*, from the Lower Devonian of the Northwest Territories of Canada, are described. These new species show several similarities to each other, including a cyclomoriform ornamentation and a median crest down the midline of the dorsal shield. All also have a well-fused median plate and have laterally barbed tubercles. The two new genera are likely related to traquairaspidids as they each have a crested median plate on the dorsal shield, though they show several key differences including the presence of tesserae lateral to the median plate, rather than having a cephalothorax composed of a single, or seven or nine plates, as is typical of known traquairaspidids.

INTRODUCTION

The phylogeny of basal heterostracans is poorly understood (Janvier, 1996), let alone their relationship to other primitive vertebrates such as *Astraspis* (Elliott, 1987). One of the key problems is that specimens of primitive vertebrates are few and far between, and when found they are typically fragmentary and contain little taxonomically useful information. Included in the basal polytomy of heterostracans are *Lepidaspis,* Traquairaspididae, and *Toombsaspis* (Janvier, 1996). For this reason, whenever specimens are found that can possibly help resolve this problem, as well as add to our knowledge of these enigmatic creatures, it is essential that they be described and introduced to the scientific community. This chapter will introduce three new taxa and significantly increase the number of known tessellate heterostracans.

Of those taxa mentioned above, *Lepidaspis* and the traquairaspidids are the taxa most similar to the species newly described here. *Lepidaspis* is a tessellate heterostracan, meaning that the armour of the cephalothorax is composed of interlocking tesserae. Upon these tesserae is a single barbed dentine tubercle. The shield is relatively flat, with no prominent protrusions present.

Traquairaspidids are slightly more diverse. The shield may be composed of a single plate, or conversely be composed of seven or nine plates. The ornamentation on these plates is also composed of dentine tubercles that are generally arranged in a cyclomoriform pattern. This means that the pattern has a large prominent tubercle surrounded by smaller tubercles (Tarlo, 1965; Dineley and Loeffler, 1976; Tarrant, 1991). Some species of traquairaspidids also have a prominent crest or spines in the posterior region of the dorsal plate along the midline of the animal (Dineley and Loeffler, 1976).

In this chapter, I give the taxonomic description of two new genera and three new species of heterostracans that show some similarities to traquairaspidids, although they also show several key differences. These new species are compared and contrasted with each other as well as with the species known from the fossil record that share some of their morphological features.

LOCALITY INFORMATION AND GEOLOGY

The 'Man on the Hill' (MOTH) locality is located in the Mackenzie Mountains of the Northwest Territories, Canada (Fig. 2.1). It is only accessible by helicopter, the closest settlement being the small mining town of Tungsten, approximately 45 minutes away. The MOTH section extends through both Silurian and Lower Devonian rock. Fossil vertebrate remains are abundant in a lower, Late Silurian, fish level called B-MOTH and the higher, Lower Devonian MOTH fish layer. The section between these two is relatively devoid of vertebrate fossils, though invertebrate breccia is common.

The B-MOTH layer has been dated as late Wenlock or early Ludlow in age (Wilson et al., 2000). This date is based both on the presence of the thelodont *Paralogania martinssoni* and on several species of the graptolite *Monograptus* being found just below and in contact with the fish level (Soehn et al., 2000; Wilson et al., 2000).

The specimens described in this study are taken from talus slopes, and have originated from the Lower Devonian MOTH fish layer. This layer is equivalent to the Geological Survey of Canada (GSC) locality 69014 or University of Alberta Laboratory for Vertebrate Paleontology (UALVP) locality 129. It is situated at MOTH 180 meters in the measured section of Adrain and Wilson (1994). The approximately 10 meters of the MOTH fish layer are bounded both on top and bottom by two turbidity deposits (Hanke, 2001). The fish layer itself comprises fine-grained carbonaceous siltstone with alternating light and dark layers (Zorn, 2003,

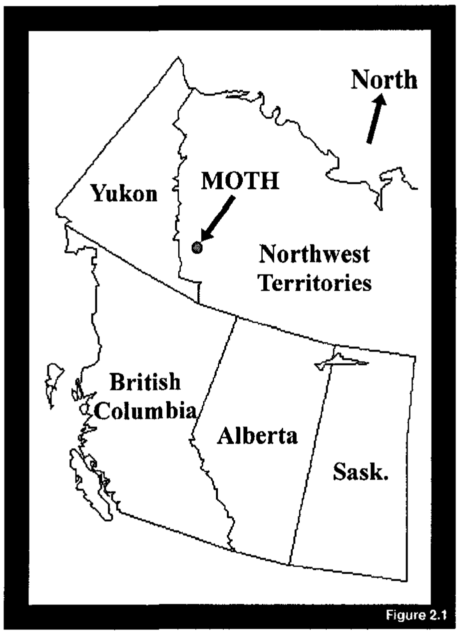

North
Yukon
MOTH
Northwest Territories
British Columbia
Alberta
Sask.

Figure 2.1

personnel communications). It was previously believed to be dolomite (Gabrielse et al., 1973; Dineley and Loeffler, 1976), and because the rock reacts strongly with acid and dissolves easily in acetic acid, it has also been described as limestone (Adrain and Wilson, 1994; Wilson and Caldwell, 1998; Soehn et al., 2000). Pyrite is present as grains, usually in small lenses of sand, as small nodules, and it has formed on some of the fossils (Zorn, 2003, personnel communications). Pyrite (FeS_2) formation begins with the oxidization of sulfur, normally from a precursor iron monosulfide (FeS) (Rickard, 1999). In this process, the sulfur is oxidized; the iron is not. The oxidization of the sulfur occurs in a liquid solution and allows pyrite to form, which tends to nucleate on biological surfaces, sulfur, and gregite (Rickard, 1999). This process occurs preferentially in an anoxic environment.

Despite the presence of organisms that lived on, near, or in the benthos (heterostracans, cephalaspidids), and other animals that were likely scavengers (ostracods, eurypterids, phyllocarids), there is no evidence of sediment reworking by large animals in the MOTH fish layer. There is evidence that the sediment was bioturbated by small organisms (Zorn, 2003, personnel communications). The fine layering suggests two things. The first is that the sediment was deposited below the storm wave base. The second is that the environment was inhospitable to large, burrowing animals.

All of this suggests a quiet and anoxic region of deposition and helps explain the high quality of preservation and diversity of the MOTH vertebrate assemblage, which includes over 70 species of vertebrates ranging from basal heterostracans to chondrichthyans and acanthodians. Of these 70+ species of vertebrates, at least 23 are heterostracans.

METHODS

Specimens were all collected from the talus slopes below the MOTH 180 m fish layer, and originated from this layer. They were collected in expeditions led by Dr. Brian Chatterton in 1983 and 1990 and Dr. Mark Wilson in 1990, 1995, 1997, and 1998, and by Chelsea Smith and the author in 2002.

Preparation of University of Alberta specimens, when necessary, was done in dilute acetic acid baths. Fossils were slowly exposed by rubbing off the sediment residue on a weekly basis using soft paintbrushes. Once exposed the fossil material was coated in vinac (plastic beads dissolved in acetone) to prevent further removal of the surrounding sediment during preparation. Once preparation was complete, fossils were covered with diluted vinac to help protect and stabilize them. All specimens are stored in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) collections and in the Canadian Museum of Nature (CMN) collection.

Thin sections were prepared by Don Resultay of the Earth and Atmospheric Sciences Department at the University of Alberta. They were photographed using normal and polarized light.

Measurements were done using 18 cm and 33 cm KAR calipers and a Wild ocular micrometer (20x/13 lens) calibrated with the 18 cm caliper. Photographs were taken using a Nikon Coolpix 4500 and Canon 10D cameras with and without the aid of microscopes.

SYSTEMATIC PALEONTOLOGY

HETEROSTRACI Lankester, 1868

Family *Incertae sedis*

GRANDIPISCIS gen. nov.

Type Species–*Grandipiscis exscopulus* sp. nov.

Etymology–Latin *grandis*, meaning large, and *piscis* (male), meaning fish, though some disagree as to whether jawless vertebrates should be considered fish.

Diagnosis–As for type and only species.

Included Species–*Grandipiscis exscopulus* new species.

GRANDIPISCIS EXSCOPULUS sp. nov.

(Figs. 2.2–2.7)

Holotype–UALVP 45700, complete anterior dorsal cephalothorax.

Paratypes–UALVP 23190, ventral shield; 32523, interior of dorsal shield; 47001 (near complete cephalothorax); 47002, 47003, interiors of dorsal shield and exterior of ventral; 47004, posterior of ventral shield and anterior part of tail region.

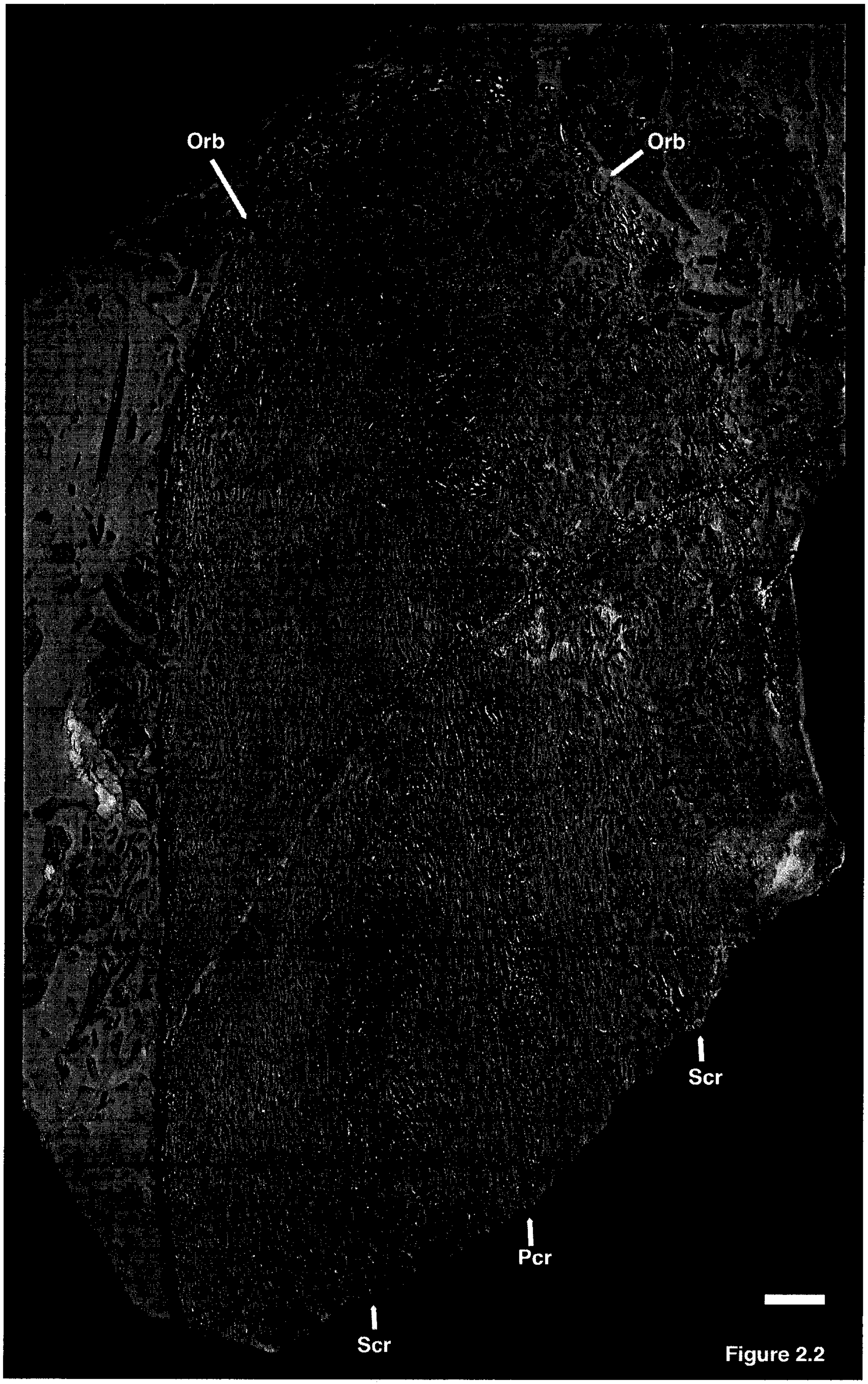
Type Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32’ N, 127° 43’ W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Etymology–Latin *ex*, meaning from, and *scopulus*, meaning cliff; species name means 'large fish from the cliff.'

Diagnosis–Large vertebrate with cephalothorax more than 25 cm long (likely approaching half a meter or more with tail); elongate-serrated dentine tubercles throughout cephalothorax; medial region of cephalothorax with elongate-serrated tubercles separated by small plate-like tubercles; three longitudinal crests, central crest taller and having secondary tubercle formation, two smaller crests lateral to median one; pineal region forming mound; orbits approximately 4 mm long, 2.5 mm wide; tail region composed of large lozenge-shaped imbricated scales.

Description

Body Form–This vertebrate was among the largest in the MOTH assemblage. The general shape of the anterior part of the cephalothorax suggests that it was more antero-posteriorly elongate in proportions when compared to other heterostracans. The specimens have been dorso-ventrally flattened and it is probable that the animal was in life as well. There are disarticulated elements surrounding the specimen that have basal plates and tubercles consistent with this species. The right side of both of the well-preserved dorsal cephalothoraces shows some disarticulation when compared to the left. The largest specimen reaches 250 mm in length and is interrupted abruptly by a fracture in the rock at the posterior end of the specimen (Fig. 2.3). The fossil has an estimated maximum width of 120 mm based on UALVP 45700 and 150 mm based on UALVP 47001 (Figs. 2.2, 2.3). The left edge of UALVP 45700 converges slightly towards the midline posteriorly, suggesting that


Orb
Orb
Scr
Pcr
Scr
Figure 2.2

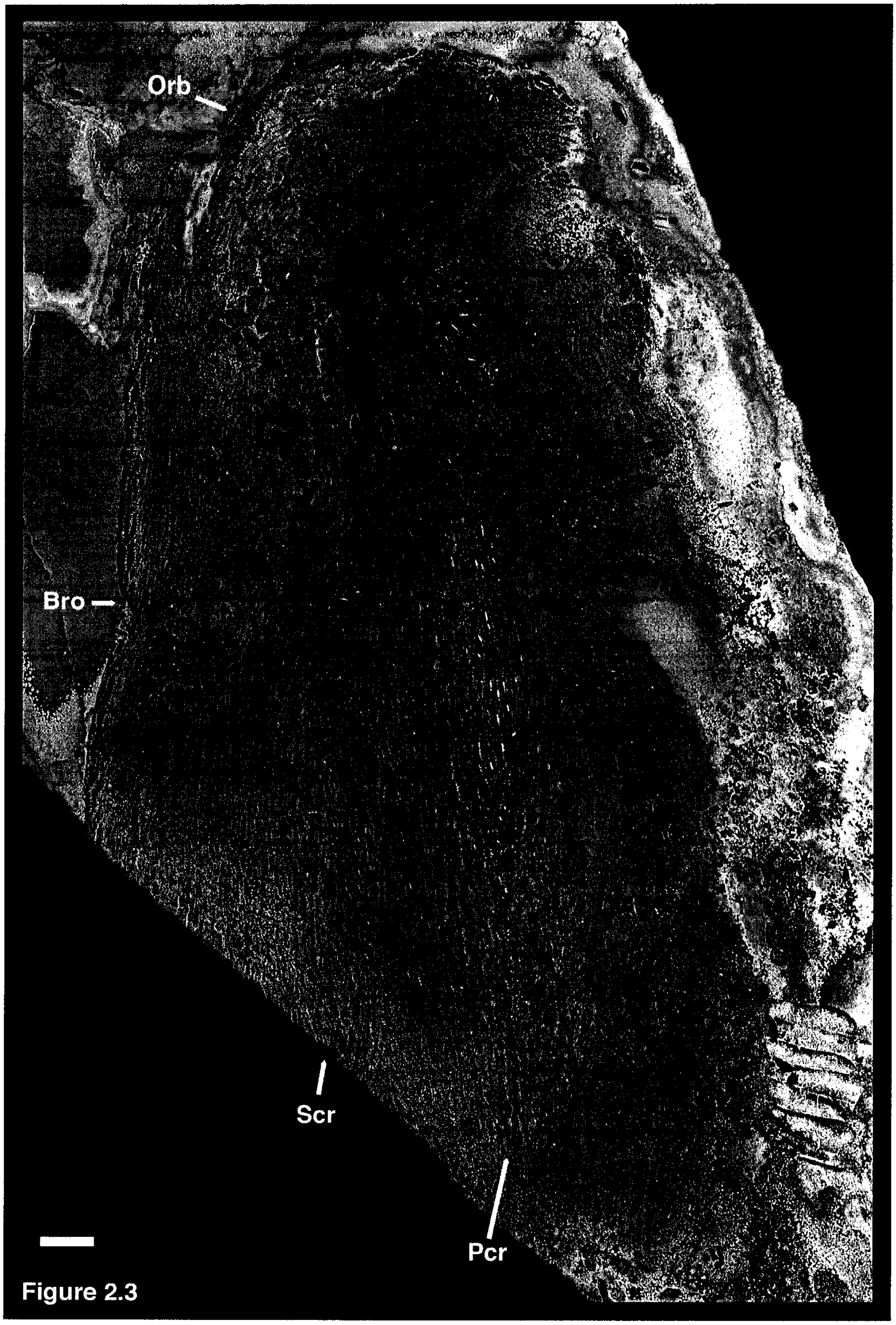


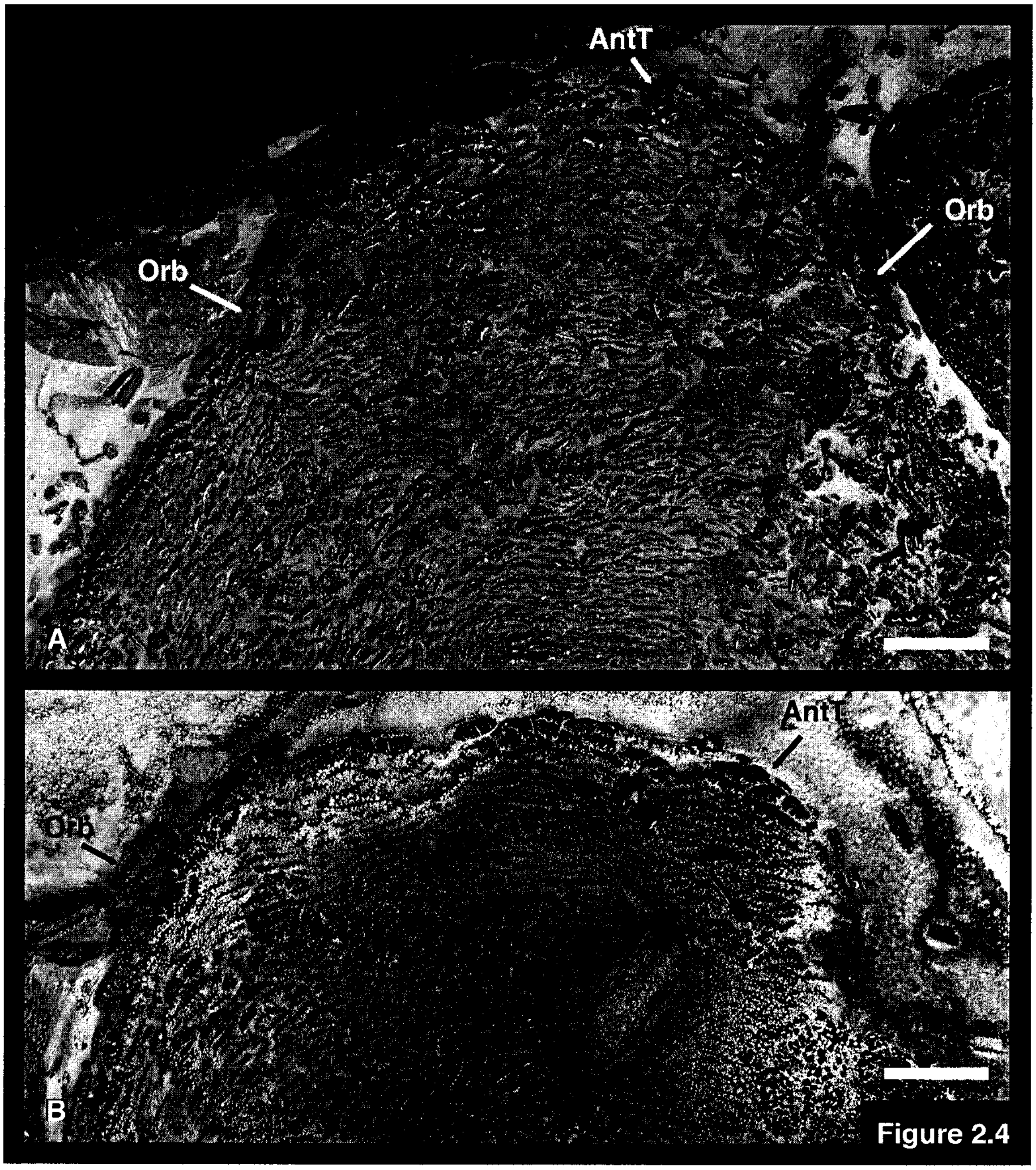
Figure 2.3

the preserved portion is more than half the cephalothorax, though the edge of UALVP 47001 is truncated short of this point. This would put the estimated size of the animal (if it has proportions similar to those of species such as *Lepidaspis serrata*) somewhere between 450-600 mm long including the tail, and likely no more than 130-150 mm wide.

Cephalothorax–There is evidence of at least one prominent crest that runs in the antero-posterior direction on the midline of the dorsal surface of the cephalothorax. This is very pronounced in UALVP 45700 and present, though to a less extreme degree, in UALVP 47001. This crest is flanked by two smaller, less prominent crests; these have been truncated by the fracture in UALVP 45700 and UALVP 47001 shows only slight formation of secondary tubercles here rather than the distinctive crests and secondary tubercle formation on UALVP 45700. These two smaller crests are separated by 55 mm and are aligned with the orbits in both specimens.

Anterior and lateral to these crests, the orientation of tubercles is generally parallel to the sides of the animal, the tubercle orientations becoming somewhat more chaotic anterior to the central crest on the cephalothorax. This is likely due to both their actual orientations in life and to some taphonomic disarticulation of the basal plates. This disarticulation is more evident on the right side of both specimens UALVP 45700 and 47001.

The orbits are 15-20 mm from the anterior tip of the specimen and have a separation of 57 mm in UALVP 45700 and at least 62 mm in UALVP 47001 (only the left orbit is exposed) (Fig. 2.4). The orbits of UALVP 45700 have a length of


AntT
Orb
Orb
A
AntT
Orb
B
Figure 2.4

4.3 mm and a width of 2.4 mm for the left and a length of 3.95 mm and width of 2.5 mm for the right. In both cases, the longer axis is in the antero-posterior direction. On UALVP 47001, the left orbit is more circular with a width of 2.55 mm. The orbits themselves are directed dorso-laterally. They are on the posterior end of a snout-like portion of the cephalothorax. The cephalothorax widens abruptly to 80 mm on UALVP 45700 and to 91 mm on UALVP 47001 in the region comprised of the 10 mm posterior to the orbits and then continues more gradually to its maximum width.

When viewed from the interior surface, the crested region of the cephalothorax is seen to be composed of a single large plate (Figs. 2.5A, 2.6 B, C). The margin of the plate, when visible, appears to have lines consistent with growth lines (Fig. 2.6B, C), particularly in UALVP 32523 and UALVP 47003. Adjacent to this plate are large tesserae that make up the rest of the dorsal surface of the cephalothorax, being most evident in UALVP 47002 (Fig. 2.5A).

The ventral surface of the cephalothorax does not appear to have any crest, though the medial region of the ventral surface seems to be absent in all cases, except in the case of UALVP 47004 (Fig. 2.6A) and UALVP 23190 (Fig. 2.5B). UALVP 47004 shows a domed transverse cross-section leading from one side of the animal to the other. This curved cross-section peaks along the midline, and posteriorly progresses into the ventral ridge scales of the tail. UALVP 23190 is limited to the exterior of the anterior ventral surface, though it appears that the region likely having the mouth has not been preserved.

The lateral margin of the cephalothorax, on both UALVP 47001 and 47003, shows an indentation towards the midline of the specimen (Figs. 2.3, 2.6C, 2.7). On

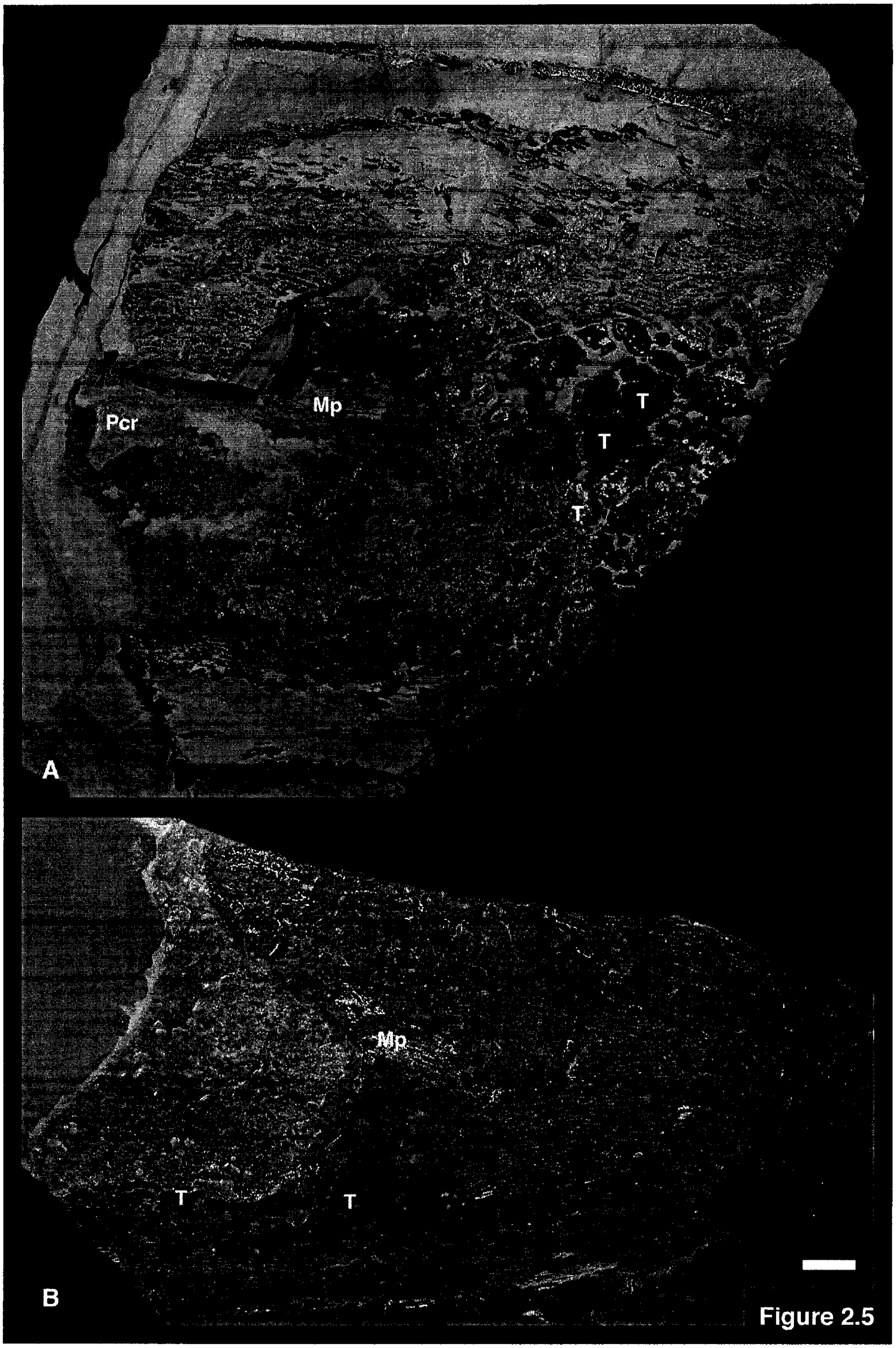


Figure 2.5

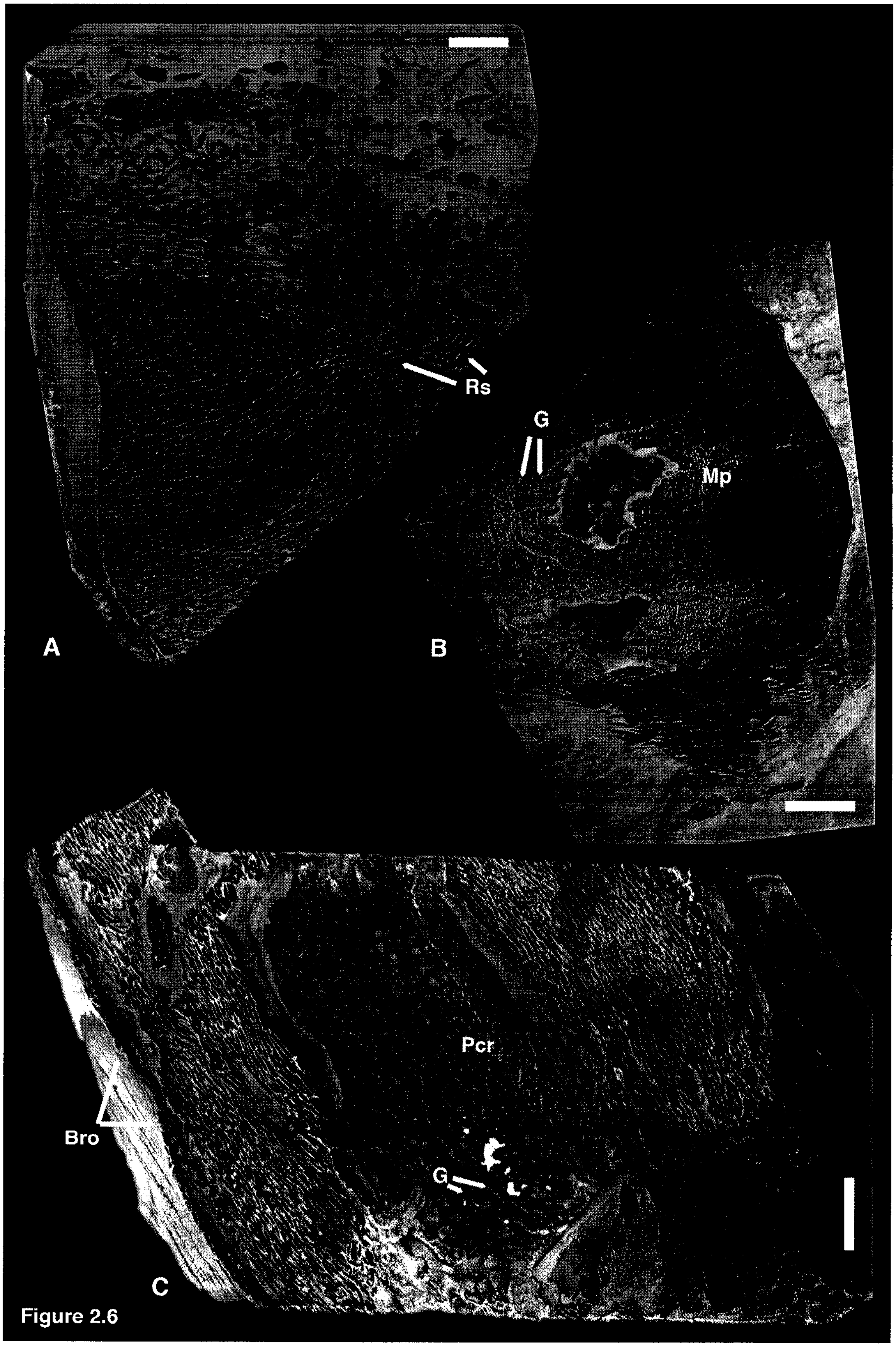


Figure 2.6

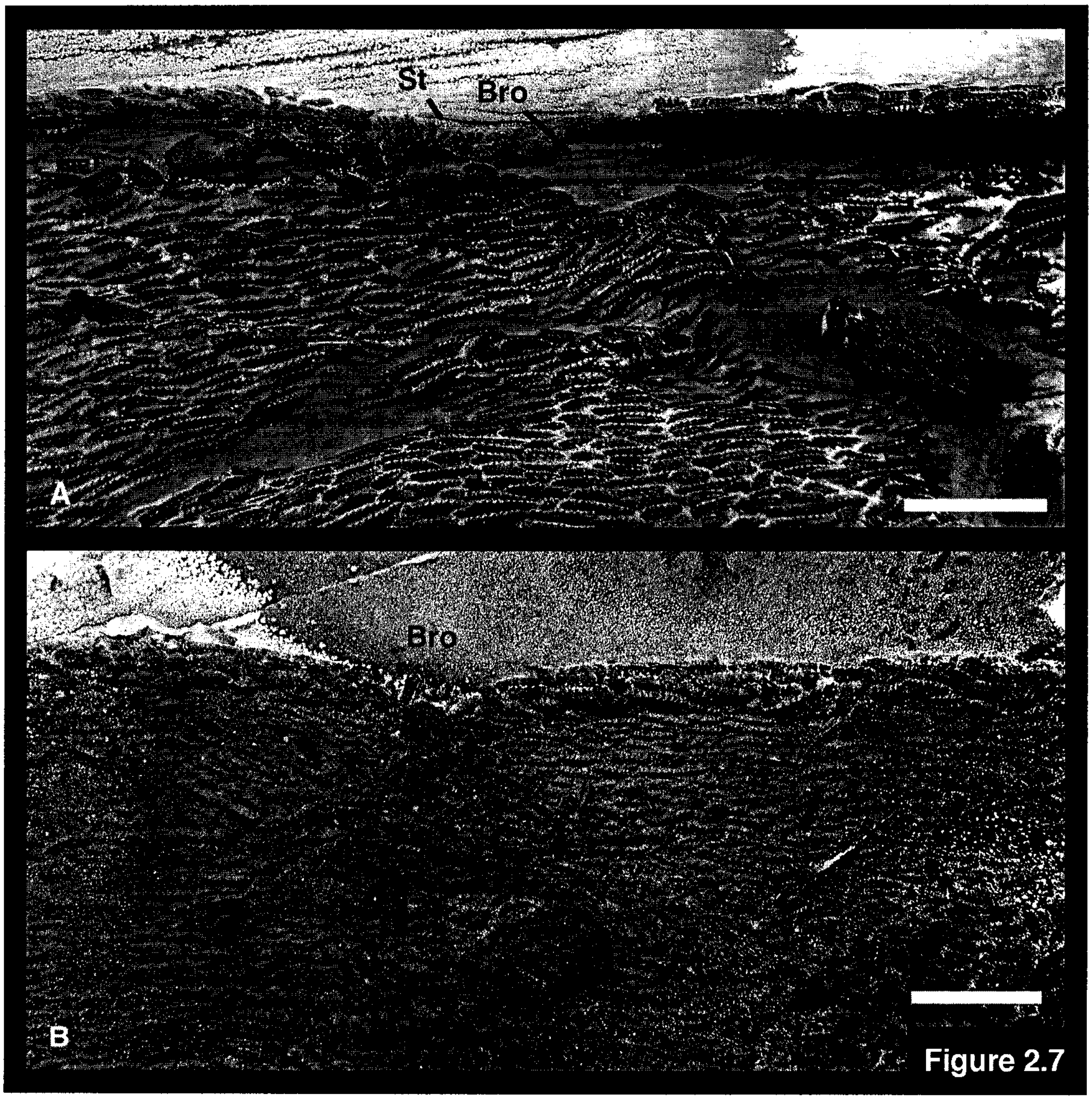


Figure 2.7

UALVP 47001 this is only a break in the continuity of the thickened lateral margin; however, on UALVP 47003, it appears as if the structure actually produces an opening on the side of the animal. Just anterior to this on UALVP 47003, the lateral margin has a very stable ridge that the ventral surface likely attached to, but that has now been crushed through taphonomic processes. Of the locations present on the cephalothorax, this appears to be the likely location of the branchial opening. Just posterior to this opening, the tubercles are short (<1 mm) compared to those on the rest of the cephalothorax. The opening would have been at most 5 mm wide and the indentation continues in an anterior to posterior direction for 16 mm on UALVP 47003 and approximately 14 mm on UALVP 47001.

In all the specimens that have the ventral surface exposed, the lateral margin appears to have been more robustly connected to the dorsal surface of the animal, as it appears as if the ventral surface has caved in towards the underlying dorsal surface. Conversely, on specimens on which the dorsal surface is exposed, the lateral margin is simply gradually covered by the surrounding sediment, with no indication of fracture. On UALVP 47003, the left lateral margin even appears intact, and the dorsal surface appears to simply wrap around onto the ventral surface for at least 6 mm to meet the collapsed part of the ventral surface.

Caudal Region–UALVP 47003 and 47004 both show a very short part of the tail region. On UALVP 47004, the ventral surface of the cephalothorax progresses into a structure similar to a ventral ridge scale. This overlaps onto the first ridge scale, which is approximately 9.5 mm long and 9.5 mm wide (exposed surface). Posterior to this is a much larger ridge scale that is 12.2 mm long and at least 14 mm wide. Lateral to these ridge scales are smaller lozenge-shaped imbricated scales. These progress from the posterior region of the cephalothorax (on the ventral surface), and on the two specimens that preserve caudal regions, these small lozenge-shaped scale are present on the sides of the animal before the medial end of the cephalothorax (the most posterior region of the cephalothorax). The scales present on UALVP 47003 and 47004 are all fairly uniform in size (ranging from 4.3 mm to 8.0 mm wide depending on the exposure and approximately 4 mm long in most cases) and appear dwarfed by the larger ridge scales. There is also one ridge scale present on UALVP 47003, but this appears to have been disarticulated and is incomplete at 7.7 mm wide and 9.9 mm long.

Histology and Tubercle Pattern–The tubercle pattern on the dorsal surface of the cephalothorax is both distinct and somewhat chaotic in some areas. The most regular pattern is discernable on both the slopes of the primary crest and the two secondary ones. This pattern consists of large (2.0-6.4 mm, average 3.7 mm), barbed tubercles that are immediately surrounded by very small (no longer than 0.4 mm) plate-like tubercles. These smaller, rarely barbed tubercles share the basal plate of the larger tubercles and, based on the interior surface of the organism, make up a single plate that forms the median crest. The top surface of all the large tubercles has been abraded and occasionally the smaller tubercles also show some abrasion. These unique basal plates, and their tubercles, are separated from each other by more, small, plate-like tubercles, and occasionally moderately long-barbed tubercles (approximately half the length of the large tubercles on the basal plates).

This pattern is not maintained over the whole dorsal surface of the animal. On top of both the primary and left secondary crest there are broad, barbed tubercles. These are sometimes up to 1.5 mm wide, but more commonly near 0.9 mm. These are not separated by smaller tubercles and are adjacent to each other. When not abraded, these are smooth topped and un-crested. It is likely these are of secondary origin, as on occasion they appear to overlap smaller, less robust tubercles. There are also similar tubercles along the rounded lateral margins of the cephalothorax. Along those margins, the large, broad tubercles cover a width of approximately 3 mm from the very edge of the specimen.

The large, barbed tubercles are also present over the pineal region of the animal, but here they are sometimes separated by small, plate-like and barbed tubercles. This region is slightly raised compared to its surrounding in both UALVP 45700 and 47001. It is just anterior to the central crest of the animal, and represents the area along the midline where the orientation of the tubercles changes from being in the antero-posterior direction to a lateral orientation. This occurs at 75.7 mm from the anterior tip of the specimen along the midline in UALVP 45700 and at 55 mm in UALVP 47001.

Anterior to the pineal region, the barbs on the tubercles are sometimes dichotomous. In this area, the basal plates are visible and are generally fused together. Where there are an obvious breaks between the bones, it can be seen that there are several tubercles sharing the basal plates. This is corroborated on UALVP 47002, where there are large plate-like structures anterior to the median plate with the crest. Occasionally there are indentations on the basal plates between tubercles marking the area that two different basal plates fused. Unlike in *Lepidaspis serrata* (see Chapter Three), there are no small tubercles acting as sutures to help bind the two basal plates together. The orbits themselves are surrounded by irregularly shaped tubercles that are found upon the fused basal plates that form the orbit itself.

On the rostral tip of the animal, the tubercles are barbed, flat-topped, and in many cases oval or almost circular in shape. These are the widest tubercles seen on the specimen and may be as much as 2 mm wide.

Based on the interior surface of UALVP 47002, the lateral region of the dorsal surface is composed of small plates, likely topped with multiple tubercles, though the surface area of each plate is smaller than that of the plates anterior to the median crest plate.

The ventral surface of the animal shows a more organized pattern of tubercle arrangement. The lateral region is composed of thin, barbed tubercles, very similar to those in *Lepidaspis serrata*, with a crest running both along their midlines and on the barbs. They are very closely spaced, with a density of approximately 14 tubercles per centimeter. In the medial region of the ventral surface, the tubercles take on a broader morphology and have a wide, flat top. They are uncrested, though the density remains as high as on the lateral regions, and this results in these tubercles nearly coming into contact with each other. The anterior region of the ventral surface has a pattern of broad flat tubercles along the midline, and orientation converging towards this midline anteriorly. The tubercles are regularly spaced and there are discernible spaces between all the tubercles in this region.

The lateral margins of the cephalothorax visible on the ventral surface are very thick, at some points reaching 2 mm in thickness (from top of tubercle to bottom of basal layer). On UALVP 47003, the left side also shows small clusters of shorter tubercles (compared to the longer ones separating these regions) approximately every centimeter. On the indentation that is likely the location of the branchial opening, the tubercles are very short, less than one millimeter in length or width.

On the caudal ridge scale the tubercles range from 1.5 mm to 7.0 mm, with the longer ones being on the medial region of the scale. The smaller imbricated scales lateral to these have many, very small tubercles with the more anterior ones being little more than stars of dentine and those on the posterior region of the scale reaching miniscule lengths of slightly more than one millimeter.

Remarks–Probably reaching half a meter, this species would have dwarfed almost all the known vertebrates and invertebrates in the MOTH assemblage, not to mention most other heterostracans, with the possible exception of some later psammosteids. The cyclomoriform arrangement of the tubercles on the median dorsal plate suggests affinities to traquairaspidids (Tarlo, 1965; Dineley and Loeffler, 1976). Also similar are the large, broad, closely spaced tubercles present on the median ventral surface of the animal as opposed to the thinner tubercles along the lateral margins. The crest along the midline of the dorsal surface is similar to those reported in *Weigeltaspis* (Tarlo, 1965) and many traquairaspidids. However, *Weigeltaspis* does not have cyclomoriform arrangement of tubercles on the shield. The branchial opening in the anterior lateral region of the cephalothorax is also consistent with the location in traquairaspidids such as *Traquairaspis mackenziensis*. The lack of complete plates making up the dorsal and ventral surfaces, however, suggests that *Grandipiscis exscopulus* should not be placed within the family Traquairaspididae.

The anterior region of the ventral surface has tubercle morphology very similar to that of *Lepidaspis*, with the exception that the basal layer of bone appears well fused and appears to grow as a large plate, rather than as separate tesserae (for the median dorsal plate at least). The morphology of the dorsal surface of the animal, with the median crest along the midline, rules out the possibility that this is another species of *Lepidaspis*.

Dineley and Loeffler (1976) also described a specimen of cephalothorax they attributed to cf. *Lepidaspis serrata*, Type 1 as well as a tail region of cf. *Lepidaspis serrata*, Type 2. The cf. *L. serrata,* Type 1 specimen shows some similarities to the ventral shield of *G. exscopulus*; however, the tubercles in the medial region of the shield are significantly larger than those of *G. exscopulus*. The tubercle pattern on the lateral region of the cf. *L. serrata,* Type 1, specimen also has interstitial ridges, similar to those seen on the dorsal surface of *G. exscopulus*. These do not appear on the ventral surface, again suggesting that the specimens described by Dineley and Loeffler are not the same as *G. exscopulus*. The *L. serrata*, Type 2 specimen does show some similarities to the tail region of *G. exscopulus*; unfortunately, the lack of any part of the cephalothorax in the specimens described by Dineley and Loeffler makes it difficult to attribute to the same species. However, since both of the specimens Dineley and Loeffler described do come from the MOTH locality (GSC 69014), there is a very strong possibility that the Type 2 specimen is an example of the tail region of *G. exscopulus*. It is also reasonable to suggest that the Type 1 cephalothorax is indeed far more similar to *G. exscopulus* than it is to *L. serrata*, and that both should no longer be referred to the species *L. serrata* or even the genus *Lepidaspis*.

The tesserae that compose the shield, with the exception of the median dorsal plate, along with the single identified branchial opening, suggest that this is indeed a classic example of a tessellated heterostracan.

GRANDIPISCIS cf. *G. EXSCOPULUS*, Type 1

(Fig. 2.8)

Material–UALVP 23254, 41680, 42045, 43846, all portions of ventral surface of cephalothorax.

Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32' N, 127° 43' W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Description

All four specimens are fairly incomplete (Fig. 2.8). When present (on UALVP 23254, 41680, and 43846) the lateral regions of the shield have a cyclomoriform pattern of tubercles. The larger tubercles in the pattern are long (approximately 5 mm), laterally barbed, and have a crest along their midlines. The barbs themselves also have crests oriented towards the midline of the tubercle posteriorly. The small interstitial tubercles are also barbed and crested along their midlines, but are typically thinner, shorter in length (one to four millimeters), and

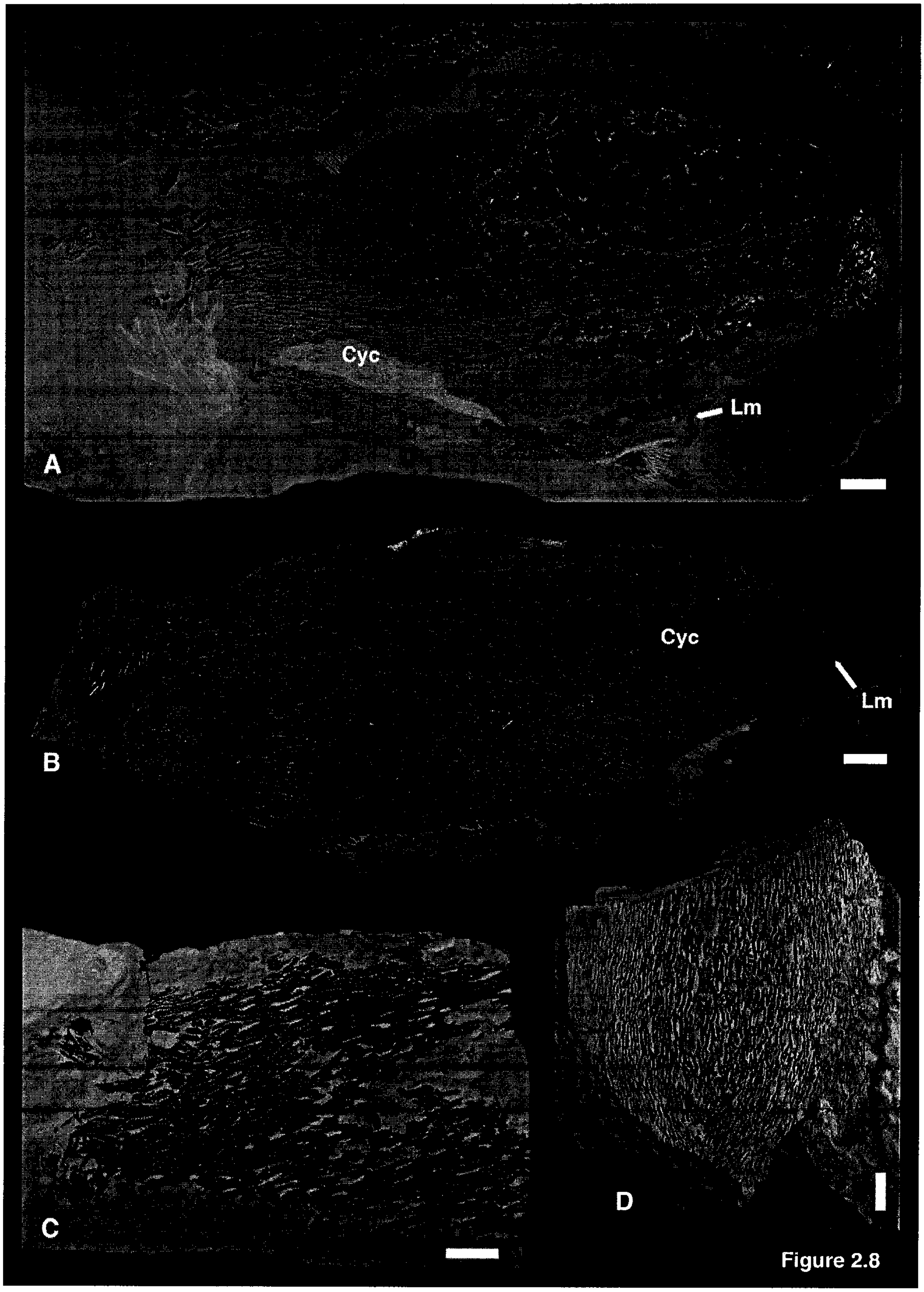


Figure 2.8

only about two thirds the height of their larger neighbors. This region has a width of approximately 3.5 cm on UALVP 43846 from the lateral margin of the specimen.

The medial region of the shield has wide (approximately 1 mm), flat, barbed tubercles. Here, tubercles are shaped as to minimize space between adjacent tubercles, and it is not uncommon for the anterior or posterior of a tubercle to fork and shape around another tubercle, though this forking normally progresses for less than half a millimeter around those tubercles. The morphology of this medial region gradually changes to the tubercle morphology of the lateral region farther from the midline of the animal. The large, broad tubercles do not appear to be secondary in origin and do not obviously overgrow their thinner neighbors from the lateral region. On the anterior of UALVP 43846, the tubercles along the midline flare out laterally until more anterior to these, the tubercles are all oriented with their long axis transverse. Tubercles closer to the lateral margin are oriented gradually towards the midline in this area following the margin of the cephalothorax. In this region where the orientations of the tubercles change, there are at least 5 examples of tubercles that take on the shape of a 'Y'. All the tubercles are flat topped and uncrested in this anterior region.

The lateral margin of the cephalothorax (preserved for 4.2 cm on UALVP 43846) is composed of short (1 to 3 mm) tubercles that are closely spaced and lack a cyclomoriform pattern.

Remarks–These specimens closely resemble cf. *Lepidaspis serrata*, Type 1, of Dineley and Loeffler (1976) and *G. exscopulus*. The tubercles in the medial region of the shield, not being excessively robust, suggest closer affinities to *G. exscopulus* than to those of *Lepidaspis* cf. *L. serrata*, Type 1. However, the cyclomoriform arrangement of tubercles in the lateral region is very similar to that of *Lepidaspis* cf. *L. serrata*, Type 1. The median tubercles are also similar to those seen in *L. loefflerae* n. sp. (described in Chapter Three); however, the morphology of the lateral region again excludes the affinities to *Lepidaspis.*

GRANDIPISCIS cf. *G. EXCOPULUS*, Type 2

(Fig. 2.9)

Material–UALVP 23158, median plate of ?dorsal shield.

Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32' N, 127° 43' W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Description

This is a portion of a cephalothorax that appears to be from the midline of the animal (Fig. 2.9). The specimen is 94 mm long and 39 mm at its widest. The whole surface of the specimen is covered with a cyclomoriform arrangement of tubercles with the larger ones being approximately 4 mm long. These large tubercles are well abraded, but when not, they have a crest running along their midline. Separating these larger tubercles are smaller (typically less than 1.5 mm long), plate-like tubercles. Occasionally these are barbed. Along the midline of the specimen are some broad (0.9 mm) secondary tubercles that overgrow the narrower primary tubercles. These secondary tubercles do not have a crest along their midline as the primary ones do. The bone of the specimen is approximately 1 mm thick, measured

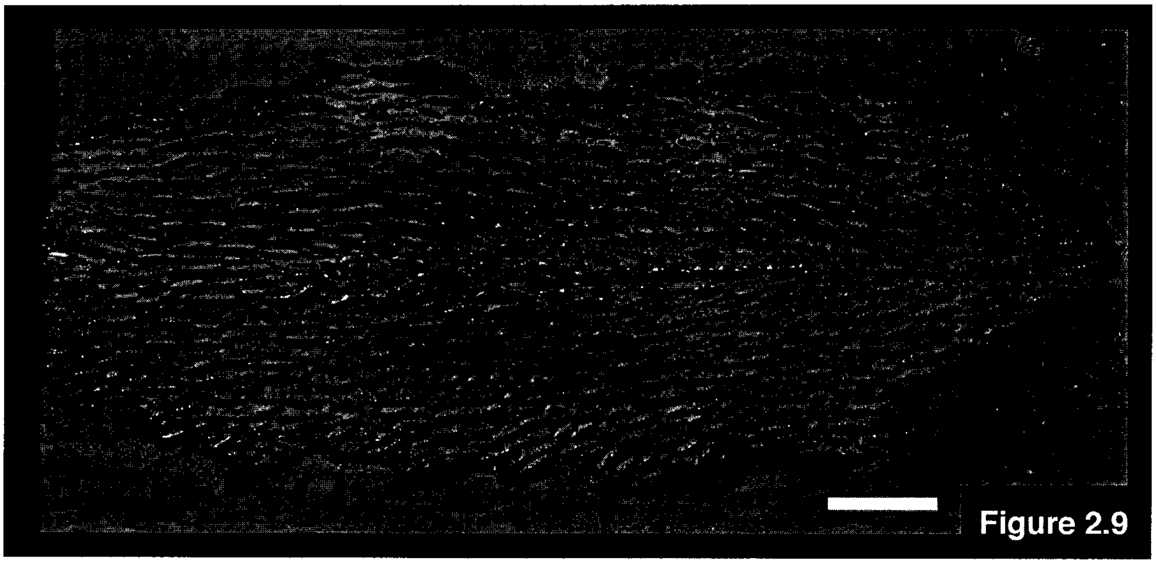


Figure 2.9

from the interior to the top of the dentine tubercle. The specimen has a slight crest along the midline; however, this may be due to the secondary tubercle formation accentuating this region.

Remarks–The presence of the small, plate-like tubercles between the larger primary tubercles is similar to the state seen on the crest of the dorsal shield in *G. exscopulus*; however, there is very little evidence on this specimen of the crest present on *G. exscopulus*. The secondary tubercles, however, are nearly identical in morphology and placement to those in *G. exscopulus*. Because of the lack of a prominent crest, this specimen cannot clearly be identified as belonging to *Grandipiscis*, though it is likely that it is a member of that genus, if not the species *G. exscopulus*.

QUASIMODASPIS gen. nov.

Type Species–*Quasimodaspis notredameensis* sp. nov.

Etymology–The Latinized form of Quasimodo, the hunchback of Notre Dame, and '*aspis*' (female) the Greek word for shield, in reference to the central crest on the cephalothorax of the animals in this genus.

Diagnosis–Tessellated heterostracan with dorsal cephalothorax with large crest along midline of median plate; bone along crest thick (more than 2 mm); surface on and around crest covered by laterally barbed tubercles with cyclomoriform arrangement of smaller dentine tubercles.

Included Species–*Quasimodaspis mackenziensis* sp. nov., *Quasimodaspis canadensis* sp. nov.

QUASIMODASPIS MACKENZIENSIS sp. nov.

(Fig. 2.10A)

Holotype–UALVP 43845, partial left side of cephalothorax.

Type Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32' N, 127° 43' W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Etymology – Referring to the Mackenzie Mountains, where the specimens were found (female).

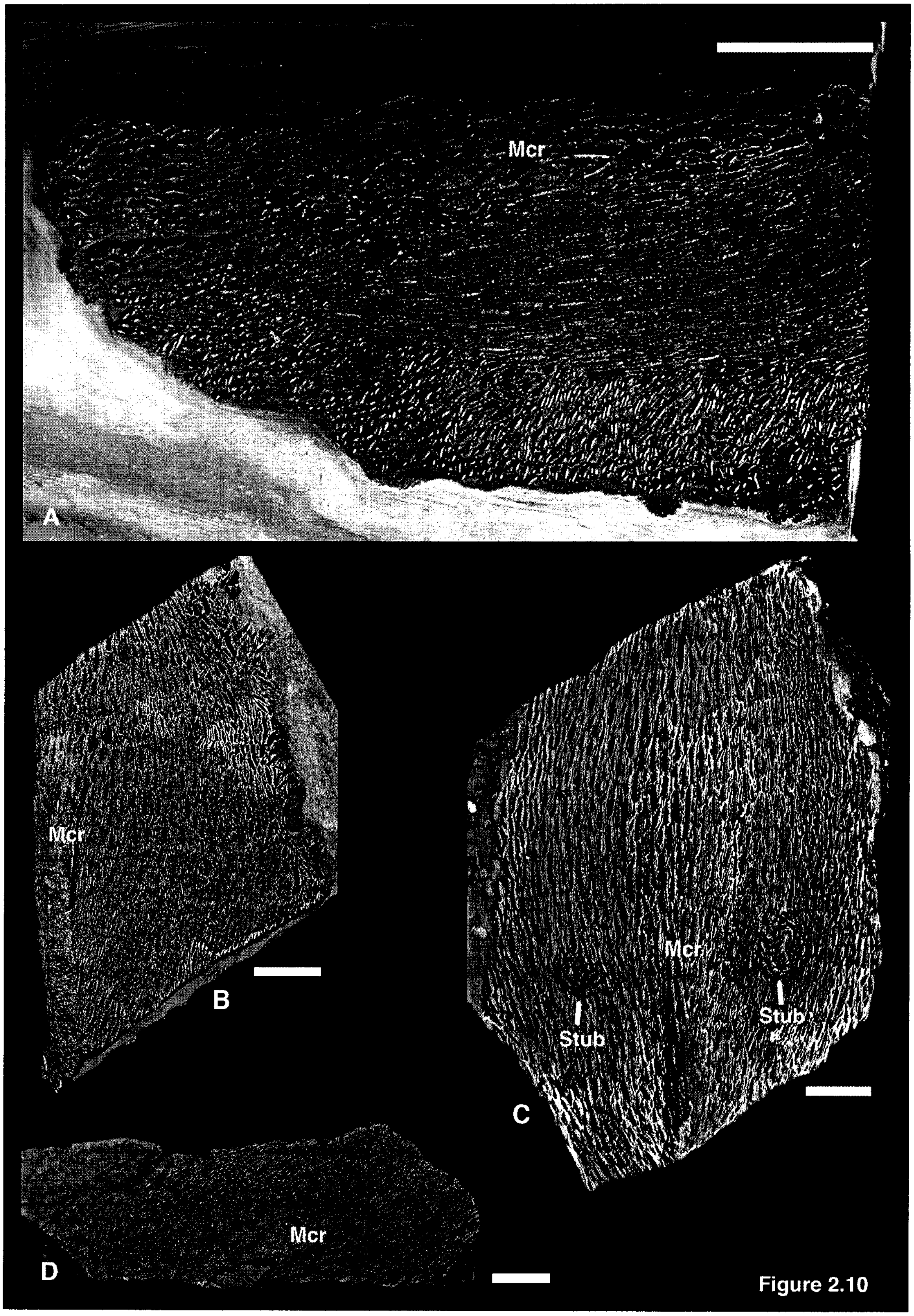
Diagnosis – Prominent median crest with large secondary tubercles; very thick bone forming cephalothorax (1.3-3 mm); tubercle pattern varying, large (3-4 mm long) secondary smooth-topped tubercles on midline, fine, barbed tubercles separated by small (<1 mm long) plate-like tubercles lateral to midline, large, smooth tubercles directed towards margin of shield lateral to region with barbed tubercles.

Description

Body Form–The one and only specimen of this species, though fragmentary, is distinct enough to separate it taxonomically from other specimens due to both the varying pattern of tubercles and to the marked thickness of the bone. The specimen itself is 77.7 mm long and 40.6 mm wide (Fig. 2.10A). Though the animal is likely dorso-ventrally flattened, the thickness of the bone has allowed the depth of the specimen to be preserved. From the lateral edge to the midline, there is a vertical depth of approximately 10 mm assuming the median crest was symmetrical. This crest along the midline is clearly distinct. The great thickness of the bone is likely the reason that the specimen was not flattened completely during preservation. There are no landmarks on the specimen such as orbits, branchial openings, or pineal macula. There is, however, a short fracture or depression on the anterior section running 12.5 mm from the anterior edge of the shield and parallel to the midline of the specimen. It passes between tubercles and does not puncture the basal layer of bone. The single example and its incompleteness makes it unclear if this is truly a characteristic of the species or if it is just a taphonomic distortion.

Histology–There are three distinct regions visible on the cephalothorax, based on tubercle type and pattern. Of these, two are evidently primary zones that were in place before any secondary tubercle formation took place. The third, distinguished by a cover of secondary tubercles, is the crest region of the cephalothorax.

The regions with primary tubercles include the zone around the midline where they take on a cyclomoriform organization, and the region around the lateral and anterior margins where the tubercles are directed towards those margins. The central region with the cyclomoriform arrangement has large, flat-topped, anteriorly barbed tubercles. These range in length from 3 mm to 4 mm and are generally abraded; however, in instances where there is no abrasion, they have a crest along the barbs and along their midline. Between these larger tubercles are small (1 mm) occasionally barbed tubercles. These smaller 'interstitial' tubercles tend to be flat



Mcr
A
Mcr
B
Mcr
Stub
Stub
C
Mcr
D
Figure 2.10

topped, though they do not appear to show abrasion. They are closely spaced and there are approximately four to five rows of these smaller tubercles between the larger ones, which are spaced 2 mm apart.

The region around the lateral and anterior margin is covered with broad (0.6 mm), flat-topped tubercles that are directed towards the margin of the plate. Many of these, though not all, lack barbs. However, they do have an oak-leaf shaped morphology. This zone of tubercles is found consistently within the first 1.1 cm from the margin of the plate. The transition from the central region with cyclomoriform tubercle arrangement to this antero-lateral zone is very abrupt, with only a few tubercles from the central region gradually bending into the lateral zone.

The zone of secondary tubercle formation along the midline consists of very broad tubercles (up to 1 mm, generally slightly thinner), with short lateral barbs. They are flat topped and show signs of abrasion. These cover the region on the crest that had been previously covered by the cyclomoriform pattern of primary tubercles. Where the secondary tubercles have been fractured and lost, the primary tubercle pattern is visible underneath. They significantly add to the thickness of the median crest of the plate, which reaches 3 mm along the midline. The rest of the plate has a thickness of at least 1.3 mm and this is maintained everywhere except along the crest.

Remarks–The thickness of the cephalothorax has probably contributed to the exceptional preservation of this specimen. It is likely a portion of the dorsal plate of the animal, as crests are rare on the ventral surfaces of heterostracan cephalothoraces. The distinct, laterally projected tubercles on the lateral margin clearly distinguish this species from the other species in this genus, as well as from similar species showing a crest such as *Grandipiscis exscopulus* and *Weigeltaspis* (Tarlo, 1965). The cyclomoriform arrangement also differentiates it from *Weigeltaspis* which does not have the interstitial tubercles. The tubercle orientation along the lateral margin differentiates it from Dineley and Loeffler's (1976) Heterostraci indet. Type 4. Though the crest of the specimen described by Dineley and Loeffler is thick as in *Q. mackenziensis*, the one they described is relatively narrow and abrupt compared to that seen in the UALVP specimens from MOTH. Also, the specimen described by Dineley and Loeffler has tubercles that are generally parallel with the long axis of the specimen and the specimen itself is small compared to that of *Q. mackenziensis*.

QUASIMODASPIS CANADENSIS sp. nov.

(Figs. 2.10B-C)

Holotype–UALVP 47005, dorsal portion of cephalothorax, median plate.

Paratypes– UALVP 32495 and 47006, both portions of the median plate of the dorsal cephalothorax.

Type Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32' N, 127° 43' W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Etymology–Specific epithet designates the species' location in Canada.

Diagnosis–Cyclomoriform arrangement of barbed, crested tubercles, with larger (3-4 mm long) tubercles tapering slightly anteriorly; interstitial tubercles (0.5-

1.5 mm long) generally barbed and crested; plate thickness ranging from 0.8 to 1.2 mm lateral to central crest and at least 2.3 mm along crested midline.

Description

Body Form–UALVP 47005, the most complete of all the incomplete specimens is 93 mm long and 60 mm wide at its largest. The half widths of the other two specimens from the margin to the midline (34 mm) suggest that this size is close to the correct width of the plate, though the unbroken length is likely significantly longer. There is a crest along the midline of the plate on all three specimens, appearing the most robust in UALVP 47006, where it has been fractured. Here, the crest is 4.4 mm wide. The height of the crest on this specimen, however, cannot be accurately measured, as there is no cross section through a complete portion of the crest.

The thickness of the plate ranges from 0.8 mm to 1.2 mm, being thicker near the midline. The cross section through the crest of UALVP 47005 is 2.3 mm thick, thought it appears that the crest has begun to taper posteriorly and this likely does not represent the full thickness of the median crest at its maximum. On UALVP 47006, the bone is still 2.0 mm thick, even though much of the crest has been broken off. UALVP 32495 shows that this thickness does not extend anteriorly on the crest as it tapers gradually. The bone of the anterior portion of the crest has a thickness similar to that of the rest of the plate.

Histology–The tubercle pattern on the surface of these plates consistently shows a cyclomoriform arrangement. Rarely is there evidence of secondary tubercle formation, with the exception of two locations, and the orientation of the tubercles is generally in the anterior to posterior direction, with these tubercles tapering gradually towards the midline at the posterior region of the crest.

The shape of the larger tubercles (3-4 mm long) in the cyclomoriform arrangement is that of an elongate teardrop. These are laterally barbed, usually flat topped (with only a few exceptions having a crest along the midline), and gradually become thinner in the anterior region of the tubercles, creating the teardrop shape. They range between three and four millimeters in length, though they are more consistently closer to three. Between these larger tubercles are smaller (0.5 to 1.5 mm in length), crested, occasionally barbed tubercles, in rows of 2-5 between the larger ones. When barbs are absent they take on a plate-like appearance.

On UALVP 47006, the lateral margin of the plate has thicker tubercles than those nearer to the midline, though they continue to have an anterior to posterior orientation. Here, the cyclomoriform arrangement, though still present, is less pronounced than in the center of the plate. This is also apparent on UALVP 32495, though to a lesser extent.

The median crest on the plate of UALVP 47005 shows extensive abrasion and the cancellous layer of bone is visible on the posterior region of the crest. Abrasion is also apparent on UALVP 47005. This area on both specimens also shows formation of secondary tubercles on the crest. These secondary tubercles are broad (0.75 - 1.6 mm) and barbed.

Lateral to the median crest of UALVP 47005 there are also two other areas of secondary tubercle formation. These secondary tubercles form a circular pattern that is 9.6 mm long and 7.8 mm wide on the right of the midline and 7.2 mm long and 6.5 mm wide in the circular pattern on the left of the midline. In both cases, these circular structures are superimposed on the cyclomoriform pattern of the rest of the shield. The tubercles producing these patterns are curved, barbed, and flat topped. Preparation from the interior of the specimen towards the circular pattern on the right side of the animal showed that the basal layer of bone is continuous and there is no physical breach of the shield under these circular patterns.

Remarks–The similarities between this species and *Quasimodaspis mackenziensis* include the cyclomoriform pattern of tubercles, the median crest down the cephalothorax, and the overall estimated size of the specimen. However, key differences are present. These include the tear-drop shape seen in the larger tubercles of the cyclomoriform pattern in *Q. canadensis*, whereas the larger tubercles in *Q. mackenziensis* tend to maintain a constant width. Secondly, the lateral and anterior margins of the plate on *Q. mackenziensis* have a unique tubercle arrangement in which they are oriented towards the margin. Though the cyclomoriform arrangement of tubercles on *Q canadensis* is limited on the margins, the tubercles do not orient themselves towards the margin as they do in *Q. mackenziensis*.

As mentioned above, the median crest of *Q. canadensis* is similar to that of *Weigeltaspis*, but the cyclomoriform tubercle arrangement is not seen in the latter. In comparison to Dineley and Loeffler's Heterostraci Type 4, the crest on *Q. canadensis*, though more significant and abrupt (especially on UALVP 47006), does not produce the bulbous structure seen in the Heterostraci Type 4 dorsal shield. The tubercles on the Heterostraci Type 4 specimens also do not taper into tear-drop shapes as seen on those in *Q. canadensis*. The very distinct crest on *Q. canadensis* also differentiates it from the other crested species, *Grandipiscis exscopulus*, found at MOTH.

CONCLUSION

The three new species described herein, along with the two types conferred to *Grandipiscis exscopulus*, all show some similarities to each other, most notably the median crest on the dorsal shield, the laterally barbed tubercles, the cyclomoriform arrangement of tubercles, and the presence of a median plate on the dorsal surface of the cephalothorax. Initially these specimens were grouped with *Lepidaspis* in the UALVP collections; however, more in-depth examinations of these specimens suggested that they are most definitely distinct from that genus, the only common feature being that barbed tubercles are seen in both the newly described species and the genus *Lepidaspis*.

The large, barbed tubercles and crests present on these new species are reminiscent of *Weigeltaspis* (Tarlo, 1965). However, the ornamentation of *Weigeltaspis* is composed of widely spaced, barbed tubercles that do not show a cyclomoriform pattern, excluding a close relationship between these new species and *Weigeltaspis*.

The cyclomoriform arrangement of tubercles is very reminiscent of those seen in traquairaspidids (Dineley and Loeffler, 1976). Traquairaspidids with crests and spines along their midlines have also been identified, and it is also common for the ornamentation to have broader and flatter tubercles near the midline of the animal, as is seen in all the newly described species with the exception of *Quasimodaspis canadensis*. The key difference from these species, particularly with respect to *Grandipiscis*, is that the dorsal shield is not formed by seven or nine plates, but by one large median plate, and then smaller tesserae of various sizes surrounding this. The position of the branchial opening in *G. exscopulus* is apparently similar in location to those seen on some traquairaspidids, and it is likely that *G. exscopulus* and the other new species described in this paper are close relatives of traquairaspidids.

These specimens likely represent another unique group of primitive tessellate heterostracans, closely related to traquairaspidids and other tessellate forms such as *Weigeltaspis* and *Lepidaspis*. Together they represent some of the most primitive vertebrates known. A detailed study of the phylogeny is in order, as the most recent phylogeny of basal vertebrates places these groups at the base of heterostracan phylogeny. The description of these exceptional specimens will help future researchers resolve these new species relationships to the other problematic taxa mentioned above, which are currently grouped together as tessellate heterostracans.

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CHAPTER 3

DESCRIPTION OF THE NEW SPECIES *LEPIDASPIS LOEFFLERAE* AND REDESCRIPTION AND DISCUSSION OF BONE GROWTH IN THE GENUS *LEPIDASPIS*

ABSTRACT

Exceptionally preserved specimens from the Mackenzie Mountains, NWT, Canada have allowed for the description and analysis of bone growth in *Lepidaspis* as well as for the description of the new species *L. loefflerae*. This genus belongs to an informal group of early basal vertebrates known as 'tessellate heterostracans,' which have dermal armour composed of interlocking tesserae. *Lepidaspis loefflerae* has a slightly broader cephalothorax than *L. serrata* and has broader, flat-topped tubercles on the tesserae of the dorsal and ventral surfaces of the cephalothorax.

The tesserae on the cephalothorax of *Lepidaspis* have a single tubercle projecting from the center of the basal plate. The basal plates themselves show varying degrees of fusion; in some specimens, the plates are completely fused and the distinction between individual plates is lost, while in others there are distinctly visible spaces between the basal plates; fusion and contact are entirely absent.

Location on the body of the tesserae also determines the extent to which they fuse. The lateral and anterior margins of the cephalothorax tend to be more robustly fused than the interior (medial) regions of the shield. However, in cases of near complete fusion, fusion along the midline and its surrounding area is more robust than between this region and the fused lateral margins.

Growth of the basal plates allowed the tesserae of some individuals to eventually fuse, though this fusion is not always associated with a larger size. The lack of significant size differences of the basal plates between well fused and poorly fused individuals suggests that tesserae were first laid down synchronomorially near

their final size. Later, limited cyclomorial growth occurred around the basal plates allowing contact and fusion with each other.

INTRODUCTION

Tessellate heterostracans are a basal group of jawless vertebrates for which phylogenetic relationships are poorly understood. At one time, they also included other tessellate vertebrates, such as *Astraspis*, before it was realized these were not heterostracans (Elliott, 1987). The tessellate pattern is produced on animals that have many small plates (tesserae) covering the cephalothorax (Tarlo, 1967). These plates form an interlocking pattern, and depending on the species these may or may not undergo some fusion to each other.

The genus *Lepidaspis*, a tessellate vertebrate thought to be a heterostracan, was first named by Dineley and Loeffler (1976) for the species *L. serrata.* They were uncertain as to its relationships to other heterostracans, and this uncertainty has yet to be resolved. They also briefly outlined the growth of the cephalothorax based on the specimens that had been collected from GSC site 69014. Recent expeditions to this site (now called MOTH) have yielded many new specimens of *Lepidaspis* allowing for a more detailed discussion of the growth, as well as the description of a new species *L. loefflerae*.

With the introduction of this new species, and the information gained from this new material, it was necessary to slightly revise the diagnosis of the previously monotypic genus *Lepidaspis*. The diagnosis and description for *L. serrata* was further refined to allow the differentiation of *L. loefflerae* sp. nov.

LOCALITY INFORMATION AND GEOLOGY

The 'Man on the Hill' (MOTH) locality is located in the Mackenzie Mountains of the Northwest Territories, Canada (Fig. 2.1). It is only accessible by helicopter, the closest settlement being the small mining town of Tungsten, approximately 45 minutes (75 km) away. The MOTH section extends through both Silurian and Lower Devonian rock. Fossil vertebrate remains are abundant in a lower, Late Silurian, fish level called B-MOTH and the higher, Lower Devonian MOTH fish layer. The section between these two is relatively devoid of vertebrate fossils, though invertebrate breccia is common.

The B-MOTH layer has been dated as late Wenlock or early Ludlow in age (Wilson et al., 2000). This date is based both on the presence of the thelodont *Paralogania martinssoni* and on several species of the graptolite *Monograptus* being found just below and in contact with the fish level (Soehn et al., 2000; Wilson et al., 2000).

The specimens described in this study are taken from talus slopes, and have originated from the Lower Devonian MOTH fish layer. This layer is equivalent to the Geological Survey of Canada (GSC) locality 69014 or University of Alberta Laboratory for Vertebrate Paleontology (UALVP) locality 129. It is situated at MOTH 180 meters in the measured section of Adrain and Wilson (1994). The approximately 10 meters of the MOTH fish layer are bounded both on top and bottom by two turbidity deposits (Hanke, 2001). The fish layer itself comprises fine-grained carbonaceous siltstone with alternating light and dark layers (Zorn, 2003,

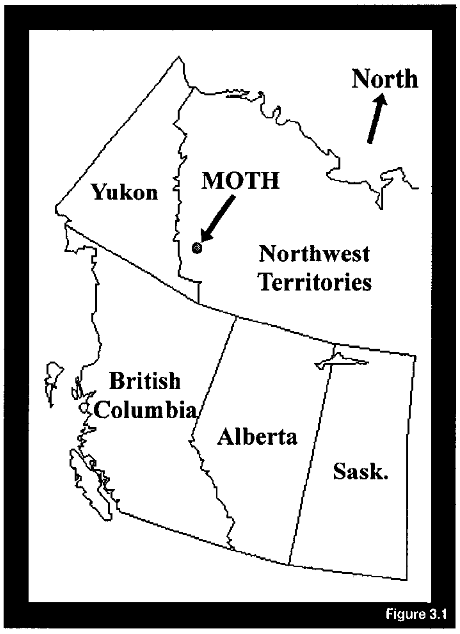

North
Yukon
MOTH
Northwest Territories
British Columbia
Alberta
Sask.

Figure 3.1

personal communications). It was previously believed to be dolomite (Gabrielse et al., 1973; Dineley and Loeffler, 1976), and because the rock reacts strongly with acid and dissolves easily in acetic acid, it has also been described as limestone (Adrain and Wilson, 1994; Wilson and Caldwell, 1998; Soehn et al., 2000). Pyrite is present as grains, usually in small lenses of sand, as small nodules, and it has formed on some of the fossils (Zorn, 2003, personal communications). Pyrite (FeS_2) formation begins with the oxidization of sulfur, normally from a precursor iron monosulfide (FeS) (Rickard, 1999). In this process, the sulfur is oxidized; the iron is not. The oxidization of the sulfur occurs in a liquid solution and allows pyrite to form, which tends to nucleate on biological surfaces, sulfur, and gregite (Rickard, 1999). This process occurs preferentially in an anoxic environment.

Despite the presence of organisms that lived on, near, or in the benthos (heterostracans, cephalaspidids), and other animals that were likely scavengers (ostracods, eurypterids, phyllocarids), there is no evidence of sediment reworking by large animals in the MOTH fish layer. There is evidence that the sediment was bioturbated by small organisms (Zorn, 2003, personnel communications). The fine layering suggests two things. The first is that the sediment was deposited below the storm wave base. The second is that the environment was inhospitable to large, burrowing animals.

All of this suggests a quiet and anoxic region of deposition and helps explain the high quality of preservation and diversity of the MOTH vertebrate assemblage, which includes over 70 species of vertebrates ranging from basal heterostracans to chondrichthyans and acanthodians. Of these 70+ species of vertebrates, at least 23 are heterostracans.

METHODS

Specimens were all collected from the talus slopes below the MOTH 180 m fish layer, and originated from this layer. They were collected in expeditions led by Dr. Brian Chatterton in 1983 and 1990 and Dr. Mark Wilson in 1990, 1995, 1997, and 1998, and by Chelsea Smith and the author in 2002.

Preparation of University of Alberta specimens, when necessary, was done in dilute acetic acid baths. Fossils were slowly exposed by rubbing off the sediment residue on a weekly basis using soft paintbrushes. Once exposed the fossil material was coated in vinac (plastic beads dissolved in acetone) to prevent further removal of the surrounding sediment during preparation. Once preparation was complete, fossils were covered with diluted vinac to help protect and stabilize them. All specimens are stored in the University of Alberta Laboratory for Vertebrate Paleontology (UALVP) collections and in the Canadian Museum of Nature (CMN) collection.

Thin sections were prepared by Don Resultay of the Earth and Atmospheric Sciences Department at the University of Alberta. They were photographed using normal and polarized light.

Measurements were done using 18 cm and 33 cm KAR calipers and a Wild ocular micrometer (20x/13 lens) calibrated with the 18 cm caliper. Photographs were taken using a Nikon Coolpix 4500 and Canon 10D cameras with and without the aid of microscopes.

SYSTEMATIC PALEONTOLOGY

HETEROSTRACI Lankester, 1868

Family *Incertae Sedis*

LEPIDASPIS Dineley and Loeffler, 1976

Type Species–*Lepidaspis serrata* Dineley and Loeffler, 1976.

Etymology–Though I am not naming the genus, the derivation of the name was not included in the original description of *L. serrata.* Latinized Greek "*lepido*", scale-like, and "*aspis*", meaning shield (female).

Amended Diagnosis–Cephalothorax broad and flat, dorso-ventrally compressed, tail narrow. Armour of small scale-units with basal plates unfused early and fused later in ontogeny. Superficial ornament of barbed dentine ridges, one ridge per basal plate on cephalothorax, two or more per basal plate on tail. Anterior and lateral margins of cephalothorax thickened and usually fused; dorsal and ventral surface of caudal region with medial row of imbricated compound scales. Mouth semicircular and placed antero-ventrally; orbits small, dorsal, and placed antero-laterally. Lateral-line system of external pores and internal network of discontinuous grooves. (After Dineley and Loeffler, 1976).

Included Species – *Lepidaspis serrata* Dineley and Loeffler, 1976, *Lepidaspis loefflerae* sp. nov.

Remarks – The similarity in structure of the tubercles and the tesserae on both species of *Lepidaspis* and the variations seen on single individuals, along with the similarity of these individual units to those of the other genera and species described in this thesis, make it very difficult to identify disarticulated remains to genus, let alone to species. This suggests that previous reports of fragmentary remains of *Lepidaspis* (Smith et al., 1995; Burrow et al., 1999) may be inaccurate and should be reexamined. In fact, the cross section used by Smith et al. (1995), lacking the median crest on the tubercle, is more similar to the cross sections of *L. loefflerae* than to those of *L. serrata.*

LEPIDASPIS SERRATA Dineley and Loeffler, 1976

(Figures 3.2, 3.7-3.10)

Holotype–NMC 19879, crushed, incomplete cephalothorax, prepared to show dorsal and ventral surfaces (Dineley and Loeffler, 1976:pl. 28, text-fig. 76b).

Referred Material–UALVP 32645, 41504, 42200, 43035, 47007, 47008.

Diagnosis–Ornamentation of thin (<1 mm) barbed tubercles on cephalothorax with crest running along midline of tubercle; smaller crests from barbs meeting this one; tubercles uncrested only on anterior region of ventral surface near mouth.

Description–The description by Dineley and Loeffler is accurate and complete, except that the length of the cephalothorax can reach lengths of up to 160 mm (Fig. 3.2); it was previously described to be 110 mm by Dineley and Loeffler, (1976).

Remarks–The location of the branchial openings is uncertain. Janvier (1996) placed them in a hypothetical location on the antero-lateral margin of the

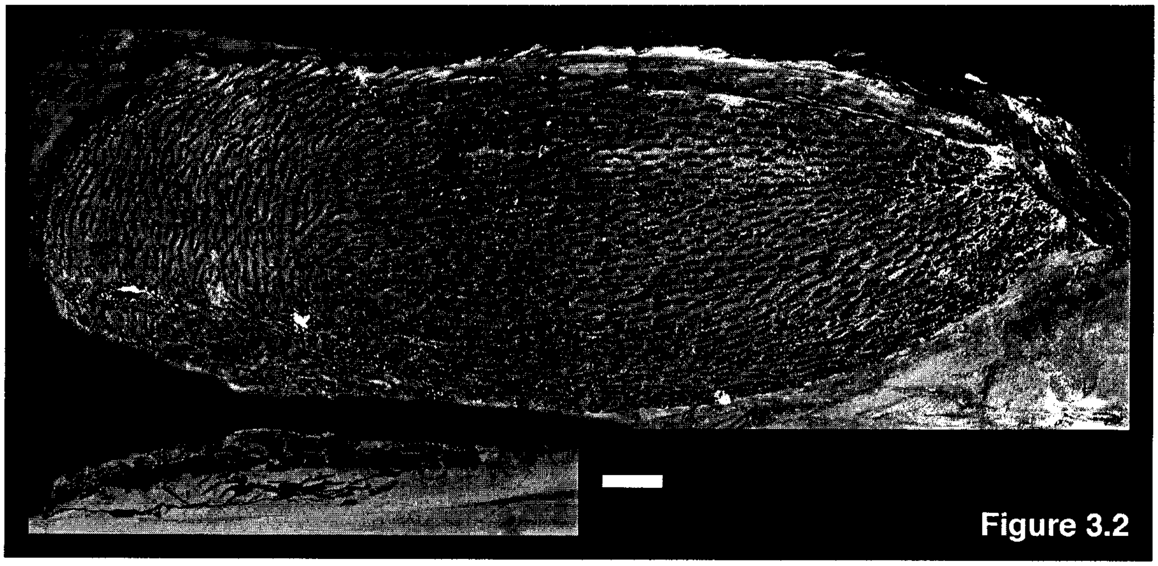


Figure 3.2

cephalothorax. However, preparation of UALVP 43035 shows that the openings are not present in that location and the cephalothorax appears fully fused (Fig. 3.2). This means that the openings must be present in the posterior region of the cephalothorax, likely opening onto the ventro-lateral surface; this is the one location that seems not to be preserved or prepared in specimens of both the CMN and UALVP collections.

LEPIDASPIS LOEFFLERAE sp. nov.

(Figs. 2.3-2.6)

Holotype–UALVP 23138, posterior part of dorsal cephalothorax and tail.

Paratypes–UALVP 43847, 23172, 23280, 47009, 47010 (thin sections A and B).

Type Locality–UALVP Locality 129, MOTH Locality, equivalent to GSC Locality 69014; 62° 32' N, 127° 43' W; Lower Devonian (Lochkovian), Northwest Territories, Canada.

Etymology–Named for Dr. Elizabeth Loeffler who has worked extensively on the ostracoderms from northern Canadian localities.

Diagnosis – Ornamentation of wide (>1 mm), flat-topped, barbed tubercles; crests sometimes present on barbs, but crests not extending to midline of tubercle.

Description

Body Form–The overall shape of individuals of this species is very similar to that of *Lepidaspis serrata*. The cephalothorax is slightly more oval, slightly wider (approximately 75 mm at the widest point), and likely longer (reaching at least 125 mm in an incomplete specimen) than that of *L. serrata* (Fig. 3.3A). The specimens themselves are all dorso-ventrally compressed, suggesting the organism itself was dorso-ventrally flattened. Though the bone is partially crushed, thin sections show that pulp cavities and much of the morphology in thin section are still preserved including fine detail such as the dentine tubules.

Cephalothorax – The orbits, associated with UALVP 43847, are slightly oval with diameters of 3.0 mm by 3.7 mm and 3.4 mm by 4.0 mm for the two orbits available (Figure 3.4A). The number of tubercles associated with the orbital plate is significantly larger than in *Lepidaspis serrata* and there are at least four rows of successive tubercles moving away from the orbit itself. These are all very closely spaced at a density of 1.25 tubercles/mm. Though the basal plates are not visible, the continuity (and otherwise disarticulated nature of the remains) suggests that they are well fused, with the exception of one edge on both, where there is a gap. These orbital plates are thought to represent the most anterior portion of the cephalothorax of *L. loefflerae* that is present in the UALVP collection.

The cephalothorax itself is slightly larger than that of *L. serrata* at approximately 75.5 mm wide and at least 125.7 mm long based on the most complete specimen, UALVP 23138. The shape of the cephalothorax is also more oval than rectangular. The lateral, and potentially the anterior, margins outline this oval and are significantly reinforced when compared to the middle of the cephalothorax (Figs. 3.3C, D). The tubercles on the margins are much more closely spaced at about 10-14 tubercles per centimeter, compared to 5-7 per centimeter on

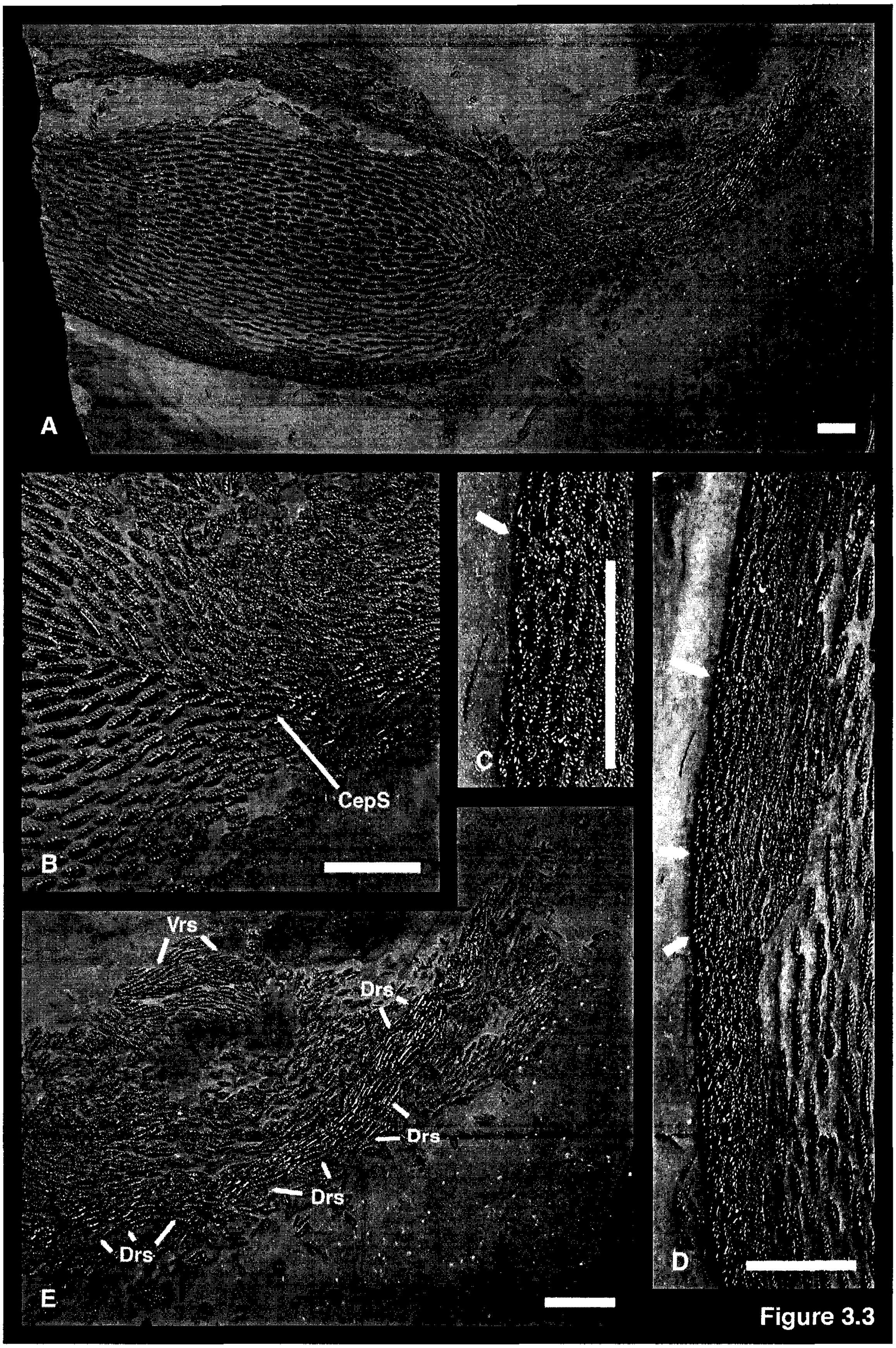
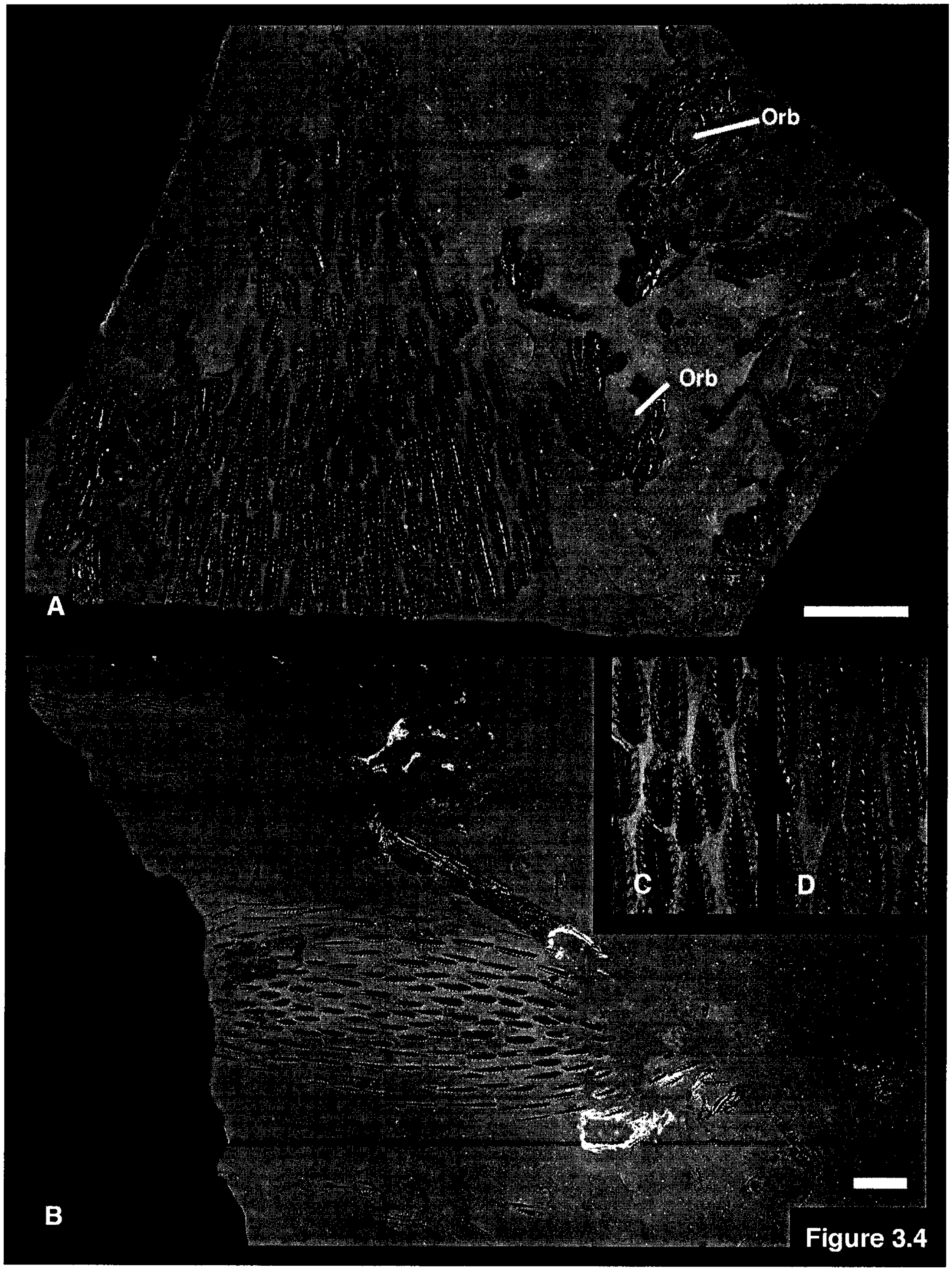


Figure 3.3


Orb
Orb
A
B
C
D
Figure 3.4

the central region of the cephalothorax. This robust lateral margin is approximately 5 mm wide and is a rounded region of fused basal plates, likely making up one pair of plate-like structures along the edge of the animal. Sporadically, in this region, there are formations of tubercles that produce a circular pattern almost as if surrounding the opening for a pore of some sort, but there is no evidence of a foramen in the basal layer of bone (Fig. 3.3C). The tubercles in this lateral region are slightly shorter in length than on the rest of the cephalothorax.

Caudal Region–The transition from the cephalothorax to the caudal region is gradual (Fig. 3.3C). The most obvious aspect of this transition is the reduction of the thickened lateral margins and the appearance of dorsal and ventral ridge scales along the midline of the cephalothorax. The most anterior ridge scale appears to be fused with the cephalothorax, or else the posterior region of the cephalothorax takes on the morphology of the scales that follow it (Figs. 3.3A, B, E).

Excluding the first, the ridge scales are all imbricated with the ones that precede them and are composed of multiple tubercles appearing over a fused basal layer of bone (Fig. 2.3E). On each individual ridge scale, the tubercles are all short (shorter than 3 mm, but normally shorter than 2 mm) on the anterior portion of the scale. These tubercles are followed by a laterally adjacent row of longer tubercles (more than 3 mm and up to 4.9 mm). These longer tubercles form rows of 7-9 tubercles in the anterior four scales and 5-7 rows in the scales posterior to the fourth and complete the posterior region of each scale. All of the tubercles found on the midline ridge scales of the tail are broad and are normally at least 0.5 mm wide on the first four scales. On the first four full scales (excluding the scale-like projection of cephalothorax), the tubercles are extensively crested. The crests run along the midlines of the barbs and then posteriorly towards the crest on the midline of the tubercle. The barbs themselves alternate on each side of the tubercle (i.e., they do not form symmetrical pairs). In a gradual progression, the crests become less prominent on the posterior scales of the series. By the fifth scale, the tubercles are flat topped and the crests are limited to being present only on the barbs themselves. During this progression, the barbs stop projecting as far laterally as they do on the first ridge scale of the tail. By the sixth and seventh ridge scales, the barbs are almost limited to being simple crests on the sides of the tubercles. The last two ridge scales of the tail have some tubercles on which barbs are insignificant or absent.

The width of the ridge scales varies from the posterior of the tail, as does the length (based on UALVP 23138, Table 3.1). Generally, the scales are wider near the cephalothorax and gradually become longer and thinner when compared to the first three anterior ridge scales.

In addition to the ridge scales discussed above, two elongate ridge scales are seen from the other side of the animal. These are extremely long (11.75 mm for the first and 9.65 mm for the second) and thin (5.60 mm and 5.10 mm respectively). The ornamentation is of crested, elongate tubercles (up to 4.95 mm on the first and 3.70 mm on the second) on a fused basal layer. Crests are also present on the barbs and these run towards the midline of the tubercles.

The scales that cover the sides of the tail are much smaller then the ridge scales. Generally, they have between one and four tubercles on a single basal plate. The compound scales with multiple tubercles are more common near the cephalothorax, while posteriorly, the scales have fewer and fewer tubercles. Near

Scale Number (caudal from cephalothorax)	Minimum Width (mm)	Minimum Length (mm)	Width/Length Ratio
1	6.85	6.60	1.04
2	7.55	7.95	0.95
3	6.95	9.40	0.74
4	5.90	10.55	0.56
5	4.25	7.70	0.55
6	4.40	6.60	0.67
7	5.35	7.60	0.70
8	6.40	7.25	0.88
9	6.25	8.90	0.70

TABLE 3.1. The minimum widths of the ridge scales associated with the cephalothorax of UALVP 23138. These are the maximum lengths measurable on the specimen as sediment or the adjacently anterior scale covers the lateral and anterior portion of each scale respectively.

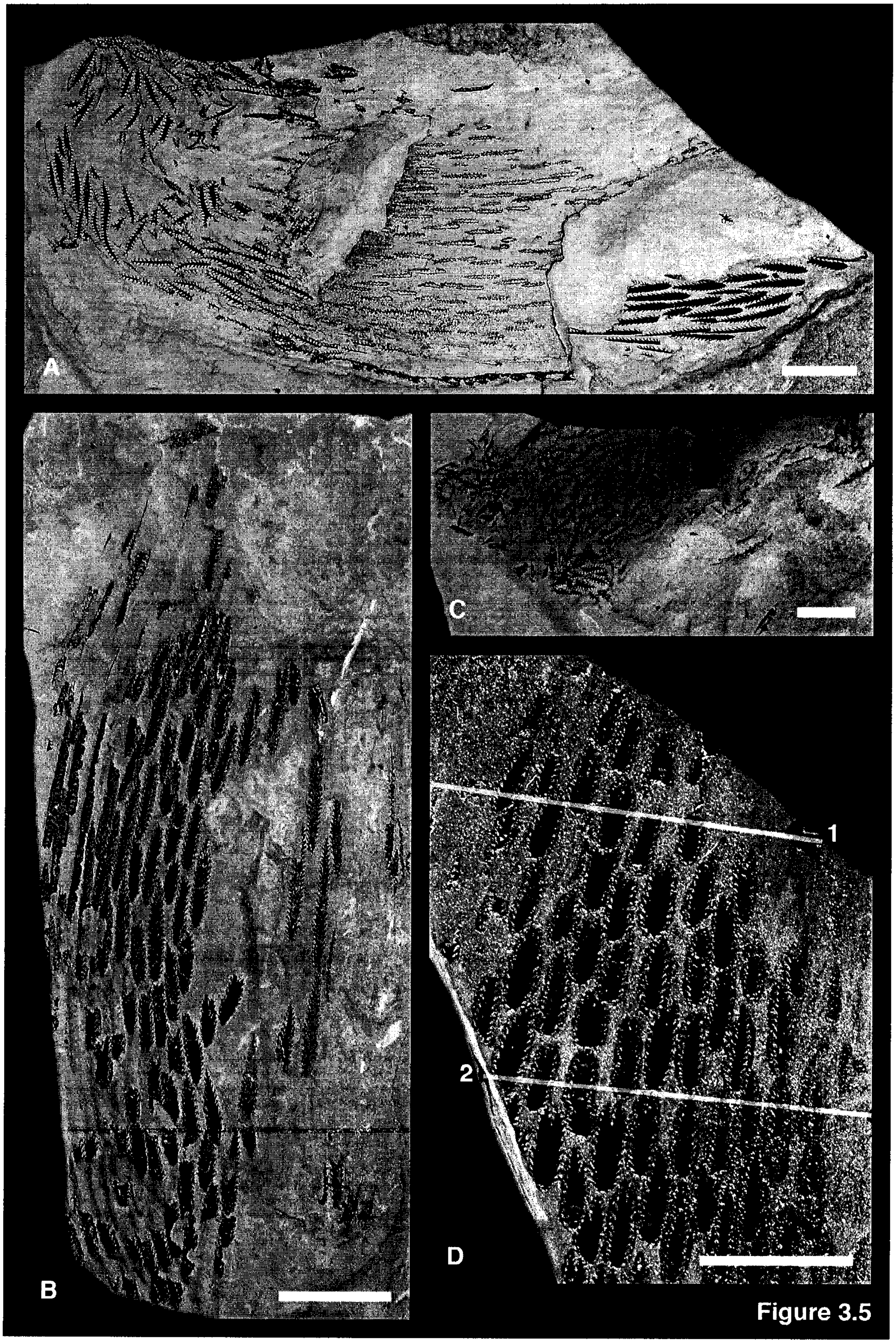
the tip of the tail, the scales consist of a basal plate with a short, barbed tubercle. All of the scales have tubercles with crests down their midline as well as on the barbs.

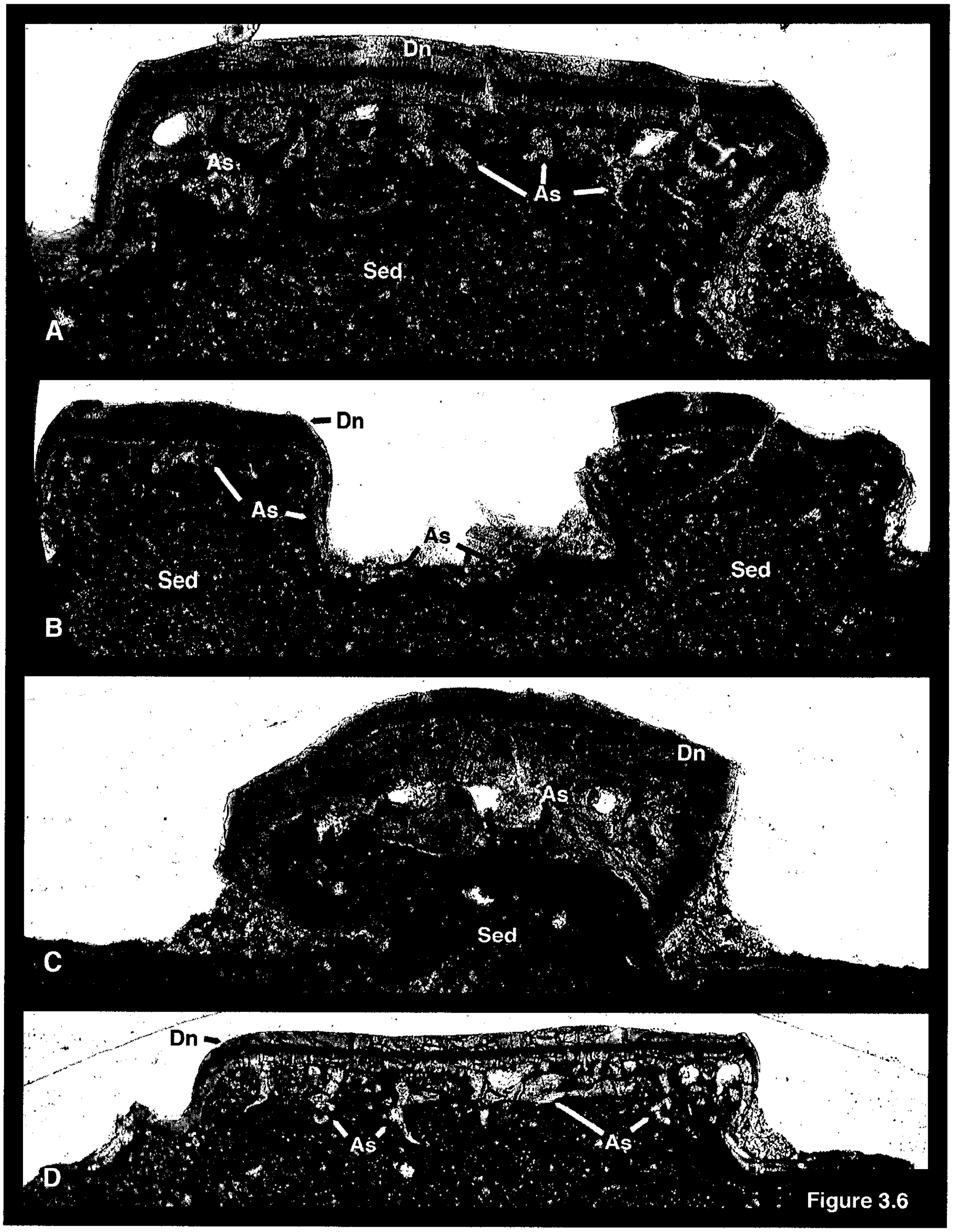
Histology–Due to the limited number of specimens, I was unable to section multiple specimens. Nevertheless, one specimen, UALVP 47010, is clearly identifiable as a portion of the cephalothorax of *L. loefflerae* (Fig. 3.5D). Using this specimen, two transverse cross sections were produced (UALVP 47010A and 47010B) and the histology of the species was examined (Fig. 3.6).

The bone is composed of dentine on the exterior surface and laminar, acellular aspidine beneath it. On the specimen, the basal layer and the cancellous layer are poorly developed. In fact, only one tubercle shows enclosed pulp cavities within the cancellous layer (Fig. 3.6C). Otherwise, the cancellous layer is composed of tendrils of bone that reach towards the interior of the animal (Fig. 3.6D). The dentine layer is limited to the top and to the sides of the tubercles, where it gradually thins and ends. The basal plates are composed of aspidine, which is continuous with the aspidine in the cancellous layer of the tubercles and the basal layer on the specimen in which one is present. The dentine tubules are clearly branched and are visible as canals that sometimes extend from the pulp cavities out into the dentine or form simple branching patterns within the dentine itself (clearest in Figure 2.6A). The only noticeable difference between thin sections of *L. loefflerae* and *L. serrata* is that on the specimens of the former (Fig. 3.6), there is no crest down the midline of the tubercle, while on *L. serrata* there is (Fig. 3.9). This characteristic makes it possible to distinguish between the two species even before they have been prepared out of the rock, provided that there is a section through the cephalothorax visible.

Remarks–There are very few examples of *L. loefflerae*. Only six specimens of *L. loefflerae* have been prepared and identified from the MOTH locality, whereas there are at least one hundred specimens of *L. serrata* from the same outcrops. The rarity of *L. loefflerae* is likely one of the reasons that Dineley and Loeffler (1976) did not recognize or describe this species.

The key distinction between the two species is the morphology of the tubercles on the cephalothorax and the tail. In *L. loefflerae,* the majority of the tubercles have a flat-topped dentine surface, while those in *L. serrata* are rarely uncrested (the exception being the anterior portion of the ventral shield near the mouth). In addition, the orbits of *L. loefflerae* are composed of plates that are more robust and have a thicker row (4-5 rows) of tubercles than the orbits of *L. serrata* (1-3 rows). On the tail, the ridge scales of *L. loefflerae* have crested tubercles, but even here there are differences between *L. serrata* and *L. loefflerae*. In *L. serrata* the barbs tend be less prominent (<0.3 mm) than on *L. loefflerae* (>0.3 mm) when


A
B
C
D
1
2
Figure 3.5


Dn
As
As
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A
Dn
As
As
Sed
Sed
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As
Sed
C
Dn
As
As
D
Figure 3.6

present in the tail region. The first ridge scales posterior to the cephalothorax on *L. serrata* are also much shorter based on specimens NMC 19873a and NMC 19873b.

The major similarities between the two species generally have to do with the overall body shapes of the animals. Both species have an ovoid shape to the cephalothorax; the orbit is placed dorso-laterally; both have a flat cephalothorax (i.e., there are no large apparent protrusions or structures on the cephalothorax). The pattern of the separate basal plates and scales.on the cephalothoraces is also very similar, with each individual basal plate having a single tubercle unless tesserae have become fused with the adjacent ones. On the tail, the differentiation of the row of dorsal and ventral median ridge scales is another important similarity.

SKELETAL GROWTH IN *LEPIDASPIS*

Heterostracans are among the most primitive vertebrates known. There have been many hypotheses put forward regarding growth in various groups of heterostracans. These include descriptions of specific examples, such as in cyathaspidids (Denison, 1964; Greeniaus and Wilson, 2003) or pteraspidids (White, 1973; Tarrant, 1991), or more general discussions of trends within heterostracan phylogenies (Tarlo, 1960, 1962). Unfortunately, the more primitive tessellate heterostracans and their ancestors are poorly understood. This may be in part because species are usually rare, fragmentary, and found as isolated specimens. However, on rare occasions when multiple, well-preserved specimens are found, some work regarding histology and ontogeny can be done. This was the case for Dineley and Loeffler (1976), who briefly discussed growth in *Lepidaspis serrata* and were able to outline some of the major details in the growth of its bones; however, much was left unsaid. The specimens recently collected from the MOTH locality will be used to add to this knowledge.

Growth in heterostracans can generally be categorized into two possible extremes that fall under the Lepidomorial Growth Theory (Tarlo, 1960). These two types of growth are known as cyclomorial and synchronomorial growth. Cyclomorial growth is characterized by a peripheral growth pattern around existing bones or primordia (centers of ossification in the dermal skeleton). The largest difference between cyclomorial growth and synchronomorial growth is that cyclomorial growth occurs over a period of time as bone is added to the margins of the developing plates and scales. This allows the animal's body to grow as the skin becomes fully ossified. Synchronomorial growth, in contrast, is characterized by the formation of the dermal plates and/or scales at one time, with no bone growth occurring later in ontogeny. In animals with determinate growth (as is hypothesized for many heterostracans), this would mean that the dermal bone only begins formation once the animal has grown to adult size. This would suggest "naked" juveniles for a heterostracan exhibiting synchronomorial and determinate growth, whereas it is likely that 'juvenile' heterostracans that have cyclomorial growth would have some bony armour covering significant portions of their bodies. These two types of growth represent the extremes along a continuum of possibilities. Likely, most growth described as cyclomorial actually involves primordia that form synchronomorially, with growth continuing along the margins later in ontogeny. The size, number, and location of these primordia on the animals at their formation, and the amount of cyclomorial growth (if any) that follows, are what appears to vary most among different heterostracan taxa.

Variation among heterostracan growth patterns is almost as varied as body shapes, but there are several similarities. In most heterostracans in which growth has been studied, there are regions along the dorsal and ventral midlines of the animals that either act as the sites of primordia or as areas showing increased bone development or fusion of tesserae. Heterostracans that show this dorsal and ventral compartmentalization of growth include irregulareaspidids (Greeniaus and Wilson, 2003) and pteraspidids (White, 1973; Tarrant, 1991). These two groups also show a tendency towards growth from the dorsal and ventral midlines towards the lateral margins of the animals. These heterostracans also include the only major groups in which growth has been described in the literature. Since they are closely related (Janvier, 1996), it was not known whether this is a feature of 'higher heterostracans' or a characteristic of all heterostracans. The examination of the bone formation of *Lepidaspis serrata* and *L. loefflerae* will help to answer this question.

Description of Growth-Related Morphology

Through the examination of various morphological features on the cephalothoraces of both *Lepidaspis serrata* and *L. loefflerae* specimens, I will develop a hypothesis on the growth of *Lepidaspis*. I will look at examples of four arbitrary categories of fusion to help describe the formation of bone on the cephalothorax with respect to both the sequence and area of fusion. These four categories are 'no contact', 'contact', 'poorly fused', and 'well fused'. Examination of histological thin sections will also be used to further resolve the processes that are taking place during bone growth.

No contact–This involves situations in which there is no contact between the basal plates of separate tesserae (Fig. 3.7A). This is both the second most common condition seen on 'articulated' cephalothoraces (both complete and fragments) and is very apparent in the large quantity of completely disarticulated material that is found at the MOTH locality. Generally, however, when present on an articulated cephalothorax, there is some fusion, or at least contact, between adjacent tesserae. No contact is also more prevalent on specimens of *L. loefflerae* than on *L. serrata.*

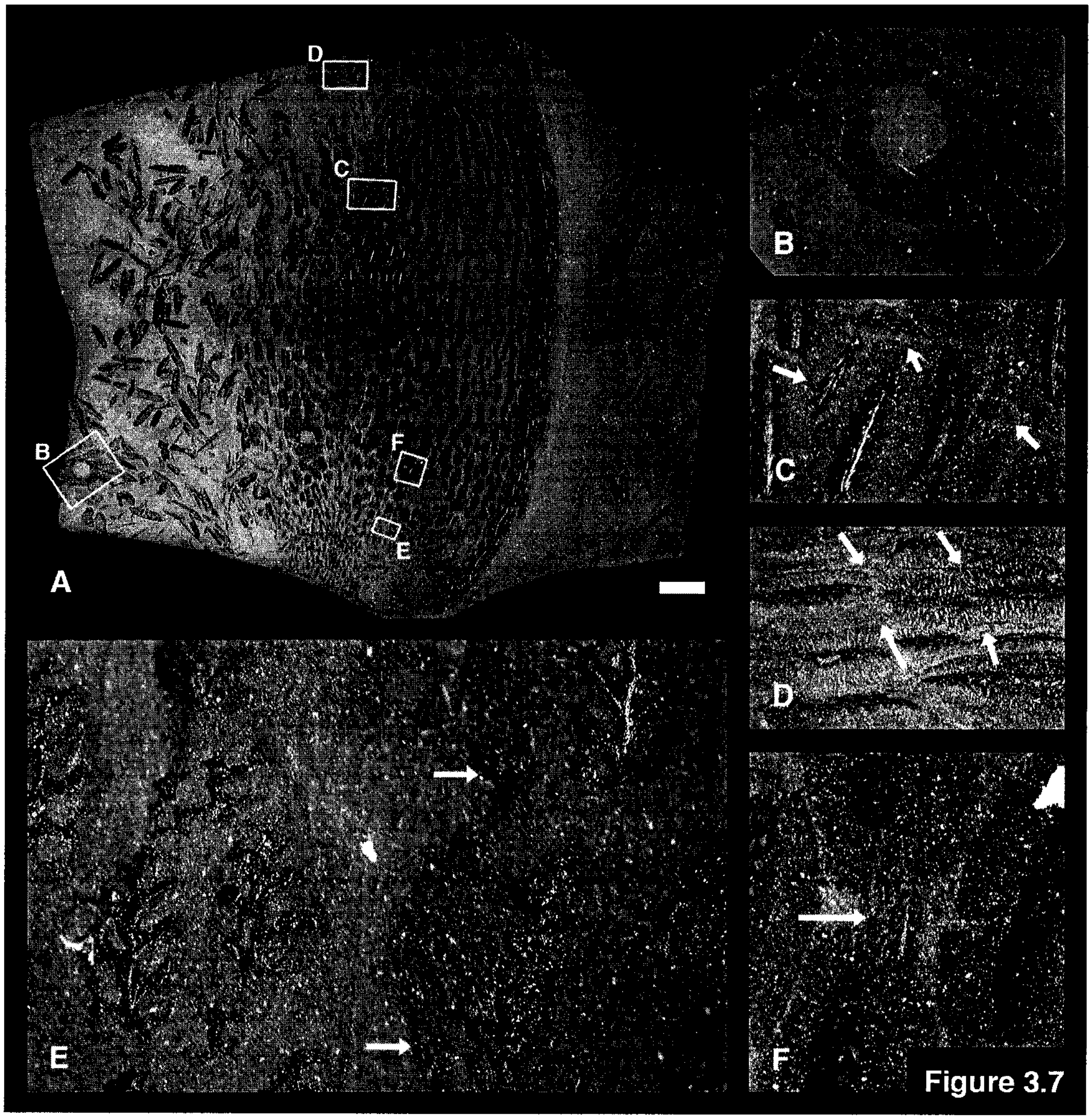
D
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Figure 3.7

On articulated specimens, the condition of 'no contact' between the basal plates of tesserae does not cover the entire cephalothorax. It is actually found in a ring around the medial region of the shield. When present, these mid-lateral regions of no contact meet along the anterior midline, though not the anterior margin of the animal. The transition on the posterior region of the cephalothorax is more complex as the mid-lateral regions of no contact gradually merge with the tail region on which compound scales are present and differentiate the two regions.

Contact–This is the most common condition in both species of *Lepidaspis*. It is characterized by contact between the individual basal plates of the tesserae, but without any fusion occurring (Fig. 3.7F). Contact may be extensive along the border of the tesserae, or it may be intermittent, with gaps along the lateral margins being most common. Contact in these cases is between the anterior corners of one basal plate and the posterior corner of another, more anterior, plate. This can create a somewhat zigzag-like pattern between the tesserae as one proceeds along the shield in the anterior to posterior direction. In the anterior part of the shield where tubercles are aligned so that the long axis is pointed laterally, the contact occurs most often between the lateral margins of the basal plates, though these tend to be more in line than those more posterior on the shield and do not produce a zigzag pattern. In all cases, by the time contact has begun along the margins of the long axis, the basal plate has begun to take on a shape similar to an elongated hexagon, filling the once present space between tesserae and normally surrounded by six other tesserae. However, there are situations where there is contact among only five other tesserae, and in some cases as many as seven.

Contact is normally seen on articulated specimens of *Lepidaspis* in the regions between the medial region and the lateral margins of well-fused specimens, and in the medial region on specimens in which fusion is poorly developed. On most specimens of articulated material of *L. loefflerae*, contact is the condition seen, though the contact between tesserae has not become very extensive (Fig. 3.4D). In these, the contact is most extensive in the medial region of the shield.

Poorly Fused–This is the third developmental stage. Tesserae are usually in contact with all those around them and some fusion of the basal plates has begun (Figs. 3.4C, 3.7C, D). This limited fusion most commonly takes place near the corners of the anterior or posterior region of the long axis of antero-posteriorly directed tubercles or on the lateral margins of the basal plates of transversely directed tubercles.

In the anterior region of *L. serrata* where the tubercles are aligned transversely, fusion is usually extensive along the lateral ends of the basal plates (Fig. 3.7D). Curiously, this is also the only location on the body where there may be an entire lack of contact between the adjacent tesserae along the long axis of the basal plate, in this case along the anterior and posterior edges of the basal plates.

Well Fused–This is the most advanced developmental stage that can be observed on the surface of the animals, i.e., without thin sections. It involves the apparently complete fusion of the basal plate to the basal plates of all the surrounding tesserae. The original outline of the basal plate is sometimes obliterated and there is always a lack of gaps between adjacent tesserae (Fig. 3.8C).

This condition is very common on the lateral margins of most specimens of *Lepidaspis* and does not significantly depend on the amount of fusion on other areas of the shield (Figs. 3.3, 3.4, 3.8, 3.10). Along with the lateral margins, the orbital region is the only other place on the cephalothorax that consistently shows this degree of fusion. In *L. serrata*, fusion is also apparent on the anterior region (Fig. 3.10A) of the cephalothorax and in the region near the midline of the animal.

Thin sections through the lateral margin of a specimen of *L. serrata* specimen show that the cancellous region of bone is very well developed (Fig. 3.9B), and is significantly thicker than on other regions of the skeleton (Fig. 3.9A). On specimens that have been prepared from the interior, the surface of the bone generally shows the honey-comb pattern that characterizes heterostracan dermal bone (Figs. 3.8E, F), likely a result of the extensive cancellous layers. It should also be noted that, on the lateral margins of the cephalothoraces in both species of *Lepidaspis*, the tubercle spacing is significantly closer than on the dorsal and ventral surfaces of the animal; it is not clear if there ever were gaps between the basal plates of separate tubercles.

The orbits, the lateral margins, and the medial regions of the cephalothoraces are the most common elements, other than individual tesserae, that can be collected from disarticulated material, and this is likely due to the high degree of fusion that they show.

Suture tubercles–One other feature of the shield may also encourage a more robust cephalothorax, what Dineley and Loeffler (1976) called 'suture tubercles.' These are smaller tubercles present throughout the cephalothorax that are located on

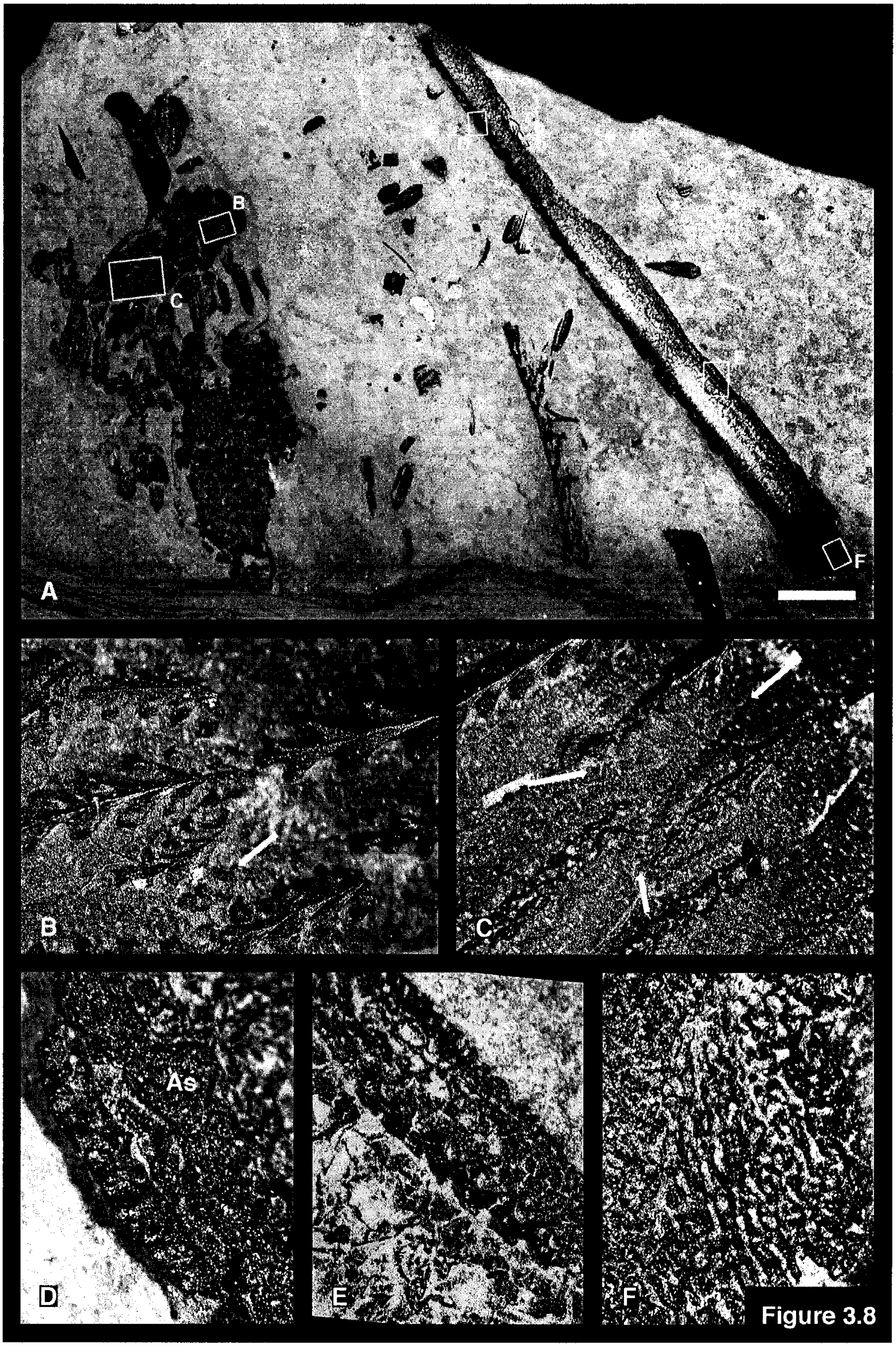

Figure 3.8

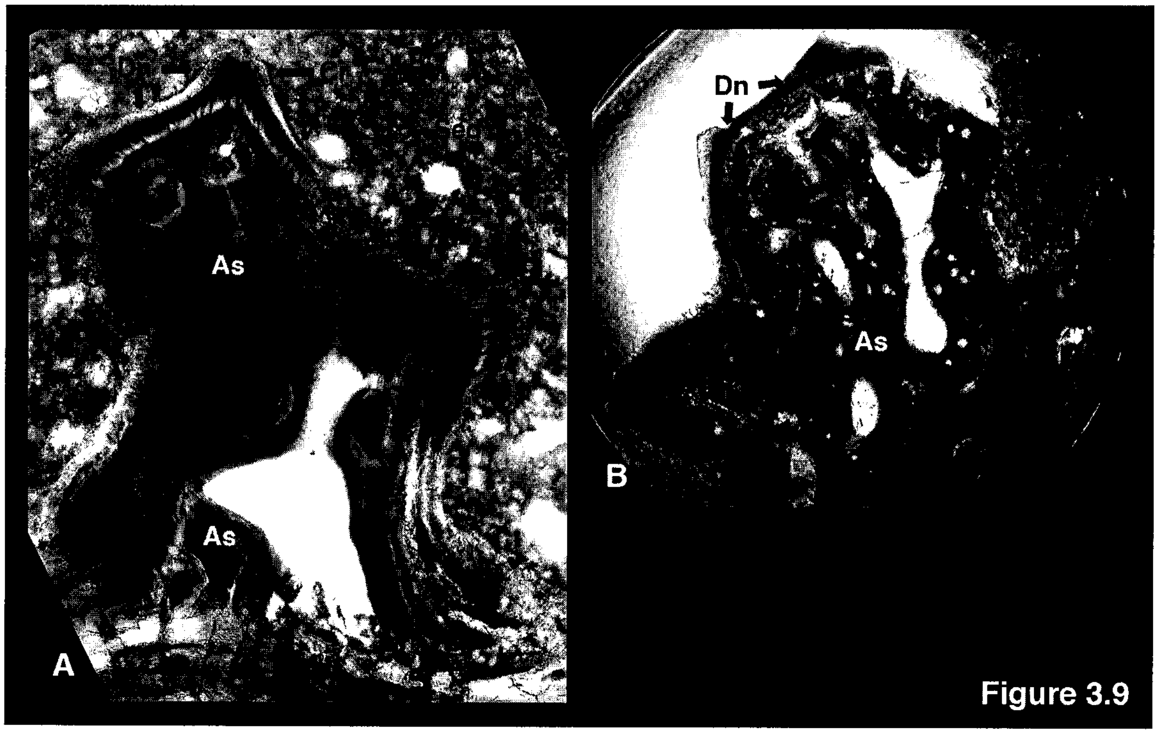

Figure 3.9

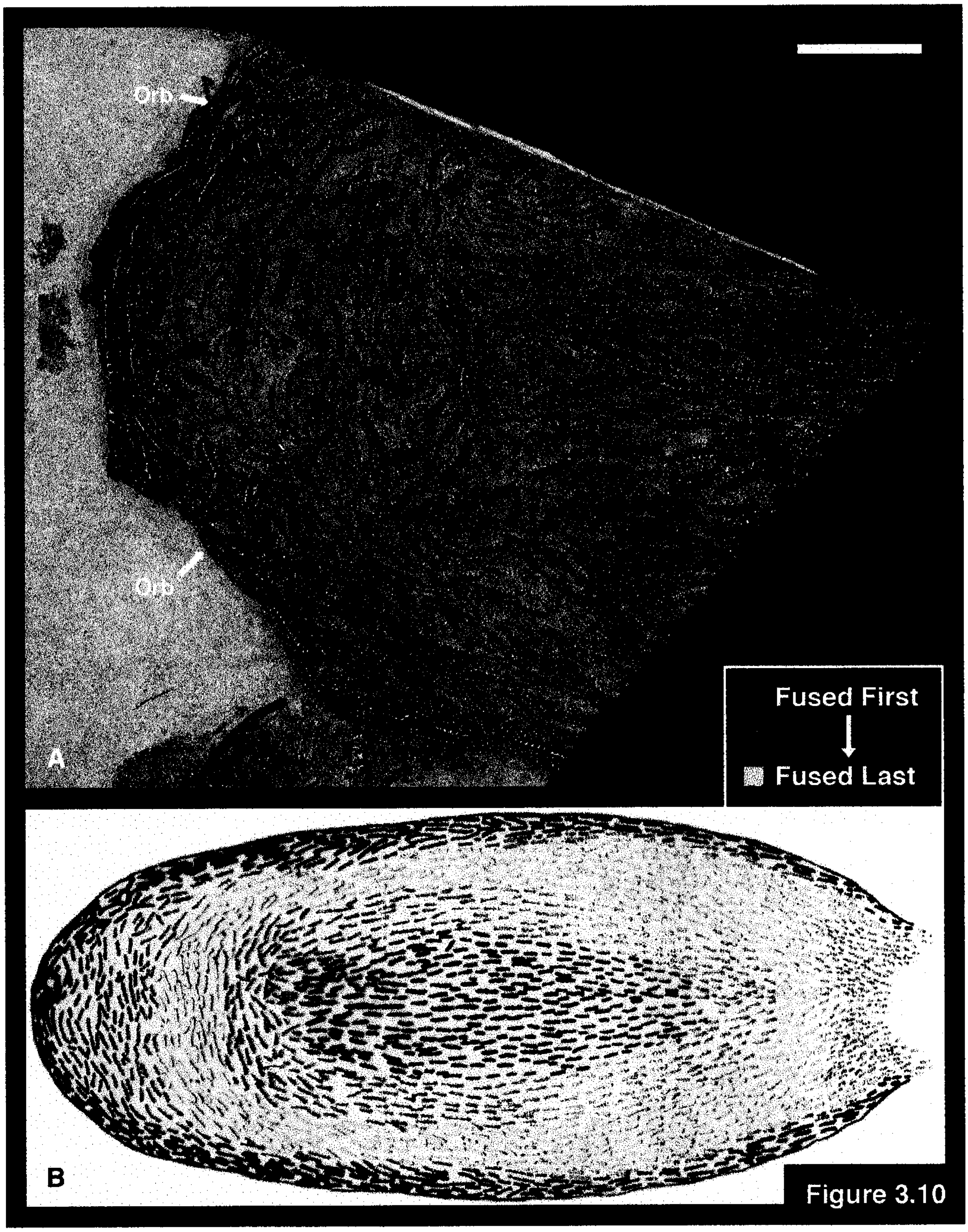

Figure 3.10

and between (when there is no contact of basal plates) the borders of two adjacent tesserae Each suture tubercle is topped with its single primary tubercle. Dineley and Loeffler reported these types of tubercles in the posterior region of the cephalothorax, but the newer material from the MOTH locality shows that they are also present on other regions of the cephalothorax.

The size of these suture tubercles varies more than that of the larger primary tubercles found on the surface of the cephalothorax. They are all shorter in length than the larger tubercles that surround them and at most half the height above the basal plates of the primary tubercles (Figs. 3.7C, E-F, 3.8B). Their orientation is also less regular. They are sometimes parallel to the surrounding primary tubercles, while in other situations they are at an oblique angle or even at a right angle to the surrounding tubercles. There is only one example in which a suture tubercle appears to have developed a basal plate, and in this case, it has fused with two larger basal plates anterior and posterior to it (Fig. 3.7F).

Discussion of Growth in *Lepidaspis*

Dineley and Loeffler (1976) noted that there was variation in the amount of fusion on the cephalothoraces of *Lepidaspis serrata.* They, however, went into little detail as to the differences between regions of the same shield and the differences in general between specimens that were well fused compared to those that showed little fusion between basal plates. The purpose of this research was to describe these differences as well as to postulate the reasons behind them.

Sequences of Fusion of Basal Plates–The first stage is the state in which each tubercle has a single and individual basal plate. There is no contact between adjacent basal plates and the margins of the plates are underdeveloped or crenulated.

As growth of the margin of the basal plate continues, contact eventually occurs between adjacent basal plates. This occurs first on the anterior and posterior corners of the basal plates, leaving a gap along the lateral margins of adjacent plates in the early stages of growth. There are several cases in which the basal plate appears fairly well developed and contact between surrounding plates is complete, if not already beginning the process of fusion.

After contact is complete, fusion of the basal plates begins. This appears to occur first in the medial region of both the dorsal and ventral plates and on the lateral and anterior margins of the animal including the orbits. The eye is likely be surrounded by an individual plate, and on all the specimens of *L. loefflerae* and *L. serrata* there is not a single occurrence of an orbit that has not been formed by a single plate-like structure that would have surrounded the eye, with the exception of the gaps seen in the two examples of *L. loefflerae*. Even on specimens in which the lateral margins have not fully fused, the orbits are present as complete structures, even when disarticulation of much of the rest of the skeleton has occurred (including the single orbital plates and fused lateral margins).

The early timing of fusion and growth of bone in the medial regions of the shield is reminiscent of bone formation patterns in more derived heterostracans such as cyathaspidids (Denison, 1964; Greeniaus and Wilson, 2003) and pteraspidids

(Denison, 1973; White, 1973; Dineley and Loeffler, 1976; Elliott, 1983). These more derived forms also show a medial to lateral polarity in bone formation; however, they show lateral growth of large bony plates covering the cephalothorax rather than the early fusion of separate tesserae.

The fusion of the lateral margins of *Lepidaspis* does not appear to be compartmentalized into a dorsal and ventral half, as in irregulareaspidids (Greeniaus and Wilson, 2003) and produces only a single fused structure. The 'lateral plate' in *Lepidaspis* that forms through the fusion of separate tesserae is usually thick (up to 5 mm) and in cross section represents an extensive layer of pulp cavities and the surrounding aspidine. Eventually this becomes a continuous structure with both the orbits and the anterior margin of the animal, creating a 'horseshoe' shaped region of fusion around the animals cephalothorax. It is normally well fused on specimens that have begun fusion of the medial region off the shield, and it should be noted also that this lateral region on the shield is where the tubercles are most closely spaced in both species of *Lepidaspis*. Posterior to the lateral plate are many smaller tesserae that make up the scales on the tail region. These do not appear to undergo fusion as they do on the cephalothorax.

The final region to fuse on the cephalothorax appears to be the area between the lateral and anterior 'plate' and the medial region of fusion. The first area to complete the process appears to be the region posterior to the orbits and anterior to the medial region of fusion. Fusion is typically very extensive in the area where the tubercles are aligned with their long axis pointing laterally; fusion then progresses along the midline through to the region of medial fusion. Eventually, the lateral-and-anterior 'plate' and the medial region are joined together to form one structure of well-fused tesserae, and the outlines of the previously separate tesserae in those two regions are scarcely visible. In the mid-lateral region, it is rare for the outlines of tesserae to be completely obliterated (Fig. 3.10B).

Fusion in the tail region seems limited to the dorsal and ventral ridge scales, and even there, it is unclear if the process of scale formation involves the coalescence of several smaller structures. This, however, seems unlikely, with the possible exception being the scales lateral to the ridge scales. These smaller scales come in combinations of two or more tubercles per scale, and in some situations it appears as if adjacent scales have undergone some fusion (whether it is the basal plates that fuse, or simply the formation of a suture tubercle between, is sometimes debatable). Either way, the exception appears limited and relatively inconsequential to the overall growth of the animal.

The Appearance of Suture Tubercles–Whether or not the actual function of the suture tubercles is to perform the function their name implies, they are definitely formed after the primary tubercles and the basal plates that form the majority of the cephalothorax. Of all the specimens in the UALVP collection, only one suture tubercle distinctly shows a basal plate to which it appears to belong. Aside from this exception, it appears that preservation of, if not formation of, suture tubercles requires that the basal plates of two adjacent tesserae to be in contact or have begun fusion. If their function is indeed to help stabilize the bone, their appearance before the fusion of tesserae suggests that they act as a bridge upon which future growth of the aspidine layer may take place. After fusion has taken place, they persist as remnants of this process.

Suture tubercles are never abundant. They occur most often on the cephalothorax just anterior to the dorsal or ventral ridge scales of the trunk region. Occasionally, they are also present elsewhere on the cephalothorax. Most commonly they occur in regions where there are large spaces between adjacent primary tubercles, again lending credence to the hypothesis that they act as bridges upon which the basal layer of bone is built.

General Discussion of Growth–Shield growth in *Lepidaspis*, especially the locations of early fusion, is suggested to be a precursor to the formation of plates or epitega that could grow independently from each other, as seen in more derived heterostracans. Similar suggestions were earlier made regarding primitive heterostracan taxa such as *Tesseraspis* (Tarlo, 1962), traquairaspidids such as *Traquairaspis* or *Phialaspis* (Tarlo, 1960, 1962, 1964, 1965; Dineley and Loeffler, 1976; Tarrant, 1991), and *Tolypelepis* (Stensiö, 1958; Tarlo, 1960, 1962, 1964, 1965; Denison, 1964).

Tesseraspis is a heterostracan with a cephalothorax composed of individual tesserae reminiscent of those of *Astraspis* and of *Lepidaspis* in its unfused form (Wills, 1935). Tarlo (1962, 1964, 1965) grouped *Tesseraspis* in the Psammosteiformes and suggested that the differentiation of the tesserae foreshadows the regions seen in more derived psammosteids. However, *Tesseraspis* is now considered a problematic heterostracan, with its position in that phylogeny indeterminate, much like that of *Lepidaspis* (Elliott and Loeffler, 1989; Janvier, 1996). Similarities with *Lepidaspis* include the medial and lateral regions of the cephalothorax where the tesserae are larger and more robust, suggesting a tendency for increased dermal development in these regions, with smaller, more gracile, tesserae in between (Tarlo, 1965).

Traquairaspidids are another group of primitive heterostracans for which the relationship to other heterostracans is unknown. Janvier (1996) places them in a basal polytomy with *Lepidaspis*. The ornamentation on the shield varies from species to species and ranges from forms with large plates making up the cephalothoracic armour to forms in which there are distinct dorsal and ventral shields. Like *Tesseraspis*, they have been previously grouped with psammosteids based on convergent similarities (Tarlo, 1965). Dineley and Loeffler (1976) suggested that primitive traquairaspidids had a fused dorsal shield that later became subdivided into smaller plates similar to those of Pteraspidiformes, together with extra 'units' (Tarrant, 1991) along the mid-lateral region of the dorsal surface. These smaller plates would have had cyclomorial growth similar to that of the tesserae of *Lepidaspis*. If this subdivision occurred, there would have been a tendency for a larger plate in the medial region of the cephalothorax, as evident from the occurrence of the dorsal disk in traquairaspidids that do show subdivisions in their armour. The uncertainty surrounding the phylogenetic relationships of traquairaspidids makes it impossible to see if this trend is correct without resolving those relationships.

Tolypelepis is a cyathaspidid that also has a cephalothorax composed of tessera-like elements. The central region is composed of many cyclomorial elements that have central tubercles surrounded by smaller ridges (Tarlo, 1960). Surrounding this central region of small units of cyclomorial growth is a region with more longitudinal ridges similar to the patterns seen on more advanced cyathaspidids. It is suggested that these regions grew and in later evolution fused to form the larger plates seen in more typical cyathaspidids such as *Poraspis* or *Corvaspis* (Tarlo, 1960; Denison, 1964). Though problematic taxa such as *Athenaegis* could refute this hypothesis (Janvier, 1996), as it appear cyathaspidid-like, but has feature that suggest it is more primitive (multiple branchial plates) and a well-fused cephalothorax.

The general trend that seems to be recurring, as reported in the literature, is the progressive fusion of many small elements on the cephalothorax towards larger, more complex, interlocking plates in more derived groups. The only major exception to this rule is the psammosteids, which are thought to have evolved small tesserae or platelets between the larger plates they inherited from their non tessellate pteraspidid ancestors. If *Lepidaspis* is indeed one of the most primitive heterostracans, it may represent the intermediate stage in the construction of the stronger, fused shield seen in later heterostracans. This transitional stage developed from ancestors similar to *Astraspis* that had an unfused (or a poorly fused) cephalothorax composed of many tesserae. Understanding their growth and ontogeny should therefore help us comprehend both the origin of the group as well as the processes behind the formation of some of the earliest bone in the fossil record.

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CHAPTER 4

CONCLUSION

Four new species of heterostracans are described, all likely closely related to the groups of unresolved taxa including the Traquairaspididae and the 'tessellate' heterostracans (Janvier, 1996; Donoghue et al., 2000). Three of the species, *Grandipiscis exscopulus*, *Quasimodaspis mackenziensis*, and *Q. canadensis* are likely most closely related to traquairaspidids as they all have a median plate and a crest that run medially down that plate, though this is also seen in other problematic taxa such as *Weigeltaspis* (Tarlo, 1965). *Grandipiscis exscopulus* also has a branchial opening in a location consistent with other traquairaspidids. Though the morphology of the tubercles themselves on these three new species is similar to that of *Lepidaspis serrata* (Dineley and Loeffler, 1976), the cyclomoriform arrangement and the median crest on the cephalothorax preclude a close relationship. On *Grandipiscis exscopulus* the tessellate nature of the rest of the cephalothorax, excluding the median dorsal plate, is also a key feature which distinguishes this species from traquairaspidids, as these tend to have a cephalothorax composed of seven or nine plates. The lack of more material for the species of *Quasimodaspis* means that it is unclear if this animal had a cephalothoracic morphology more similar to that of *Grandipiscis* or to that seen in traquairaspidids. There is, however, no doubt that these three new species will also be added to the group of problematic taxa at the base of heterostracan phylogeny.

The new species of *Lepidaspis*, *L. loefflerae*, is distinct from its likely sister species based on external morphology, the obvious difference is the central region of the cephalothorax which has flat-topped tubercles in *L. loefflerae* rather than crested ones as on *L. serrata*. The bone surrounding the orbits of *L. loefflerae* is also more robust than that of *L. serrata*, having a plate composed of more rows of tubercles.

Similarities between the two, including their gross body form and the covering of tesserae with single barbed tubercles, preclude creating a new genus and suggest that these two organisms were closely related. This new species, and additional specimens of *L. serrata*, have allowed a more in-depth study of the bone growth of *Lepidaspis*.

The tesserae of *Lepidaspis* appear to go through four stages of growth in relation to the surrounding tesserae. These stages progress from one of no contact between tesserae, to contact, to some fusion between adjacent tesserae, to the final stage in which fusion has progressed to the point of obliterating any hint of the previous subdivisions in the bone. These final two stages of bone growth are most commonly found on the lateral and anterior margins of the cephalothorax, as well as in the medial region of the shield. Later, fusion may occur on other regions of the shield and produce a solidly fused cephalothorax. This process of fusion appears to also be supplemented by the formation of smaller secondary tubercles that Dineley and Loeffler (1976) termed suture tubercles. These smaller tubercles tend to appear in regions where the tubercles of two adjacent tesserae are uncommonly far apart. Suture tubercles may act as bridges around which the aspidine of the basal layer may form, and eventually help fill the space between tesserae. This process of fusion, in which the lateral and medial regions fuse first, is similar to the bone growth polarity seen in other more derived heterostracans such as pteraspidids and cyathaspidids and may hint at an evolutionary ancestry of this pattern (White, 1973; Greeniaus and Wilson, 2003).

With the addition of four new species of primitive vertebrates, as well as the examination of growth in *Lepidaspis*, future researchers will be able to produce a more complete phylogeny of the Heterostraci. Hopefully, this will include the resolution of the basal polytomy which currently includes *Lepidaspis*, traquairaspidids, and other tessellate forms.

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