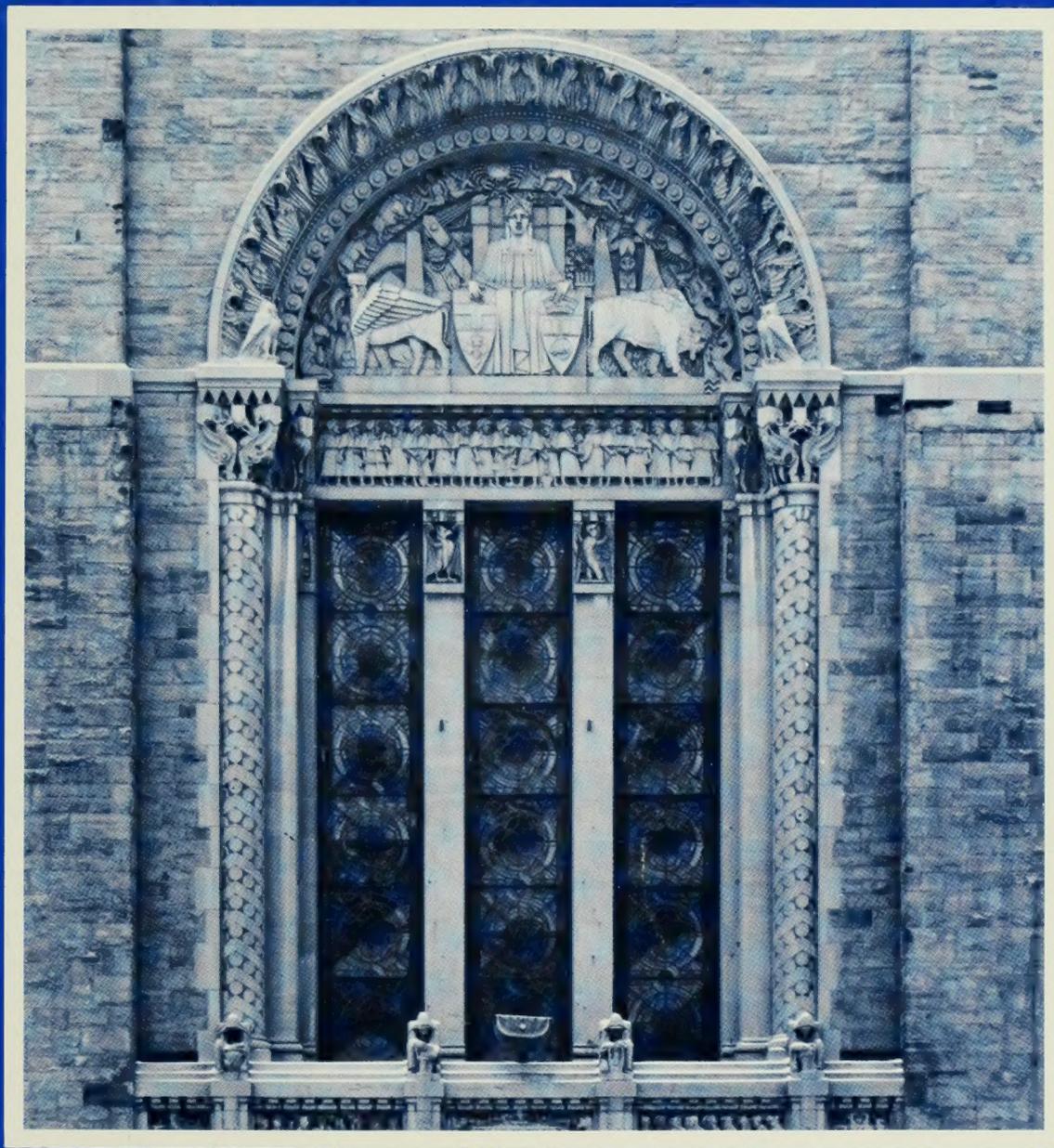


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Phylogeny, Speciation, and Palaeoecology
of the Early Carboniferous (Mississippian)
Conodont Genus *Mestognathus*

Peter H. von Bitter, Charles A. Sandberg,
and Michael J. Orchard

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Conodont Genus *Mestognathus*

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Phylogeny, Speciation, and Palaeoecology of the Early Carboniferous (Mississippian) Conodont Genus *Mestognathus*

Abstract

Mestognathus, an important Early Carboniferous conodont genus whose appearance has generally been thought to coincide with, and define, the base of the Viséan, evolved from *Clydagnathus* during the Tournaisian and ranges from that stage into the Namurian. Five species, including *M. harmalai* sp. nov. and *M. praebeckmanni* sp. nov., are distinguished by the gradual phyletic development of the parapet, the fixed blade, the anterior notch, the position of the carinal deflection, and the increasing tendency to evert the basal cavity. *Mestognathus dhuensis* and *M. neddensis* are demonstrated to be synonyms of *M. beckmanni*, *M. bipluti*, or *Mestognathus* spp.

Mestognathus apparatuses apparently contained only asymmetrically paired Pa elements that belong to symmetry Class IIIa. We hypothesize that ramiform elements may have been lost because of environmental stress. Juveniles of *Mestognathus* are small and have a noticeably large open basal cavity. This structure everts with growth and increase in size of the platform to form a well-defined large basal pit in mature specimens of the three oldest species. It everts almost totally in the two youngest species, leaving only a small basal pit in large individuals. Parallel changes in the development of the parapet and of the carina accompany this ontogenetic development.

Mestognathus is one of the asymmetric cavusgnathoid conodonts characteristic of Carboniferous nearshore environments. We hypothesize that it lived in and defined the most nearshore community, the *Mestognathus* biofacies, members of which lived mainly in the hypersaline tidal lagoonal-sabkha biotope. Rocks formed in such extreme depositional environments have not often been preserved or sampled for conodonts, which accounts for the apparent rarity of *Mestognathus*. Complicating factors for palaeoecologic analysis of the genus include both seaward and downslope secondary transport into other biofacies and biotopes.

Mestognathus, until now regarded as a provincial taxon, was remarkably cosmopolitan. It was recently reported from Asia and is being found increasingly in western North America. Palaeogeographically the genus was apparently restricted to a narrow equatorial belt lying between latitudes 40°S and 25°N.

A fourfold *Mestognathus*-based shallow-water zonation is proposed for the Tournaisian to Namurian time interval. The lowest known occurrence of *M. beckmanni* neither coincides with, nor defines, the base of the Viséan.

Introduction

The genus *Mestognathus* and its type species *M. beckmanni* were defined and named by Bischoff (1957) on the basis of approximately 50 platform elements from the Lower *Goniatites* Stufe (cu III α) in the Lower Carboniferous of Germany. Higgins (1961) described a second species of the genus, *M. bipluti*, having available 25 specimens from the

Namurian of North Staffordshire, England. The third and fourth described species of *Mestognathus*, *M. dhuensis* and *M. neddensis*, were named by Globensky (1967) and Rhodes, Austin, and Druce (1969) from the Viséan of Nova Scotia and Wales, respectively, each having available 5 specimens. Recently, Belka (1983) erected a fifth species

of *Mestognathus*, *M. groessensi*, utilizing 16 specimens from the Tournaisian of Poland—all from boreholes.

Since *M. beckmanni* was described by Bischoff (1957), not only have four additional species of the genus been described, but *Mestognathus* has been found widely distributed in strata of Early Carboniferous age in Europe, Africa, Asia, Australia, and North America. The genus has attained biostratigraphic importance and is considered “of great value in Anglo-German correlations” (Rhodes and Austin, 1971:341). Druce (1973) believed the genus to be “essentially a Viséan form”, Higgins (1981) stated that it “appears in the early Viséan”, and Austin (1973) and Groessens (1974) considered *M. beckmanni* to mark the base of the Viséan.

The erection of new species on the basis of very limited material or from subsurface sections that preclude recollection, the lack of proper diagnoses, and the absence of clear and sufficiently large illustrations (photographs of the types are reillustrated on Plate 1 at approximately their original magnifications) provided the impetus for our re-evaluation of the taxonomy and phylogeny of species of *Mestognathus* and for photographic documentation in conventional orientations of the type species of the first four described species of *Mestognathus* by scanning electron microscopy (Pls. 2–4; 12–15; 20 [fig. 6 only]; 21–23; 25–29). Additional motivation was provided in 1981 by the first reports of mestognathids from western North America and the existence of pre-Viséan mestognathid faunas. These new finds were by Orchard (1981) in western Canada, Sandberg (based on specimens of John Harmala) in western Utah, and I. S. Johnston (pers. comm., 1981) in the Republic of Ireland. The discovery of Tournaisian mestognathids directly contradicted the Upper Mississippian (Viséan) lower limit for the genus given about the same time by Austin and Rhodes (*in* Robison, 1981:W172).

GENERIC CONCEPT

Mestognathus and *Scaphignathus* are homeomorphs that are based primarily on probably paired platform elements (Pa, P, or Sp elements, according to different notation systems) that have a Class IIIa symmetry (not Class IV as given by Druce [1973] and Belka [1983]). These genera

have a generally right-sided anterior blade and a basal opening that everts ontogenetically from a large basal cavity to a smaller basal pit.

The two genera are distinguishable by the distinct morphology of their carinas. The carina of the type species of *Scaphignathus*, *S. velifer*, is straight and ends in a medial position in the anterior half of the platform. The lectotype of *S. velifer* differs from *Mestognathus* in that it has a subcentral blade (Helms, 1959, pl. 5, fig. 20). *Scaphignathus ziegleri* and *S. peterseni*, the two other known species of the genus, both lack a carina. *Mestognathus*, in contrast, always possesses a carina, one that is deflected sharply to the left in the anterior half of the platform.

The two genera have mutually exclusive ranges. *Scaphignathus* is apparently restricted to the Late Devonian *Palmatolepis trachytera*, *P. postera*, and Lower *P. expansa* zones (Ziegler and Sandberg, 1984), making its highest occurrence well below the base of the Carboniferous. *Mestognathus* is apparently restricted to the Carboniferous and ranges upwards from the late Tournaisian (late Kinderhookian) *Siphonodella isosticha* – Upper *S. crenulata* Zone, well above the base of the Carboniferous. A gap of 11 m.y. (Sandberg et al., 1983) is represented by the stratigraphic interval between the lowest known occurrence of *Mestognathus* and the highest known occurrence of *Scaphignathus*. Finally, *Scaphignathus* and *Mestognathus* are interpreted to have had different ancestors. *Scaphignathus* evolved from *Pandorinellina* (Sandberg and Ziegler, 1979, fig. 2), whereas we recognize a *Clydagnathus* ancestor for *Mestognathus*.

As presently conceived, *Mestognathus* comprises five species: in phyletic succession, *M. harmalai* sp. nov., *M. groessensi* Belka, *M. praebeckmanni* sp. nov., *M. beckmanni* Bischoff, and *M. bipluti* Higgins. *M. dhuensis* Globensky and *M. neddensis* Rhodes, Austin, and Druce are synonymized. *M. harmalai* sp. nov. apparently evolved from a species of *Clydagnathus*—*C. gilwernensis* Rhodes, Austin, and Druce that had developed a completely right-sided blade, a posterior carina extending anteriorly at least past midlength of the platform, and a rounded parapet area. Thus all species of *Mestognathus*, even the earliest, possess a right-sided blade and a long carina.

Materials and Methods

Mestognathus specimens studied firsthand are deposited at a variety of institutions. The abbreviations for these used within the text and captions are BMNH = British Museum (Natural History); GSC = Geological Survey of Canada; IGS = Institute of Geological Sciences (Leeds); PUM = Philipps University (Marburg); ROM = Royal Ontario Museum; TCD = Trinity College (Dublin); UNB = University of

New Brunswick; US = University of Sheffield; USNM = United States National Museum.

Specimens of *Mestognathus* from Austin (1974) and Austin and Husri (1974), examined by us, are housed at the University of Southampton. The holotype and paratype of *M. bipluti*, described and illustrated by Higgins (1961), are now at the British Museum (Natural History), where they

have been given register numbers BMNH X 1063 and 1064, respectively. The term "type specimens" is used by us to refer to the holotype and paratype(s) of a species.

Photographs shown on Plates 2 to 29 were produced by scanning electron microscopy. The bulk of these were taken of gold-coated specimens on a Cambridge S1 electron microscope in the Department of Geology at the University of Toronto.

The use of ? preceding a taxon in our synonymies indicates our inability to confirm the identification of the author(s) cited or to identify the illustrated specimen.

Generally the question mark applies to the specific identification and is the result of poor illustrations, of poorly preserved specimens, or of specimen orientations that make identification or confirmation impossible. In a few cases, such as *Scaphignathus?* sp. B of Rhodes, Austin, and Druce (1969, pl. 2, figs. 12a–c) and *Cavusgnathus unicornis* of Kalvoda (1983, pl. 1, fig. 7), the ? preceding a taxon in our synonymies applies to both the genus and the species. In our text, a ? after a genus or species name indicates doubts as to the generic or specific assignment, respectively.

Morphology

TERMS AND ORIENTATION

We continue to use many of the morphologic terms for *Mestognathus* named in German by Bischoff (1957) and translated subsequently. These, together with others that are newly applied (or applied in a different manner), are shown in Text-figure 1. Our most noticeable departure has been in calling the structure labelled the "outer parapet" by Higgins (1961) and Belka (1983) the "anterior blade" and dividing it into the free and fixed blades. This brings the terminology of the genus into line with that of other cavusgnathoids (cf. Lane, 1967). Our use of the term "parapet" is consistent with the use of that term by Sandberg and Ziegler (1973:101), but is distinct from that employed by Sweet (*in* Robison, 1981:W16) for *Cavusgnathus*. We note that *Cavusgnathus* lacks parapets and we use this term in the manner defined by Sweet later in the same publication (W65): "Parapet (Brüstung)—wall-like longitudinal structure on platform of pectiniform element, or on flange of ramiform element."

The terms used for orientation of the genus depart from those employed by Bischoff (1957), Higgins (1961), Rhodes, Austin, and Druce (1969), and Belka (1983). We prefer to use right side for outer side, left side for inner side, upper surface for oral surface, and lower surface for aboral surface. We continue to use the terms anterior and posterior.

We are unable to account for at least four authors' having reversed the negatives of photographs of *Mestognathus beckmanni* and *M. bipluti* (see synonymies). We have been able to verify this reversal only for specimen E1.E.1 of Higgins (1961) and specimens Z.1.45 and Z.2.46 of Austin and Husri (1974). None of the five species of *Mestognathus* are known to have a platform with a left-sided anterior blade.

MORPHOLOGIC STRUCTURES

Examination and photographic documentation, by scanning electron microscopy, of the type specimens of species

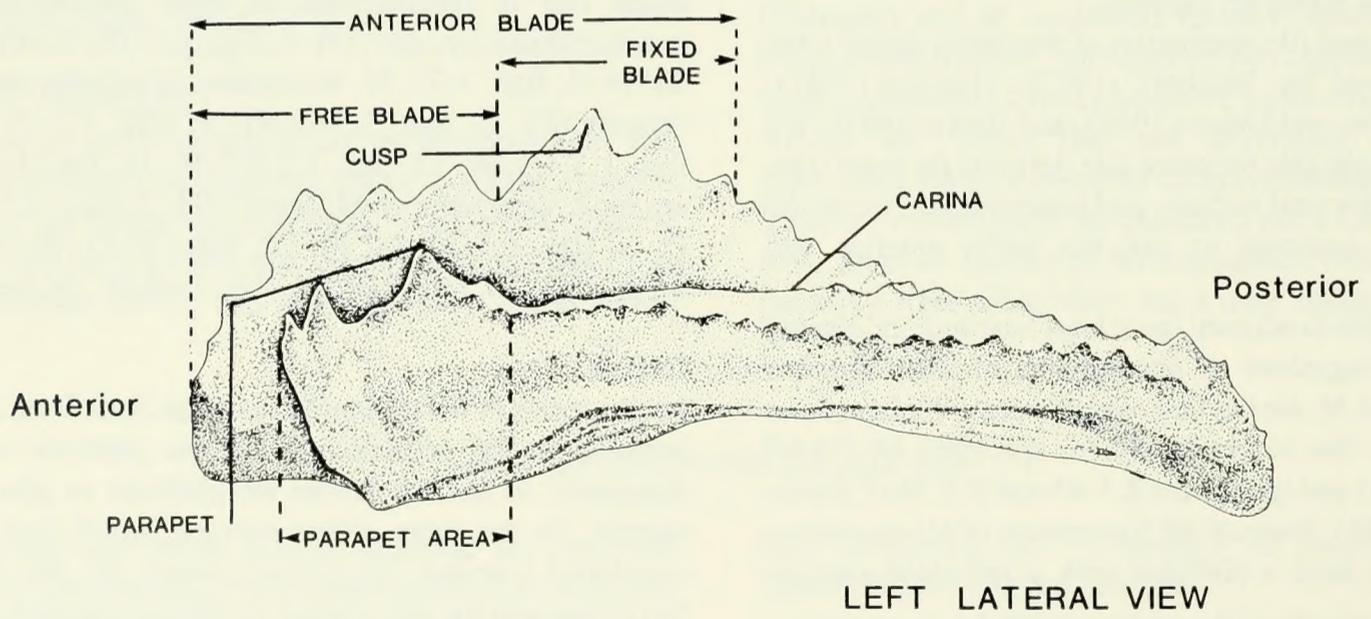
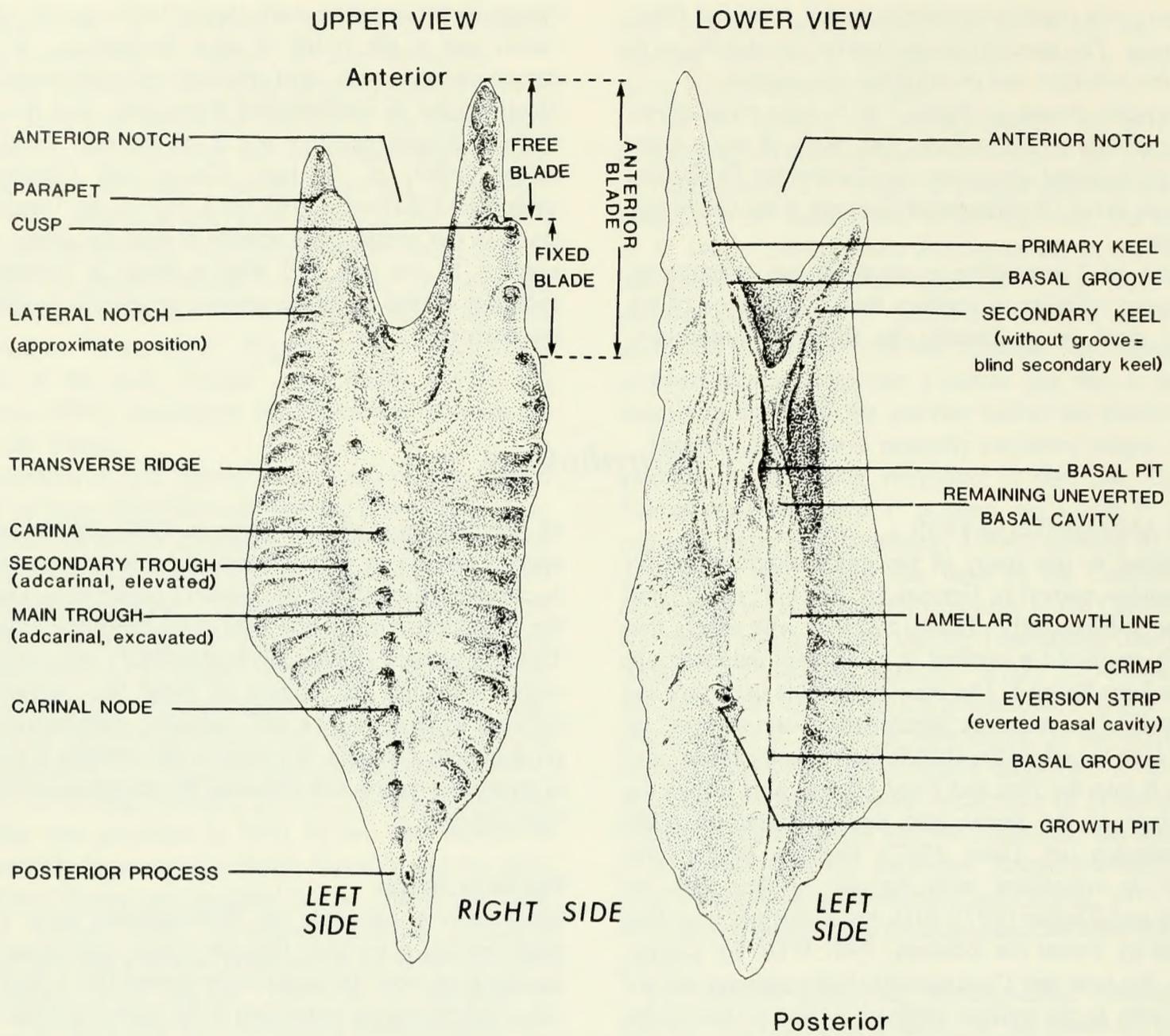
of *Mestognathus* erected prior to 1983, of the two new species erected by us, and of many new specimens of *M. beckmanni* Bischoff and *M. bipluti* Higgins have resulted in the collection of much new data on morphologic structures. These structures change phylogenetically and ontogenetically. Although the effects of these two variables are difficult to separate, we will, initially, concentrate on the phylogenetic changes. We discuss the changes in individual structures below and illustrate the morphologic terms in Text-figure 1.

Platform Shape

Most mature elements of *Mestognathus* have a wide platform that is variably sinuous. Some specimens of *M. harmalai* sp. nov. are moderately slender (Pl. 5, figs. 1–3); other specimens are expanded in the central portion (Pl. 6, figs. 4–9). *M. groessensi* already has the typical broad sinuous form of younger species (Pl. 1, figs. 27–31), a shape that is characteristic of most specimens of *M. praebeckmanni* sp. nov. (Pl. 8, figs. 6,7; Pls. 9,10), but not all (Pl. 8, figs. 1,2). *M. beckmanni* is variably broad and sinuous (Pl. 2, figs. 1,3–5; Pl. 3, figs. 1,3–5; Pl. 12, figs. 1,3,4,6; Pl. 13, figs. 1,2,6,7; Pl. 16, figs. 1–4,8), as are most specimens of *M. bipluti* (Pl. 2, figs. 6,7,10–14; Pl. 3, figs. 6,7,10–14; Pl. 20, figs. 10,11; Pl. 21, figs. 1,2,8,9; Pl. 22, fig. 3; Pl. 26, figs. 5–8; Pl. 28, figs. 1,4).

Carina

In all species of *Mestognathus* a carina starts from a central position at the posterior tip of the platform and cuts diagonally to the left across the platform to join the left margin. In the three oldest species, which had not yet developed a strong, distinctive parapet, the join between the carina and the left margin is generally nearly opposite the anterior terminus of the fixed blade. In *M. harmalai* sp. nov. the join is at approximately four-fifths the distance from the posterior end of the left margin (Pl. 5, figs. 1,5; Pl. 6, figs. 2,3,6,7). In *M. groessensi* (Pl. 1, figs. 26,28) and



Text-fig. 1. Morphologic terms of *Mestognathus* used in this study. Specimen illustrated is *M. bipluti*, ROM 43422, "D₁ Limestone", sample PHI-D₁-2, locality 20. Note that some structures, such as the free blade in upper view, are foreshortened considerably.

morphotype 1 of *M. praebeckmanni* sp. nov. (Pl. 11, fig. 7), it is at about the same point. Morphotypes 2 and 3 of the latter species possess an adcarinal trough, and in these the carina joins the left margin directly posterior to that structure (Pl. 8, figs. 1,6). In the two species that had developed a strong parapet, the junction between carina and left margin is distinctive in that the carina climbs the right side of the highest parapet denticle and terminates in its tip. This is particularly noticeable in *M. beckmanni* (Pl. 16, figs. 1,8).

The carina is strong and ridgelike in *M. harmalai* sp. nov. (Pl. 5, figs. 1,5; Pl. 6, figs. 2,3,6,7), the only species of *Mestognathus* that has a high bladelike posterior process. The carina becomes progressively weaker and is already composed of individual nodes in the two next younger species, *M. groessensi* (Pl. 1, figs. 26,28) and *M. praebeckmanni* sp. nov. (Pl. 8, figs. 1,6,10). *M. beckmanni* possesses a variably strong carina that is composed of nodes (Pl. 2, figs. 1,3–5; Pl. 12, fig. 1; Pl. 13, figs. 1,2) and may be ridgelike anteriorly (Pl. 2, fig. 2; Pl. 12, fig. 2; Pl. 16, figs. 1,3,5,7–9). In some specimens of *M. beckmanni* the carina is less prominent (Pl. 2, figs. 1,4,5; Pl. 12, fig. 1; Pl. 13, figs. 1,2). Similarly, *M. bipluti* possesses a variably strong carina composed of discrete nodes (Pl. 18, figs. 9,10; Pl. 20, fig. 9; Pl. 21, figs. 1,2; Pl. 23, fig. 4). Anteriorly the nodes may disappear and the carina may become more ridgelike.

Adcarinal Trough

In all species of *Mestognathus* the carina is bordered on the right side by a deep, excavated main adcarinal trough that extends along the longitudinal axis of the platform. The carina is bordered on the left side by a shallow (elevated) secondary trough that turns from the carina and either exits the left side of the platform or climbs the parapet (Pl. 1, figs. 26–31; Pl. 2; Pl. 5, figs. 1,5; Pl. 6, figs. 2,3,6,7; Pl. 8, figs. 1,6,10). The greater depth of the main trough can be seen in a cross-section of *M. beckmanni* paratype PUM Bi 1957/39 (Pl. 20, fig. 6), although left and right are reversed because the view is towards the posterior end. The main trough of *M. bipluti* is seen particularly well in Plate 18 (figs. 9,10), Plate 20 (fig. 9), and Plate 23 (fig. 4). The right part of the main trough is shallowest posteriorly, becoming deeper anteriorly. The shallow elevated trough is characteristic of the genus and is not known in other cavusgnathoids.

Transverse Ridges

Transverse ridges of different length and strength extend more or less at right angles to the long axis of the element from the right and left margins of the platform. Although development of transverse ridges is closely related to ontogeny, some generalizations about the transverse ridges of the five recognized species of *Mestognathus* may be

made. The transverse ridges tend to be strong and regular in *M. harmalai* sp. nov. (Pl. 5, figs. 1,5; Pl. 6, figs. 2,3,6,7), but are apparently weaker, less regular, and at more of an angle to the platform margin in *M. groessensi* (Pl. 1, fig. 28) and *M. praebeckmanni* sp. nov. (Pl. 8, figs. 1,6). In *M. beckmanni* these transverse ridges, still variably strong, may be composed of partly fused nodes (Pl. 2, fig. 2; Pl. 12, fig. 2) or may be sharply crested and solid (Pl. 2, fig. 4; Pl. 13, figs. 1,2). Although not well preserved in the type specimens of *M. bipluti* (Pl. 2, figs. 6,7; Pl. 21, figs. 1,2), the transverse ridges of adult specimens of the species are strong (Pl. 18, figs. 9,10; Pl. 20, fig. 9; Pl. 23, fig. 4).

Anterior Notch

At the anterior end of younger species of *Mestognathus* a variably developed anterior notch is generally present. This feature, dependent on the degree of parapet development and commonly best seen in lower view, is not developed in *M. harmalai* sp. nov. (Pl. 5, figs. 1,2,5; Pl. 6, figs. 1,3–7; Pl. 11, fig. 12). It is slightly developed in *M. groessensi* (Pl. 1, figs. 27–31), and is slightly to moderately well developed in *M. praebeckmanni* sp. nov. (Pl. 8, figs. 4,6,7,9,10; Pl. 9, figs. 1,3–5,7,8,10,11; Pl. 10, figs. 3,6–10). This anterior notch is better developed, being moderately deep, in the younger mestognathid species *M. beckmanni* (Pl. 2, figs. 1,5; Pl. 12, fig. 1; Pl. 13, fig. 2; Pl. 16, fig. 1). It is deepest in *M. bipluti* (Pl. 1, figs. 9,10; Pl. 2, figs. 6,7; Pl. 3, figs. 6,7; Pl. 21, figs. 1,2,4,5,10).

Anterior Blade

The anterior blade of *Mestognathus* varies in shape, in outline, and in the development of fixed and free blades. The anterior blade characteristics of *Mestognathus* species, particularly those of *M. beckmanni* and *M. bipluti*, have, because of foreshortening, been difficult to document when utilizing such longitudinal views of the upper surfaces as shown on Plate 2 (figs. 1,5), Plate 12 (fig. 1), Plate 13 (fig. 2), Plate 19 (figs. 6–10), and Plate 20 (figs. 4,7).

There is a general phylogenetic trend from possession of only a long free blade, with a very short or no fixed blade (*Mestognathus harmalai* sp. nov.) to an increasingly long fixed blade, with a short free blade, in younger species. The anterior blade of *M. harmalai* sp. nov. is distinctive because of the arrangement of the cusp and/or the blade denticles; furthermore, it lacks the offset towards the left side directly posterior to the cusp that is characteristic of younger mestognathids. The holotype has a cusp that is part of the short fixed blade and three denticles anterior to the cusp that form the longer free blade (Pl. 5, figs. 1,5). Paratype USNM 257753 lacks both a recognizable cusp and a fixed blade and shows three denticles of equal size forming a free blade (Pl. 6, figs. 1,4). The anterior blade of *M. groessensi* (Pl. 1, figs. 26,28), a short abbreviated structure consisting almost entirely of a fixed blade, is more like the

blade of the three younger species of *Mestognathus* and consists of a slightly offset cusp with two denticles anterior to it.

Mestognathus praebeckmanni sp. nov. also has an advanced mestognathid anterior blade, one that starts with a cusp that is offset towards the trough and ends with a variable number of anterior blade denticles that diminish in size anteriorly. The fixed blade is appreciably longer than the free blade and consists of the cusp and two to three anterior denticles (Pl. 1, figs. 32–34; Pl. 8, figs. 3–6, 10, 11; Pl. 9, figs. 1, 2, 5, 6, 8–10; Pl. 10, figs. 1, 4–6).

The anterior blade of *Mestognathus beckmanni* is variable in appearance, particularly when damaged (as in the case of three of the type specimens, Pl. 4, figs. 2–4; Pl. 13, figs. 4–8). The fixed blade of *M. beckmanni* is more than twice the length of the free blade (Pl. 1, fig. 1; Pl. 16, figs. 1, 3, 5; Pl. 20, figs. 10, 12). The anterior blade of this species is longer anteriorly than is the parapet, and it is dominated by a reclined cusp, the steep posterior margin of which overhangs the platform slightly (Pl. 4, figs. 1–5; Pl. 13, figs. 3–5, 8, 9; Pl. 16, figs. 7–9, 11; Pl. 17, figs. 1–13; Pl. 19, figs. 1–5). The number and arrangement of denticles vary with ontogenetic development. Small specimens have fewer, more regularly arranged denticles (Pl. 17, figs. 8, 11, 12; Pl. 19, figs. 4, 5; cf. *Mestognathus* spp., Pl. 19, figs. 11–14), whereas larger specimens have a greater number of more irregularly arranged denticles (Pl. 4, fig. 5; Pl. 13, fig. 9; Pl. 16, figs. 7, 9, 11; Pl. 17, figs. 2–4; Pl. 19, figs. 1, 2).

Mestognathus bipluti, like *M. beckmanni*, has a fixed blade at least twice the length of the free blade (Pl. 20, figs. 11, 13). The maximum number of anterior blade denticles observed on *M. bipluti* is six in large specimens (Pl. 24, fig. 6) and the minimum is four in smaller specimens identifiable as *M. bipluti* (Pl. 19, fig. 10; Pl. 24, fig. 13). The anteriormost one or two blade denticles are nearly vertical; however, the more posterior blade denticles are slightly reclined. The denticles of well-preserved Viséan specimens increase in height progressively towards the posterior (Pl. 19, figs. 8–10; Pl. 24, figs. 1, 6, 8–10, 12, 13); those of type specimens and of topotypes do not follow this pattern but have a prominent notch anterior to the cusp (Pl. 4, figs. 6, 7; Pl. 21, figs. 3, 7; Pl. 23, fig. 6). The cusp varies in prominence; it is only slightly more prominent than the adjacent denticle in Viséan specimens from Atlantic Canada (Pl. 19, figs. 7–10; Pl. 24, figs. 2, 6, 8, 10, 12, 13), but is somewhat more so in Namurian specimens from North Staffordshire (Pl. 4, figs. 6, 7; Pl. 21, fig. 7; Pl. 23, figs. 6–10).

Parapet Area

The morphology of the left anterior part of the platform, the parapet area, is the single most important criterion for separating adult *Mestognathus* into five species. *M. har-*

malai sp. nov. possesses a low parapet area with a convex or rounded termination of the left anterior platform (Pl. 5, figs. 1, 5; Pl. 6, figs. 1, 3, 4, 6, 7). *M. groessensi* similarly has a nearly horizontal, anteriorly inclined, and featureless parapet area (Pl. 1, figs. 26, 29), as does *M. praebeckmanni* sp. nov. (Pl. 8, figs. 4, 5, 10, 11; Pl. 9, figs. 2, 6, 9; Pl. 10, figs. 1–6, 8, 9).

A single large parapet denticle, anterior to which a single smaller denticle may be present, is the key to identification of *Mestognathus beckmanni* (Pl. 1, fig. 8; Pl. 4, figs. 5, 9; Pl. 13, fig. 9; Pl. 16, figs. 8, 9, 11; Pl. 17, figs. 10, 13; Pl. 19, figs. 2, 3; Pl. 20, figs. 2, 5; Pl. 26, fig. 4). The parapet area of some of the type specimens is broken, and probably for this reason Bischoff (1957) did not mention that feature in the original diagnosis. The denticulation of the holotype consists of two denticles, a smaller one anterior to a larger one (Pl. 4, fig. 1; Pl. 13, fig. 3). The large parapet denticle of paratype PUM Bi 1957/39, a very large specimen, is atypically large and well defined (Pl. 4, fig. 5; Pl. 13, fig. 9). The parapet denticles of three of the paratypes are broken off or damaged (Pl. 4, figs. 2–4; Pl. 13, figs. 4–8). The parapet-denticle variation between the holotype and paratype PUM Bi 1957/39 is caused, we believe, by changes during ontogeny.

The parapet of *Mestognathus bipluti* is characterized by three or more denticles, two or more of which are anterior to the highest denticle (Pl. 4, figs. 6, 7, 10, 12; Pl. 19, figs. 6–10; Pl. 20, figs. 4, 7; Pl. 21, figs. 3, 7; Pl. 23, figs. 5–10; Pl. 24, figs. 1–13; Pl. 26, fig. 7; Pl. 28, fig. 6).

Eversion Strip

The lower surface of the five recognized species of *Mestognathus* is convexly rounded and bears a variety of morphologic structures. Most noticeable among these is an eversion strip that extends the length of the element on either side of the basal groove and the basal cavity and/or pit (Pl. 3). The eversion strip widens with increasing size of the conodont. Corresponding with this widening is a gradual flattening—that is, in smaller individuals the eversion strip is raised as a pseudokeel, whereas in larger individuals it is gradually engulfed by succeeding lamellae to become lower and more an integral part of the lower surface.

The eversion strip of *Mestognathus harmalai* sp. nov. is poorly developed and is known only as a raised pseudokeel (Pl. 5, figs. 2–4; Pl. 6, figs. 5, 8, 9). The eversion strip of the holotype of *M. groessensi* is low (Pl. 1, fig. 27), but that of one of the paratypes (Belka, 1983, pl. 1, fig. 2 [here reproduced as Pl. 1, fig. 31]) is noticeably raised. The eversion strip of *M. praebeckmanni* sp. nov. (Pl. 8, figs. 7, 9; Pl. 9, figs. 3, 4, 7, 11; Pl. 11, figs. 2, 3, 8, 9) is narrow and raised in small specimens (Pl. 9, figs. 3, 4, 7), becomes increasingly less raised with an increase in size, and is broadest and flattest in mature specimens (Pl. 8, figs. 7, 9; Pl. 9, fig. 11). *M. beckmanni* possesses an eversion strip

that is narrowest at the posterior end of the platform, is widest at about the basal cavity, and then narrows and splits to follow the contours of the primary and secondary keels (Pl. 3, figs. 1–5; Pl. 12, figs. 4–6; Pl. 13, figs. 6,7). The eversion strip of *M. bipluti* is narrowest at the posterior end of the platform, is widest at about the basal cavity, and divides anteriorly to rim the inner and outer margin of the primary and secondary keels (Pl. 21, figs. 8,9; Pl. 22, figs. 1,2). Mature specimens of *M. bipluti* have a flat eversion strip that does not project above the crimp (Pl. 13, figs. 6,7; Pl. 21, figs. 8,9; Pl. 22, figs. 1,2,4,6), the smooth rounded lower surface formed by the last deposited lamella.

Basal Groove

In the five recognized species of *Mestognathus* a basal groove divides the eversion strip and extends the full length of the platform from its posterior tip into the primary keel at the anterior end of the outer blade (Text-fig. 1). Little variation can be observed in the length or configuration of the main basal groove. Noticeable variation exists, however, in the lateral extension of the basal groove into the secondary keel, and we suggest that whether or not the basal groove extends into a secondary keel varies phylogenetically. *M. harmalai* sp. nov. (Pl. 5, figs. 1,3,4; Pl. 6, figs. 5–10; Pl. 11, fig. 11) and *M. groessensi* (Pl. 1, figs. 27,30,31) lack both secondary keels and basal grooves. As a parapet develops in *M. praebeckmanni* sp. nov., a secondary keel forms on the lower surface (Pl. 8, figs. 7,9; Pl. 9, figs. 3,4,7,11; Pl. 11, figs. 2,3,8,9); however, the basal groove does not extend into this structure.

We have been unable to document the presence of a secondary basal groove, or its entry into the secondary keel, in any of the types of *Mestognathus beckmanni*. The best-preserved types, the holotype and paratype PUM Bi 1957/39, have diagnostic rounded keels with well-developed swirling eversion strips but lack any sign of a basal groove (Pl. 3, figs. 1,5; Pl. 12, fig. 4; Pl. 13, fig. 7; Pl. 14, figs. 1,3; Pl. 15, figs. 7,10). The remaining types have poorly preserved lower surfaces (Pl. 3, figs. 2–4; Pl. 12, figs. 5,6; Pl. 13, fig. 6). Other specimens of this species, although showing well-developed keels, also lack a basal groove in their secondary keels (Pl. 3, fig. 9; Pl. 16, figs. 2,4,10,12; Pl. 25, figs. 8,9).

The continuation of the basal groove into the secondary keel of *Mestognathus bipluti* is difficult to demonstrate unequivocally from the types. This structure is moderately well developed and visible in the holotype (Pl. 13, fig. 6; Pl. 21, fig. 8; Pl. 22, fig. 1), whereas it is not well developed in the paratype (Pl. 3, fig. 7; Pl. 21, fig. 9; Pl. 22, fig. 2). The basal groove is visible in some additional specimens of the species (Pl. 3, figs. 12,14; Pl. 28, figs. 4,5; Pl. 29, figs. 1,2), but it is partly or entirely filled in and obscured in others (Pl. 3, figs. 10,11,13; Pl. 26, figs. 2,6; Pl. 27, figs. 1,2; Pl. 28, fig. 7).

The preceding discussion suggests that the basal groove does not extend into a supporting lobe to form a secondary keel in the three older species of *Mestognathus* but does so in some specimens of the two younger species. Whether this structure was developed ontogenetically in these species and was covered or partially resorbed with age must remain an open question.

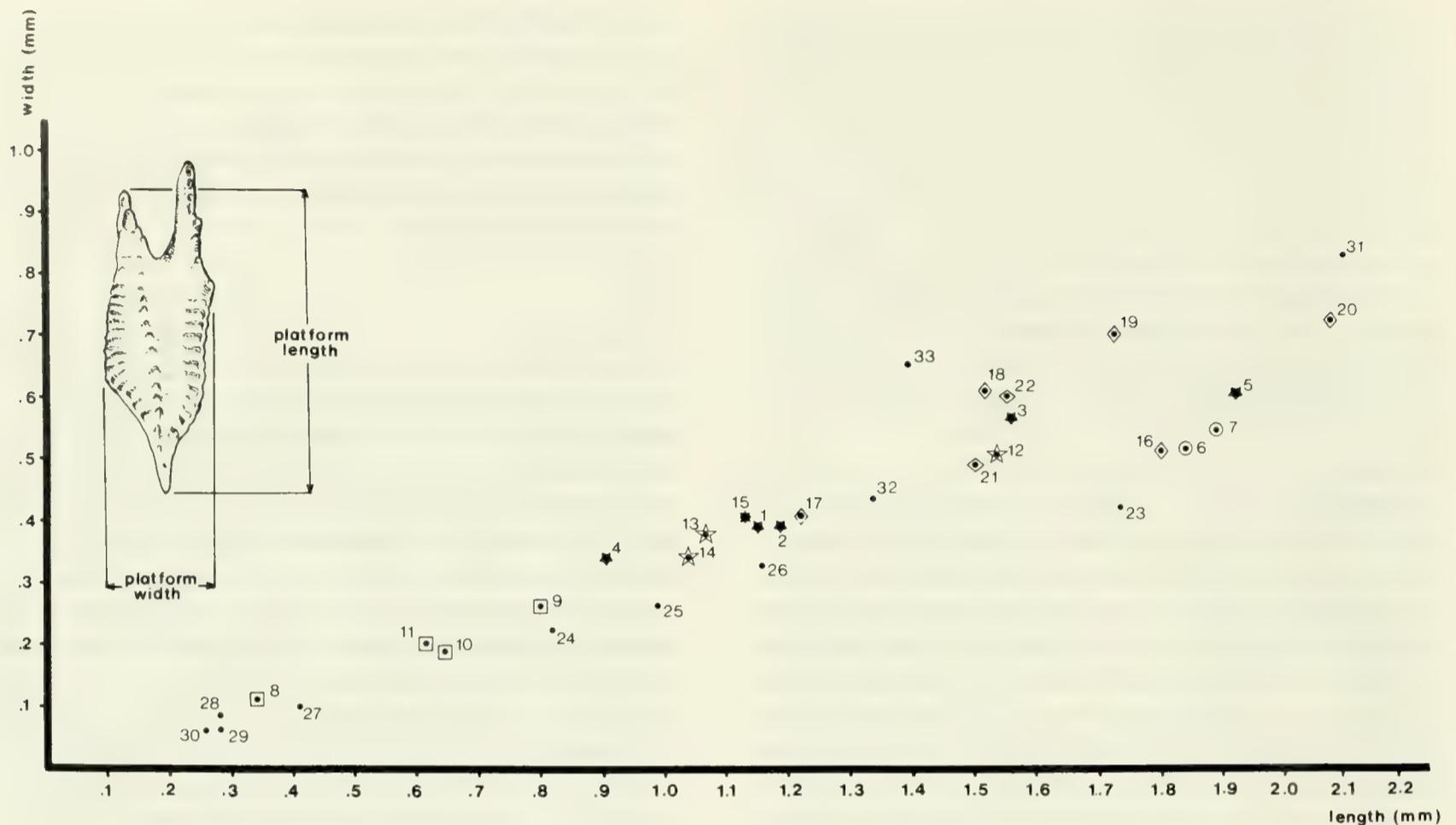
ONTOGENY

The morphology of species of *Mestognathus* changes most noticeably and dramatically during ontogenetic development. This generalization is based largely on rare ontogenetic growth series of *M. beckmanni* and *M. bipluti* that have been recovered and assembled from Viséan rocks laid down in specialized palaeoenvironments of Atlantic Canada.

Small specimens of species of *Mestognathus* are rare, probably for sedimentologic and/or environmental reasons, and because in some studies they have been incorrectly assigned to *Cavusgnathus*, owing to their open basal cavities. For example, the type specimens of *M. bipluti* are both rather large individuals (Text-fig. 2; Pl. 1, figs. 9,10; Pl. 2, figs. 6,7; Pl. 3, figs. 6,7; Pl. 4, figs. 6,7; Pl. 21), as are topotypes from North Staffordshire (Text-fig. 2; Pl. 23, figs. 5–10). In fact, A. C. Higgins (pers. comm., 1982) noted that he (1961, 1975) had “never come across small specimens of this species—which is presumably due to sorting”. Whatever the reasons for the dearth of small growth stages, which are considered further in the section dealing with palaeoecology and downslope transport and the one discussing *M. bipluti*, we are able to document important ontogenetic changes during the growth of one or more species of the genus.

The most obvious measure of ontogenetic development is change in overall size, as expressed by increase in length and width (Text-fig. 2; Pls. 17–19). Accompanying this are a number of ontogenetic changes in individual morphologic structures that are more subtle and are best documented photographically. Thus smaller immature mestognathids tend to be slenderer and less sinuous than mature specimens, and for this reason, too, they may be confused with *Cavusgnathus*. This tendency is particularly noticeable in some specimens of *Mestognathus beckmanni* (Pl. 3, fig. 2; Pl. 12, figs. 2,5; Pl. 16, figs. 5,6), *M. bipluti* (Pl. 3, fig. 11), and *Mestognathus* sp. (Pl. 3, fig. 9).

The development of transverse ridges and the differentiation of the two trough areas involve a noteworthy series of morphologic changes. The smallest specimens of *Mestognathus* studied have only a longitudinal row of nodes on either side of a poorly defined trough (Pl. 18, figs. 6,7). As the conodont increases in size, these nodes elongate laterally and “stretch” into ridges. The nodes of the left margin become more elongate; one swollen part remains at the left margin, whereas the other part, still connected to the



Text-fig. 2. Length/width plot of key specimens of species of *Mestognathus*. Note that length is platform length rather than total length because anterior blade is often broken. Measurement of number 15 (*M. groessensi*, holotype) calculated from illustrations of Belka (1983).

1. *M. beckmanni*, holotype, PUM Bi 1957/35.
2. *M. beckmanni*, paratype, PUM Bi 1957/36.
3. *M. beckmanni*, paratype, PUM Bi 1957/37.
4. *M. beckmanni*, paratype, PUM Bi 1957/38.
5. *M. beckmanni*, paratype, PUM Bi 1957/39.
6. *M. bipluti*, holotype, US E1.E.1.
7. *M. bipluti*, paratype, US E1.E1.2.
8. *M. dhuensis*, holotype, UNB 64-F-216 (MH-2-19) (here considered *Mestognathus* sp.).
9. *M. dhuensis*, paratype, UNB 64-F-215 (KD-6) (here considered *Mestognathus beckmanni*).
10. *M. dhuensis*, paratype, UNB 64-F-217 (MV-1) (here considered *Mestognathus bipluti*).
11. *M. dhuensis*, paratype, UNB 64-F-214 (KD-6) (here considered *Mestognathus bipluti*).
12. *M. neddensis*, holotype, BMNH X 250 (here considered *Mestognathus bipluti*).
13. *M. neddensis*, paratype, BMNH X 251 (here considered *Mestognathus* sp.).
14. *M. neddensis*, paratype, BMNH X 252 (here considered *Mestognathus* sp.).
15. *M. groessensi*, holotype, no depository designated by Belka (1983, 1985).
16. *M. harmalai* sp. nov., holotype, USNM 257751.
17. *M. harmalai* sp. nov., paratype, USNM 257752.
18. *M. harmalai* sp. nov., paratype, USNM 257753.
19. *M. harmalai* sp. nov., paratype, USNM 257754.
20. *M. harmalai* sp. nov., paratype, USNM 257755.
21. *M. praebeckmanni* sp. nov., holotype, USNM 257757.
22. *M. praebeckmanni* sp. nov., paratype, USNM 257758.
23. *M. beckmanni*, BMNH X 245.
24. *M. bipluti*, BMNH X 246.

marginal node by a ridge, moves increasingly towards the trough area, where it forms the developing carina (Pl. 18, figs. 8,9). It is the apparent stretching of the left-margin nodes that produces the elevated adcarinal trough. The nodes of the right margin similarly elongate to form the transverse ridges of that side (Pl. 18, figs. 8–10).

The number and arrangement of denticles in the anterior blade of *Mestognathus* vary with ontogenetic development. For example, small specimens of *Mestognathus* have fewer, more regularly arranged denticles (Pl. 19, figs. 11–14), whereas larger specimens have a greater number of more irregularly arranged denticles (Pl. 17; Pl. 19, figs. 1–10). As the number of anterior blade denticles increases, so do the lengths of the free and fixed blades (Pls. 17,18,19,24).

The taxonomically most important change during the growth of the two youngest species of *Mestognathus* appears to be the development of parapet denticulation. Below a platform length of approximately 0.5 mm (Text-fig. 2), the denticulation of the parapet is undeveloped, and the two species are indistinguishable from one another and can be identified only to genus (Pl. 19, figs. 11–14). In specimens longer than 0.5 mm, specific determination is generally possible because the parapet develops distinctly in the two species. As the parapet develops and enlarges, the anterior notch also deepens and becomes better defined (Pl. 18).

As *Mestognathus beckmanni* increases in size, the single large parapet denticle becomes more prominent. Moderately mature specimens of *M. beckmanni*, including the holotype (Pl. 4, fig. 1; Pl. 13, fig. 3), commonly possess an additional small denticle anterior to the highest parapet denticle (Pl. 16, fig. 7). This extra denticle is observable even in some juvenile specimens of *M. beckmanni*. This structure, plus the general ontogenetic variation of the parapet denticulation, is best demonstrated in the ontogenetic growth series from Atlantic Canada (Pl. 17, figs. 1–13; Pl. 19, figs. 1–5). In this series the single larger parapet denticle is commonly joined anteriorly by a single

smaller denticle (Pl. 17, figs. 2,4,5,7–9,11; Pl. 19, figs. 1,4). The types of *M. beckmanni*, and growth stages of the species from Atlantic Canada, suggest that presence of a smaller denticle anterior to the main parapet denticle is an intermediate ontogenetic feature that disappears by overgrowth in fully mature specimens of *M. beckmanni*, such as paratype PUM Bi 1957/39 (Pl. 4, fig. 5; Pl. 13, fig. 9).

Growth series of *Mestognathus bipluti* from Atlantic Canada demonstrate that the smallest specimens identifiable as *M. bipluti* (Pl. 19, fig. 10; Pl. 24, fig. 13) possess a single parapet denticle that is, with an increase in size, added to anteriorly by new denticles (Pl. 19, figs. 8,9; Pl. 24, figs. 10,12) to form the spatulate parapet.

Specimens of *Mestognathus bipluti* from Atlantic Canada apparently did not attain the same large size as specimens from North Staffordshire. The largest specimens of *M. bipluti* recovered from Atlantic Canada not only are noticeably smaller (Text-fig. 2), but also possess a less massive, spatulate parapet. Smaller size and a less spatulate parapet also appear to characterize other documented Viséan occurrences of *M. bipluti*. Polish, Irish, Welsh, Scottish, and Belgian Viséan specimens appear to possess a smaller, more delicate, less denticulate parapet than do the larger Namurian specimens: Polish (Skompski and Sobon-Podgorska, 1980, pl. 5, figs. 11,13,14; Belka, 1983, pl. 1, figs. 5–8, pl. 2, figs. 3a,b,4,8a,b); Irish (Austin, 1974, pl. 1, fig. 22; Austin and Husri, 1974, pl. 5, figs. 9,10); Welsh (Rhodes, Austin, and Druce, 1969, pl. 15, figs. 2a–c,6a–c,8a,b; Varker and Sevastopulo, 1985, pl. 5.4, figs. 17,18); Scottish (Rhodes, Austin, and Druce, 1969, pl. 15, figs. 1a–c,3a–c); Belgian (Bless et al., 1976, pl. 14, fig. 14).

The comments by A. C. Higgins (pers. comm., 1982) regarding sorting in this species may be both the simplest and the most likely explanation of the size difference noted in Viséan and Namurian populations of *Mestognathus bipluti*. An alternative hypothesis involves incomplete ontogenetic growth because of hypersaline environmental conditions. This hypothesis interprets the lack of really

25. *M. bipluti*, BMNH X 248.

26. *M. bipluti*, BMNH X 249.

27. *M. bipluti*, ROM 43414.

28. *Mestognathus* sp., ROM 43418, Wallace Point Member, sample WaPt-1-3, locality 17.

29. *Mestognathus* sp., ROM 43416.

30. *Mestognathus* sp., ROM 43417.

31. *M. beckmanni*, USNM 257759.

32. *M. beckmanni*, USNM 257760.

33. *M. beckmanni*, USNM 257761.

large individuals of *M. bipluti* with large spatulate parapets as the result of individuals' failing to reach adulthood because of the hypersaline conditions. Shimer (1908) cited hypersalinity as the cause of the relatively small size of Windsor Group invertebrates. Although Bell (1929) regarded this conclusion as unwarranted, it has been demonstrated that other species of conodonts have been dwarfed by hypersaline environments (Sandberg and Ziegler, 1979: 189).

The most striking aspect of the lower surface of small specimens of *Mestognathus* is the large elongated basal cavity that becomes proportionately smaller and shorter as the conodont increases in size. Although it was the discovery in recent years of mestognathids with large basal cavities that was, in part, responsible for the recognition of Tournaisian mestognathids, this is a misconception, since juvenile specimens of the two youngest species of *Mestognathus*, *M. beckmanni* and *M. bipluti*, have large, elongated basal cavities (Pl. 18, figs. 1–4).

We believe it to be likely that all species of *Mestognathus* (including the poorly known *M. groessensi*) started life with large basal cavities and that these were then everted to different degrees as the conodont grew. The basal cavities of the three oldest species, *M. harmalai* sp. nov. (Pl. 5, figs. 2,6,7; Pl. 6, figs. 5,8–10), *M. groessensi*, and *M. praebeckmanni* sp. nov. (Pl. 8, figs. 7,8), were everted sufficiently to leave a moderately large, well-defined basal pit, whereas those of the two youngest species (Pl. 18, figs. 1–3,6–8) were almost totally lost, leaving only a very small basal pit.

Another size-related feature of immature specimens of *Mestognathus beckmanni* (Pl. 12, fig. 5; Pl. 13, fig. 6) and *M. bipluti* (Pl. 18, fig. 4; Pl. 20, fig. 8) is a pronounced liplike raised pseudokeel, consisting of an eversion strip bisected by a basal groove. This feature is most pronounced in the posterior half of the platform. Moderately mature to mature specimens of *M. beckmanni* (Pl. 3, figs. 1,5; Pl. 12, fig. 1; Pl. 13, fig. 7) and *M. bipluti* (Pl. 18, fig. 10) have had this earlier raised pseudokeel engulfed by the deposition of many later lamellae, so that it is flush with the crimp.

The four type specimens of *Mestognathus dhuensis* (= *M. beckmanni*, *M. bipluti*, and *Mestognathus* sp.) possess a pronounced raised pseudokeel (Pl. 3, figs. 8–11; Pl. 25, figs. 2,6,8–10; Pl. 26, figs. 2,6; Pl. 27, figs. 5,6), a feature that is least prominent in paratype UNB 64-F-217 (MV-1). The holotype of *M. neddensis* (= *M. bipluti*) lacks a raised pseudokeel (Pl. 3, fig. 12; Pl. 28, fig. 4), whereas the two paratypes (= *Mestognathus* spp.) have this feature developed to a moderate degree (Pl. 3, figs. 13,14; Pl. 28, fig. 7; Pl. 29, fig. 5). We interpret the well-developed pseudokeel of six of the seven type specimens of the two synonymized species to be a juvenile characteristic, an interpretation supported by the relatively small size of these specimens (Text-fig. 2). The holotype of *M. neddensis*, in lacking a

pseudokeel, is the most mature specimen of the seven specimens (Text-fig. 2, no. 12). The presence of a well-developed pseudokeel in many mestognathids, particularly those from Atlantic Canada (Pl. 18, figs. 1–4; Pl. 20, fig. 8), is directly attributable to their small size.

In the ontogenetic development of the types of the synonymized *Mestognathus dhuensis* (= *M. beckmanni*, *M. bipluti*, and *Mestognathus* sp.) the right side of the eversion strip becomes constricted and then flattens out just after reaching its broadest expansion (Pl. 3, figs. 8–11; Pl. 25, figs. 2,3,8,9; Pl. 26, figs. 2,6; Pl. 27, figs. 1–3). This constriction then develops into a diagnostic crease on the lip of the adjacent basal cavity and gives it an asymmetric appearance (Pl. 25, fig. 3; Pl. 27, figs. 1–3). This crease, although not present in all immature mestognathids from Atlantic Canada (Pl. 18, figs. 1–4), is interpreted as an ontogenetic feature that, like the pseudokeel, is lost with additional growth.

Although we have discussed the evolutionary and phylogenetic significance of the extension of the basal groove into the secondary keel, we are unable, from available Viséan specimens, to relate the presence or absence of a basal groove in the secondary keel to ontogenetic development. For example, the types of *Mestognathus dhuensis* (= *M. beckmanni*, *M. bipluti*, and *Mestognathus* sp.) and of *M. neddensis* (= *M. bipluti* and *Mestognathus* spp.)—specimens that we have studied in great detail—do not follow a regular ontogenetic pattern with regard to entry of the basal groove into the secondary keel. The secondary keels of the types of *M. dhuensis* either lack a basal groove (or have one that is completely blocked; Pl. 25, figs. 2,3,8,9), or possess one that is visible only intermittently (or have one that is only partially blocked; Pl. 26, figs. 2,6; Pl. 27, figs. 1,2). The holotype and paratype BMNH X 252 of *M. neddensis*, on the other hand, have a completely open basal groove in the secondary keel (Pl. 3, figs. 12,14; Pl. 28, figs. 4,5; Pl. 29, figs. 1,2), whereas in paratype BMNH X 251 the junction of the primary and secondary keels is blocked (Pl. 3, fig. 13; Pl. 28, fig. 7). More study of this characteristic in Viséan mestognathids, particularly those from Atlantic Canada, may show that the basal groove of the secondary keel fills up randomly without regard to size or maturity.

ULTRASCULPTURE

So-called "golf-ball" surfaces, the honeycombed microstructure commonly present on the upper platform of conodonts, are observed in better-preserved specimens of *Mestognathus*. A honeycombed network is present on the left lateral edge of the holotype of *M. praebeckmanni* sp. nov. (Pl. 8, fig. 10; Pl. 10, figs. 10,11) and is better developed on the upper surface of some specimens (e.g., the holotype and paratype PUM Bi 1957/38) of *M.*

beckmanni (Pl. 14, figs. 10–12; Pl. 15, fig. 6). The honeycombed network has also been observed on the lateral edges of the upper surface of a specimen of *M. bipluti* (ROM 43422; Pl. 18, fig. 10).

The crimp of *Mestognathus beckmanni* and *M. bipluti* is often altered by corrosion, recrystallization, and/or the development of overgrowths. We do not know, however, whether the crystals observable on the crimp of these species are in crystallographic continuity with those of the underlying lamellar sheets. The smooth crimp is best seen in some of the types of *M. beckmanni* (Pl. 3, figs. 1,2,4,5; Pl. 12, figs. 4,5; Pl. 13, figs. 6,7; Pl. 14, figs. 1,3,7,8), whereas an irregular altered crimp is observable in numerous specimens of both species (Pl. 3, figs. 3,7–13; Pl. 12, fig. 6; Pl. 21, fig. 9; Pl. 25, figs. 2,3,6,8–10; Pl. 26, figs. 2,6; Pl. 27, figs. 3,5,6; Pl. 28, figs. 4,7; Pl. 29, figs. 4,7,10). The type specimens of *M. dhuensis* and *M. neddensis*, species synonymized by us with *M. beckmanni*, *M. bipluti*, and *Mestognathus* spp., have, for unknown reasons, a particularly noticeable tendency towards recrystallization and/or overgrowth of the crimp (Pl. 25, figs. 9,10; Pl. 26, figs. 2,6; Pl. 27, figs. 3,5,6; Pl. 28, figs. 4,7; Pl. 29, figs. 1,4,7,10).

The parallel and overlapping lamellae making up the eversion strip in younger mestognathids often form circular, in part hollow, growth pits of unknown function, similar to some types of secondary growth centres illustrated by Müller (*in* Robison, 1981:W37). These structures, most noticeable in the types of *Mestognathus neddensis* (= *M. bipluti* and *Mestognathus* spp.; Pl. 3, figs. 12–14; Pl. 28, figs. 4,5,7; Pl. 29, figs. 1,5,6) and the holotype of *M. dhuensis* (= *Mestognathus* sp.; Pl. 3, fig. 8; Pl. 25, figs. 2–5), are expressed as hollow or solid nodes slightly anterior to and left of (in lower view) the basal cavity. In specimen ROM 43422 of *M. bipluti* (Text-fig. 1) these structures are present at the posterior end of the conodont (Pl. 20, figs. 1,2). In the types of *M. beckmanni* and *M. bipluti*, rather than hollow growth pits being present in this position, there are consistently one or more swellings (Pl. 3, figs. 1–7; Pl. 12, figs. 4–6; Pl. 13, figs. 6,7; Pl. 14, figs. 1,5,6; Pl. 15, figs. 7,8; Pl. 21, figs. 8,9; Pl. 22, fig. 2); however, the holotype and paratype PUM Bi 1957/39 of *M. beckmanni* bear hollow growth pits enclosed in the swirling lamellae of the supporting lobe on the right side (seen in lower view) of the conodont (Pl. 14, figs. 5,6; Pl. 15, figs. 7–10).

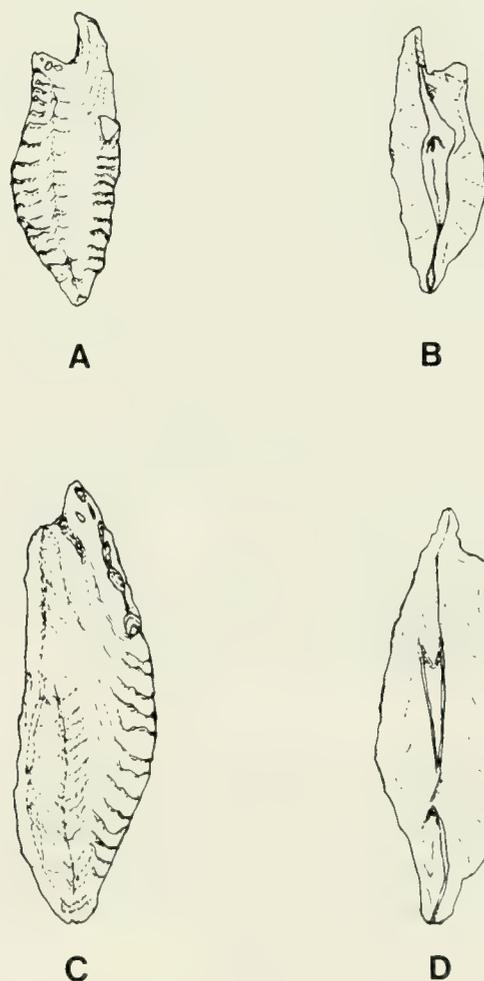
SYMMETRY

The apparatus of *Mestognathus* most likely included one or more sets of paired asymmetric Pa elements. Sinistral and dextral elements of these pairs may be distinguished, though often with difficulty, by differences in curvature of the left margin (in upper view) and of the basal groove (in

lower view) (Text-fig. 3). Thus the symmetry between pairs of Pa elements of *Mestognathus* is similar to that of *Cavusgnathus* (*sensu* Lane, 1967). It is not a mirror image but rather is expressed more subtly by differences of curvature, etc.

Mestognathus is placed, by our interpretation, in symmetry Class IIIa of Lane (1968). *Mestognathus* did not, in our view, ever exist as unpaired platform elements, as implied by Druce (1973) and Belka (1983) in placing this genus in symmetry Class IV of Lane (1968). Although Higgins (1961) believed that *M. bipluti* was unpaired because “the curvature of individual specimens is independent of the inner and outer sides as defined on the size of the parapets”, he nevertheless went on to suggest three possibilities that may have existed: *Mestognathus* elements were not paired, the right and left elements were considerably different, or the different pairs had different directions of curvature.

We believe that the second and third of Higgins’s possibilities existed and point out that our criteria for distinguishing sinistral or dextral elements of this genus are similar to, and compatible with, those used by others



Text-fig. 3. Sinistral and dextral *Mestognathus*.

A,B. Sinistral *M. praebeckmanni* sp. nov. morphotype 3, upper and lower views, respectively. Paratype USNM 257758, locality 3.

C,D. Dextral *M. praebeckmanni* sp. nov. morphotype 1, upper and lower views, respectively. TCD 23164, locality 5.

(Norby, 1976; Rexroad, 1981; von Bitter and Plint, in press) to differentiate left and right elements of another cavusgnathoid, *Cavusgnathus*.

APPARATUS

Whether or not *Mestognathus* bore ramiform elements in its apparatus is uncertain. The reasons for this uncertainty include a lack of natural assemblages, the relative rarity of the genus, and the apparently common downslope transport of current-sorted disjunct elements.

From available data, it seems probable that this cavusgnathoid bore only one or more pairs of Pa or platform elements. We cannot, however, rule out the possibility that ramiform elements may have been present in the apparatus of *Mestognathus* living under optimum conditions. As *Mestognathus* was subjected to increasing environmental stress, its ability to retain ramiform elements may have decreased (see Merrill and von Bitter, 1984:256,257, fig. 5). Other cavusgnathoids, some of them contemporaneous with one or more species of *Mestognathus*, are known to have borne a full complement of platform and ramiform elements (Scott, 1942; von Bitter, 1972; Baesemann, 1973; Norby, 1976; Rexroad, 1981; von Bitter and Plint-Geberl, 1982). The ramiform elements of these cavusgnathoids were not always retained—especially under conditions of environmental stress (Merrill and von Bitter, 1984:256,257).

Among the methods available for analysing conodont collections for recurrent associations is cluster analysis. Of the authors known by us to have applied this technique to their data, only Druce, Rhodes, and Austin (1972, 1974) analysed Lower Carboniferous conodont collections that contained *Mestognathus*, or *Mestognathus*-like conodonts. Although these authors did not use collections stratigraphically younger than those from the K and Z coral zones (and therefore did not include *Mestognathus sensu* this study), *Scaphignathus?* sp. A and *S.?* sp. B (considered to be *Mestognathus groessensi* by Belka, 1983 and Varker and Sevastopulo, 1985) were included. Druce, Rhodes, and Austin (1972:62) included these taxa in their groups 5 and 6 but were unable to ascribe any significance to the associations.

Other determinants of biologic association, such as the presence of symmetry transitions or similarity of colour or of denticulation, are apparently not applicable. Among the reasons for this is the fact that *Mestognathus* is relatively rare and that *Mestognathus* ramiforms have either not been preserved or not been identified.

von Bitter and Plint-Geberl (1982:202) speculated about a close biologic relationship between *Mestognathus* and *Spathognathodus scitulus*, *Ozarkodina laevipostica* and

Apatognathus spp. Nicoll (1980:137) suggested, and Rexroad and Thompson (1979:240) concluded, that the last three conodonts belonged to the same multielement species.

Hindeodus? [formerly *Spathognathodus*] *scitulus* and *Apatognathus* spp. are known from a fused cluster and were biologically probably a part of the same apparatus (Austin and Rhodes, 1969). Such a biologic link between these two-element types is supported by occurrences in Atlantic Canada, the central United States, Scotland, and North Wales (Table 1). Except for *Hindeodus?*, we use the taxonomic names utilized by previous authors (Table 1) rather than the multielement designation *Apatognathus scitulus* proposed by Rexroad and Thompson (1979:240). We do this because of our own uncertainty about whether *Ozarkodina laevipostica* is a part of that apparatus, because Nicoll (1980:137) suggested the genus *Apatognathus* is restricted to the Devonian, and because these names are well established in the literature (Table 1).

The infrequent and unpredictable occurrence of *Ozarkodina laevipostica* with *Hindeodus? scitulus* and *Apatognathus* (Table 1) makes it seem unlikely to us that *O. laevipostica* belonged to the same apparatus of which *H.?* *scitulus* and *Apatognathus* were a part. Although *O. laevipostica* may have been an irregularly and/or infrequently occurring part of an *H.?* *scitulus*-*Apatognathus* apparatus (cf. the rare hornlike M element of *Ellisonia conflexa* (Ellison) of von Bitter and Merrill, 1983), supporting distributional and morphologic data would be required to demonstrate this.

Mestognathus is as unlikely to have been part of an apparatus with *Ozarkodina laevipostica* as part of one with *Hindeodus? scitulus* and *Apatognathus*. *Mestognathus* is only rarely associated with *O. laevipostica*. *H.?* *scitulus* and *Apatognathus*, although commonly found together with *Mestognathus*, nevertheless are often found by themselves, without *Mestognathus* (Table 1). This lack of common or consistent association of *Mestognathus* with any of the conodonts under consideration is most noticeable in the Mississippian of the central United States. It was from this region that Rexroad and Collinson (1963:19) originally described *O. laevipostica*. *H.?* *scitulus*, *Apatognathus*, and *O. laevipostica* have a common distribution here (Rexroad and Collinson, 1963; Nicoll and Rexroad, 1975), whereas *Mestognathus* has not been reported from the central United States.

We conclude that there is reasonably strong evidence that *Hindeodus? scitulus* and *Apatognathus* were biologically part of the same multielement species. *Ozarkodina laevipostica* and *Mestognathus*, on the other hand, were only sometime ecologic associates of one another and of that multielement species.

Table 1. Occurrences of *Hindeodus? scitulus*, *Ozarkodina laevipostica*, *Apatognathus* spp., and *Mestognathus* spp. in Atlantic Canada, U.S.A., Scotland, and Wales.

Except for our usage of *Hindeodus? scitulus*, the taxonomic names utilized are those of the papers cited. Abbreviations: U = uncommon; P = present; R = rare; C = common.

		Conodont Taxa			
		<i>Hindeodus?</i> <i>scitulus</i>	<i>Apatognathus</i> spp.	<i>Ozarkodina</i> <i>laevipostica</i>	<i>Mestognathus</i> spp.
Illinois, Indiana, and Missouri (Rexroad and Collinson, 1963)	St Louis Limestone	R-C	R-C	U-C	
Indiana and Kentucky (Nicoll and Rexroad, 1975)	St Louis Limestone	P	P	P	
Newfoundland (von Bitter and Plint-Geberl, 1982)	Cod-1-15	1	1		6*
	Cod-1-9	2	1	1	4
	Cod-1-7		1		
Nova Scotia (von Bitter, 1976)	PHI-E ₁ -4	C	R		
	PHI-E ₁ -3		C		
	PHI-D ₁ -3		C		C
	PHI-D ₁ -2	C	C		C
Quebec (Plint-Geberl, 1982; Plint and von Bitter, 1986; von Bitter and Plint, in press)	PHI-C ₃ -4				C
	IDM-3-21				9
	IDM-7-8	1	1		
Scotland (Clarke, 1960)	IDM-7-7		1	1	
	Index Limestone and Shale	P			
	Upper Limestone Group				
	Lin Spout		P		
	Glencart	P	P	P†	
North Wales (Aldridge, Austin, and Husri, 1968)	Monkcastle	P			
	Skateraw Middle Limestone and shales	P	P		
North Wales (Aldridge, Austin, and Husri, 1968)	4D		1		6
	4Bf	2	8		9
	4Bc	1			
	4Bb		3		5
	4Ba	2	4		4
	4Ae	2	3		45
	4Ad	4	10		5
	4Ac	4	4		58
	4Ab	2	3		9
	4Aa	1			15
	2b		3		
2a		2		1	
1c		1			

*Original published count of 5 revised to 6.

†*Euprioniodina glencartensis* of Clarke (1960) is taken as a possible *Ozarkodina laevipostica*.

Palaeoecology

PALAEOECOLOGICAL INTERPRETATIONS

Our survey of the authors who have placed *Mestognathus* in a community or biofacies context appears at first glance to show a great divergence of views (Table 2). Not only is there variation in the code applied to designate the biofacies, community, or group that each author believed included *Mestognathus* (row 1), but other apparent differences result from interpretation of whether or not an author was able to recognize one or more conodont communities shorewards of the one that included *Mestognathus* (row 2). These differences, interestingly enough, are based more on terminology than on substance.

Mestognathus and its ecologic associates were thought by all six authors surveyed (Table 2) to have lived in shallow water, commonly nearshore environments. Austin (1976:201) included *Mestognathus* in his shelf-related genera, Sandberg and Ziegler (1979) grouped the genus among the asymmetric platform genera interpreted as shallow-water forms, and Higgins (1981:47) stated it to be

“typically a shelf genus” that “is only common in very shallow-water facies”. Most recently, Sandberg and Gutschick (1984, fig. 14) proposed a mestognathid(?) biofacies as the landwardmost of seven conodont biofacies of the *Scaliognathus anchoralis*–*Doliognathus latus* Zone. They interpreted this biofacies to be present in the tidal lagoon and sabkha environment(s).

It is the similarity, rather than the difference, of opinions regarding *Mestognathus*'s habitat that is striking—nearly all authors view this as a shallow-water “shelf” genus. In those cases where *Mestognathus* was recovered from deep-water sediments, not only did its relative abundance drop off (Higgins, 1981:40, fig. 4.3), but its presence is best interpreted as indicating downslope transport (this study; also Belka, 1983:81,82). The conditions in the shallow-water environments that were the habitat of *Mestognathus* ranged from high energy (intertidal, oolite shoal, and reefoid) to low energy (lagoonal). Although Higgins (1981, fig. 4.3) recovered Viséan species of *Mestognathus*

Table 2. *Mestognathus*—its biofacies, biofacies associates, and environmental conditions.

	Druce (1973)	von Bitter (1976)	Austin (1976)	Merrill and von Bitter (1979)
Conodont association	Biofacies II	Biofacies II*	Community I‡	Community I
Relative biofacies position to shore	2nd	2nd	1st	1st
Age	Viséan	Viséan–?Early Namurian	Viséan	Late Early Carboniferous
Taxa present	<i>Mestognathus</i> <i>Cavusgnathus</i> <i>Taphrognathus</i> <i>Gnathodus</i> (simple) <i>Spathognathodus</i>	<i>Mestognathus</i> † <i>Cavusgnathus regularis</i> – <i>C. unicornis</i> Group <i>Taphrognathus</i> <i>Gnathodus scotiaensis</i> <i>Spathognathodus</i> <i>Apatognathus</i>	<i>Mestognathus</i> <i>Cavusgnathus</i> <i>Taphrognathus</i> <i>Spathognathodus cristulus</i> <i>Apatognathus</i> <i>Polygnathus</i> <i>Pseudopolygnathus</i> <i>Patrognathus</i> <i>Bispathodus</i> <i>Streptognathodus</i>	<i>Mestognathus</i> spp. <i>Cavusgnathus altus</i> <i>Taphrognathus</i> spp.
Environmental conditions/lithologies, etc.	Intermediate water depth (<50 m?)	Inner shelf and reefoid environments; <i>Mestognathus</i> recovered in intertidal, high-energy reefoid and oolitic shoal carbonates	Oolites, pale thick-bedded bioclastic limestones, dark thin-bedded bioclastic limestone	Nearshore, shallow-water, euryhaline, often high-energy

*Here designated Biofacies II.

†von Bitter (1976) likely misinterpreted this group of conodonts to have been derived from more basinward deeper-water biofacies.

‡Austin (1976, fig. 4) did not designate this association as a biofacies but included these in his “shelf associated” genera.

most abundantly in "black fine limestones" interpreted as [quiet-water] lagoonal deposits, most authors (Table 2) have observed the frequent occurrence of the genus in carbonate rocks, the composition of which is indicative of higher energy. Austin (1976, figs. 4,7), for example, recognized that *Mestognathus* was most at home in the shallow-water environment in which pale, thick-bedded bioclastic limestones were deposited. Although the genus was still present in oolitic limestone and dark, thin-bedded bioclastic limestones deposited shorewards and seawards, respectively, of the depositional sites of the thick-bedded bioclastic limestones, Austin recognized that it nevertheless decreased in these two kinds of lithologies. These observations agree with data presented by von Bitter (1976) for some occurrences of *Mestognathus* in the Viséan of Atlantic Canada. On Port Hood Island, Nova Scotia, *Mestognathus* was present and common in only three samples taken from beds classified petrographically by Schenk (1969) as algal biolithite, biosparite, and oosparite. These lithologies were thought by Schenk to represent intertidal, reefoid, and oolitic shoal conditions, respectively—

all conditions that require a high-energy environment.

Two other common occurrences of *Mestognathus* noted by von Bitter (1976) were in the type sections of the Herbert River and Wallace Point members of the upper Windsor Group (Appendix, localities 15, 17). Since then *Mestognathus* has also been recovered in moderate abundance from the type section of the Avon Member of the upper Windsor Group (Appendix, locality 16). There is, in the samples from these three type localities, a directly observable relationship between lithology and energy and the presence or absence of *Mestognathus*. The Herbert River Member at locality 15 (Appendix), containing *Mestognathus*, is a noticeably bioclastic carbonate unit containing much evidence for a high-energy, shallow-water depositional environment (Moore, 1967:253). The lower parts of the Avon and Wallace Point members, containing *Mestognathus*, are also bioclastic carbonates that have been interpreted as having been deposited under high-energy, intertidal conditions (Moore, 1967:257,261). Overlying the basal bioclastic units of both members, at their type sections, are characteristic sublithographic limestones that

Higgins (1981)	Kalvoda (1983)	Belka (1983)	Sandberg and Gutschick (1984)	This Study
Community III	Group I			Biofacies I
3rd	1st		1st	1st
Viséan	Early Carboniferous		Early Carboniferous	Early Carboniferous
<i>Mestognathus</i> <i>Cavusgnathus</i>	<i>Mestognathus</i> <i>Cavusgnathus</i>	" <i>Mestognathus</i> occurrences correspond to <i>Eotaphrus</i> biofacies" of Lane, Sandberg, and Ziegler (1980).		<i>Mestognathus</i> defined the most nearshore biofacies. <i>Mestognathus</i> was transported seawards into both shallow-water and deeper-water marine environments. Consequently, it became secondarily mixed with <i>Cavusgnathus</i> , <i>Clydagnathus</i> , <i>Hindeodus</i> , <i>Gnathodus</i> , etc.
<i>Gnathodus homopunctatus</i> and <i>G. commutatus</i>	<i>Apatognathus</i> <i>Cloghergnathus</i> <i>Laterignathus</i> <i>Clydagnathus</i>			
Lagoonal, black, fine limestones	Shallowest parts of shelf; inner shelf		Tidal lagoon and sabkha; sandy dolomite(?) and anhydritic dolomite(?)	Tidal lagoon and sabkha; sandy dolomite(?) and anhydritic dolomite(?)

have been interpreted to signify low-energy, lagoonal depositional environments (Moore, 1967:257,261). *Mestognathids* have not been recovered from the sublithographic, platy limestones.

Although we suggest that *Mestognathus* is commonly found in sediments indicative of shallow-water, high-energy conditions, we are, nevertheless, cautious about attributing too great a significance to wave energy as a controlling factor. For example, we do not necessarily agree with Belka (1983:82), who concluded that the distribution of *Mestognathus* was "controlled more by the water-energy than by the conditions prevailing on the sea floor". On the contrary, Higgins (1981) reported the genus from presumably quiet-water [?hypersaline] lagoonal deposits. Moreover, we are aware (as were Merrill and von Bitter, 1976) that what we often view, when recognizing that a particular fossil occurs in a specific sediment type, is a secondary effect rather than a primary cause. We suggest that the overriding factor in the nearshore, shallow-water environments of Early Carboniferous seas was salinity rather than wave energy. The distribution of *Mestognathus*, like that of other *cavusgnathoids* (Merrill and von Bitter, 1976, 1979), was more likely affected by variations in salinity than by wave energy. The recovery in Atlantic Canada of *mestognathids* from marine rocks deposited in or near hypersaline environments (as evidenced, for example, by *mestognathid*-bearing samples HerbR-8-4 and Avn-5-1 (Appendix, locality 18) associated with anhydrite nodules) supports this thesis. These rocks are often, as they are on Port Hood Island, Nova Scotia, noticeably impoverished faunally but rich in algal stromatolites.

Salinity is a factor that greatly influences the distribution of modern nearshore marine organisms, and this factor is in turn controlled by a number of subfactors, such as temperature, eh, and pH. In the nearshore, shallow parts of Early Carboniferous tropical seas, salinity levels would have varied considerably (according to the amount of fresh-water runoff and evaporation) in any of the high- or low-energy environments. We therefore suggest that a tolerance by *Mestognathus* of variations in salinity takes into account the numerous reports of moderately abundant *mestognathids* in high-energy carbonate rocks on the one hand and their occurrence in quiet-water lagoonal deposits (Higgins, 1981) on the other.

The marine rocks of the Windsor (von Bitter, 1976) and Codroy (von Bitter and Plint-Geberl, 1982) groups of Atlantic Canada were deposited in or near hypersaline environments, and thick evaporites in the form of sulphate and chloride deposits are common. von Bitter (1976) interpreted that *Cavusgnathus* [now assigned by him to *Clydagnathus*] *windsorensis* was tolerant of rather extreme environmental conditions, such as shallow-water, high-energy settings, in which there were considerable variations in salinity, and that this species defined a biofacies by

the same name.

Clydagnathus, until now considered to be a Tournaisian conodont genus (Rhodes, Austin, and Druce, 1969; Druce, 1973; Austin, 1976), is acknowledged (Druce, 1973; Austin, 1976; von Bitter, 1976; Lane, Sandberg, and Ziegler, 1980; Higgins, 1981; Kalvoda, 1983) to have lived in the shallowest, most restricted part of the Early Carboniferous marine shelf. The genus is commonly found in supratidal sediments (Austin, 1976:213), and Higgins (1981, fig. 4.3) indicated that the genus lived under hypersaline conditions. We suggest that although *Clydagnathus*, like the other *cavusgnathoids*, *Mestognathus* and *Cavusgnathus*, was tolerant of variable salinities (i.e., was euryhaline), it nevertheless lived consistently under shallow, variably saline conditions and defined a very shallow-water, nearshore conodont biofacies during the Tournaisian and Viséan. During this time interval *Mestognathus*, another asymmetric *cavusgnathoid*, lived in a biofacies landwards of its ancestor *Clydagnathus* and the biofacies it defines. The salinity of these more landward *Mestognathus* environments would have been even more extreme because of evaporation.

If *Mestognathus* was restricted by similar, but more extreme, environmental factors than was *Clydagnathus*, then the probable explanation for the relative rarity of *Mestognathus* would be the fact that the specialized, harsh, and uncommon nearshore environments that were the main habitat of the genus have either not been sufficiently sampled or have not been available for study. The Windsor and Codroy groups of Viséan age in Atlantic Canada apparently represent shallowest-water depositional settings, where such relatively uncommon environments have been sampled and where the complicating factor of downslope transport has been avoided.

The presence of relatively abundant *Mestognathus* in sediments that have clearly not been transported downslope or that have not been reworked appreciably permits the testing of the environmental hypotheses above. Such a situation may also exist, for example, in the Viséan carbonate rocks of the *Cyathaxonia* beds of North Wales from which Aldridge, Austin, and Husri (1968) recovered relatively abundant *Mestognathus*. The carbonate-depositing environments contrast noticeably with goniatite-bullion shale facies of the same age in the Republic of Ireland, from which these authors did not recover a single specimen of *Mestognathus*.

If, as discussed, *Clydagnathus* gave rise to *Mestognathus* and if there were really differences in the salinity (and ?depth) tolerances of the two genera, then it follows that the transition species between *Clydagnathus* and *Mestognathus* must have invaded and adapted to new environments during the early Tournaisian. The general agreement of various authors as to the relative position of *Mestognathus* in particular biofacies belts (a shelf versus a basinal

genus) suggests that the genus quickly attained environmental stability.

The interesting, but unlikely, possibility that Namurian *mestognathids* migrated from shallower-water (i.e., lagoonal) environments into inner-shelf and deeper-water settings was suggested by Higgins (1981, fig. 4.3). We suspect this interpretation to be the result of the lack of shallower-water environments available for sampling in Namurian sequences, as well as of possible reworking and downslope transport of sediment.

We agree with Higgins (1981) that *Mestognathus* was likely nekto-benthic, that is living on the shallow sea bottom and being influenced by its environmental factors during part of its life cycle, but likely swimming actively during another (?larval) stage. This hypothesized life cycle would explain the wide distribution of the genus on the one hand and its relative restriction to certain kinds of sediment, in particular depositional belts, on the other. We are unable to support the strictly nektonic interpretation of Belka (1983:82) for *Mestognathus*.

Our survey of those authors who previously attempted to group *Mestognathus* with possible ecologic associates in the same biofacies or conodont community indicates that all six authors agreed that *Cavusgnathus* was an environmental associate of *Mestognathus* (Table 2). In the case of *Taphrognathus*, agreement decreased to four authors, followed by three for each of the simple gnathodids, *Spathognathodus* (= *Hindeodus* and *Hindeodus?* of authors in part) and *Apatognathus*. Although all authors described a Viséan marine community, because the genus was, at the time, thought to be "essentially a Viséan form" (Druce, 1973), slight complications were introduced by Austin (1976, fig. 4), who, because of biofacies overlap and conodont occurrences in the British Viséan, interpreted *Patrognathus*, *Streptognathodus* [!], *Bispathodus*, *Polygnathus*, and *Pseudopolygnathus* to be part of the same biofacies as *Mestognathus*. Kalvoda (1983) attempted to formulate broad environmental generalizations for Early Carboniferous conodonts, using symmetry in the same manner as had Druce (1973), Merrill and von Bitter (1979), and Sandberg and Gutschick (1979). We suspect that Kalvoda's inclusion of *Clydagnathus*, *Cloghergnathus*, and *Laterignathus* in the same ecologic group is a reflection of the relatively broad interval of time for which he was attempting to generalize biologic events, of the likelihood that he has not worked firsthand with these conodont genera, and of the fact that he was attempting to put all "asymmetrical conodont genera" into one environmental niche.

DOWNSLOPE TRANSPORT

A complicating factor in evaluating the palaeoecologic aspects of *Mestognathus* is that many occurrences are in

rocks that formed as a result of downslope movement. The recognition of sediments that have undergone this type of transport poses the initial difficulty. This is compounded by the fact that the biologic components of a variety of environments (to say nothing of ages) may be mixed and therefore difficult to use for palaeoecologic and other analyses. For example, the fact that juvenile specimens of species of *Mestognathus* were until now undocumented can in large measure be attributed to sorting and destruction during downslope and other transport. Clearly, for palaeoecologic and other analysis it is desirable to eliminate those occurrences in which this type of transport has taken place and to concentrate on those occurrences in which *Mestognathus* is still in or near its original habitat.

We will, in the following section, document occurrences involving downslope transport.

Mestognathus harmalai sp. nov. occurs at locality 1 (Appendix) in Utah, 0.76 to 1.5 m above the base of a 2.1 m thick coarse crinoidal (= encrinitic) wackestone bed, the top of which is 13.4 m below the top of the Joana Limestone. The crinoidal wackestone bed is interpreted as a debris flow from a shallow-water setting surrounding a nearby island (Gutschick and Sandberg, 1983). The debris flow is intercalated in a sequence of thin-bedded micrites and crinoidal biomicrites that are interpreted as clinoform limestones. Processing of 29 kg of rock from this debris flow has yielded 1843 normal-size (0.5 to 1.0 mm) conodonts, with eight large (1.6 to 2.6 mm long; mean = 2.2 mm) specimens of *M. harmalai* sp. nov. Because they are unusually large, are mixed with smaller conodont species that are of slope origin (Sandberg and Gutschick, 1979), and are mostly badly corroded or have pieces broken off, the specimens of *M. harmalai* sp. nov. are interpreted to be the remaining individuals of the species that had the greatest distance of transport in the debris flow. Other elements of the fauna are mainly *Polygnathus communis communis*, with some *Bispathodus utahensis* and *Hindeodus* spp. (shallow-water or euphotic zone forms); and fewer specimens of *Hindeodella segaformis*, *Pseudopolygnathus multistriatus* morphotypes 1 and 2, and *Bactrognathus* sp. nov. Lane, Sandberg, and Ziegler (1980), all moderately deep-water or slope species, as interpreted by Sandberg (Sandberg and Gutschick, 1979; Lane, Sandberg, and Ziegler, 1980).

Mestognathus praebeckmanni sp. nov. is known from North America and Europe from rocks that are, like those in which *M. harmalai* sp. nov. occurs, best interpreted to have resulted from downslope movement of sediment. For example, van den Boogaard and Vazquez Guzman (1981:2,7), although believing their nine Spanish specimens of *M. beckmanni* (= *M. praebeckmanni* sp. nov. either entirely or in part by our interpretation) to have come from a shallow, nearshore, high-energy environment, nevertheless described the crinoidal limestones from which they

recovered them, together with other conodonts, as being "intercalated in a flysch sequence of slates and grey-wackes". We believe that it is more likely that this occurrence represents a debris flow, an interpretation that is not only more consistent with the data provided by van den Boogaard and Vazquez Guzman (1981), but also agrees with a slope to deeper-water origin postulated for Lower Carboniferous limestones in Spain (cf. Lane, Sandberg, and Ziegler, 1980:125) and with many of the environmental situations from which *Mestognathus* has been recovered elsewhere. A case in point involves the rocks from which *M. praebeckmanni* sp. nov. (and to some degree *M. beckmanni*) have been recovered at localities 2, 3, and 4 (Appendix) in Belgium and in Germany. At these localities, as at locality 1 (Appendix) in Utah, carbonate and fossil clasts are common in the limestones from which *Mestognathus* has been recovered. The specimens of *Mestognathus* are not only larger than the accompanying conodonts but are all of one size range, and conodonts of different environments (but not ages) are mixed. All the preceding interpretations suggest that at these localities upper-foreslope to shelf-margin rocks were transported downslope as debris flows.

Another European occurrence of *Mestognathus praebeckmanni* sp. nov. in transported sediments is documented by Belka (1983:82) in the Sosnowiec borehole of southern Poland (see synonymies for *M. groessensi* and *M. praebeckmanni* sp. nov. for our interpretation of the taxonomy of his faunas). Belka pointed out that the conodont fauna and the sediments are of an "allodapic nature" and concluded by interpreting the "*Mestognathus* setting" in this borehole to be the "result of seaward transported debris-flow".

Mestognathus praebeckmanni sp. nov. is known in North America only from two metamorphic terranes in British Columbia here referred to as the Cariboo and the Toodoggone occurrences. Their settings are remarkably similar to those of Spanish occurrences of *Mestognathus* documented by van den Boogaard and Vazquez Guzman (1981). In a number of the British Columbia samples (Appendix, localities 6–10), *M. praebeckmanni* sp. nov. occurs with *M. beckmanni*, although rocks containing these species are poorly exposed and highly metamorphosed. However, the unusual abundance of *Mestognathus* and its presence in an unexpected geologic setting (a highly metamorphosed terrane) create a special interest in examining some of the depositional factors of these occurrences.

The Cariboo occurrence (Appendix, localities 6–8) shows equivocal evidence for downslope movement of sediments (Orchard and Struik, 1985). Sample MC81/32A (the sample containing the most specimens of *Mestognathus*) is from locality 7 (Appendix), where bedding planes contain large articulated crinoid stems. The stems appear to be *in situ*, although *en masse* movement could have taken

place. Supporting the idea of *en masse* movement is the interpretation of the conglomerates of the Guyet Formation, underlying the limestones of the Greenberry Formation, as a debris flow. Of possible significance here are Sandberg's observations (Sandberg and Dreesen, 1984) of similar bedding-plane occurrences of articulated crinoid stems with broken transported horn corals in upper-slope settings of the Devonian Pinyon Peak Limestone in Utah.

The Toodoggone occurrences (Appendix, localities 9 and 10) involve *Mestognathus*-bearing carbonate rocks that probably were deposited in an island-arc system, although they show little evidence of biofacies mixing and/or downslope movement.

The preceding discussion regarding post-mortem transport of species of *Mestognathus*, although centred on occurrences of *M. harmalai* sp. nov. and *M. praebeckmanni* sp. nov., probably applies equally to many, but not necessarily all, occurrences of *M. beckmanni* and *M. bipluti*. Occurrences such as those described by Matthews and Thomas (1974) in southwest England are difficult to explain without invoking downslope post-mortem transport. These authors recovered *M. beckmanni* from Lower Carboniferous (cu II and cu III) rocks regarded as possible proximal and distal turbidites, an interpretation supported on sedimentologic and faunal grounds, such as conglomeratic limestones, much bioclastic debris, and reworked conodont faunas.

Mestognathus bipluti morphotype 2 is known only from the Namurian of North Staffordshire, England (Higgins, 1961, 1975) and is represented only by large specimens (A. C. Higgins, pers. comm., 1982). These youngest forms of the genus, like many of their predecessors, may also have been involved in current sorting and/or downslope movement. Higgins (1981:42) stated that "the majority of late Viséan and Namurian environments in NW Europe are of the basin variety consisting of black or grey shales and mudstones with thin argillaceous limestones near the base." This statement, considered together with descriptions of the type locality provided by Higgins (1975:86,87), suggests that *M. bipluti* morphotype 2 was recovered from deeper-water sediments. The restricted size range of this form and the fact that it composes less than 10 per cent of the fauna (Higgins, 1975, fig. 4.3), taken together with the rock types yielding this species, support the interpretation that these youngest *mestognathids* lived on a shallow shelf, but that their remains were transported and redeposited downslope into deeper water.

ENVIRONMENTAL HYPOTHESES

The preceding discussions of palaeoecology and downslope transport suggest the following concerning the probable habitat of *Mestognathus* (see Text-fig. 4 for a partial summary of these hypotheses):

- a) *Mestognathus* lived mainly in harsh, nearshore,

shallow-water, hypersaline marine environments. It may also have been tolerant of nearshore brackish-water environments.

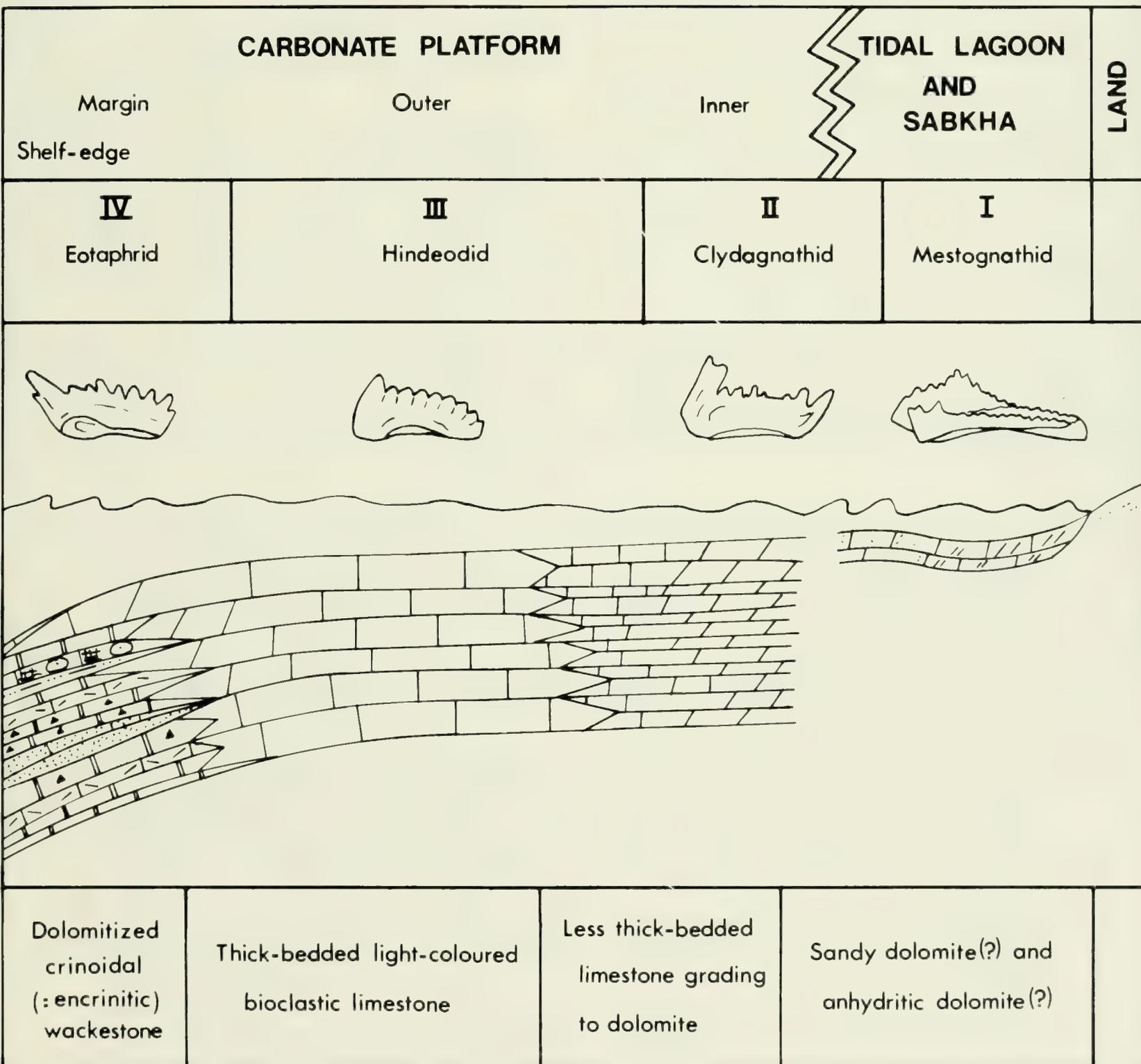
b) *Mestognathus* lived mainly above light-coloured, well-oxygenated, aerated ocean bottoms. It may also have been tolerant of dark, restricted, lagoonal bottom sediments.

c) *Mestognathus* apparently inhabited an even more nearshore environment than its *Clydagnathus* ancestor and migrated landwards concurrently with the demise of *Patro-*

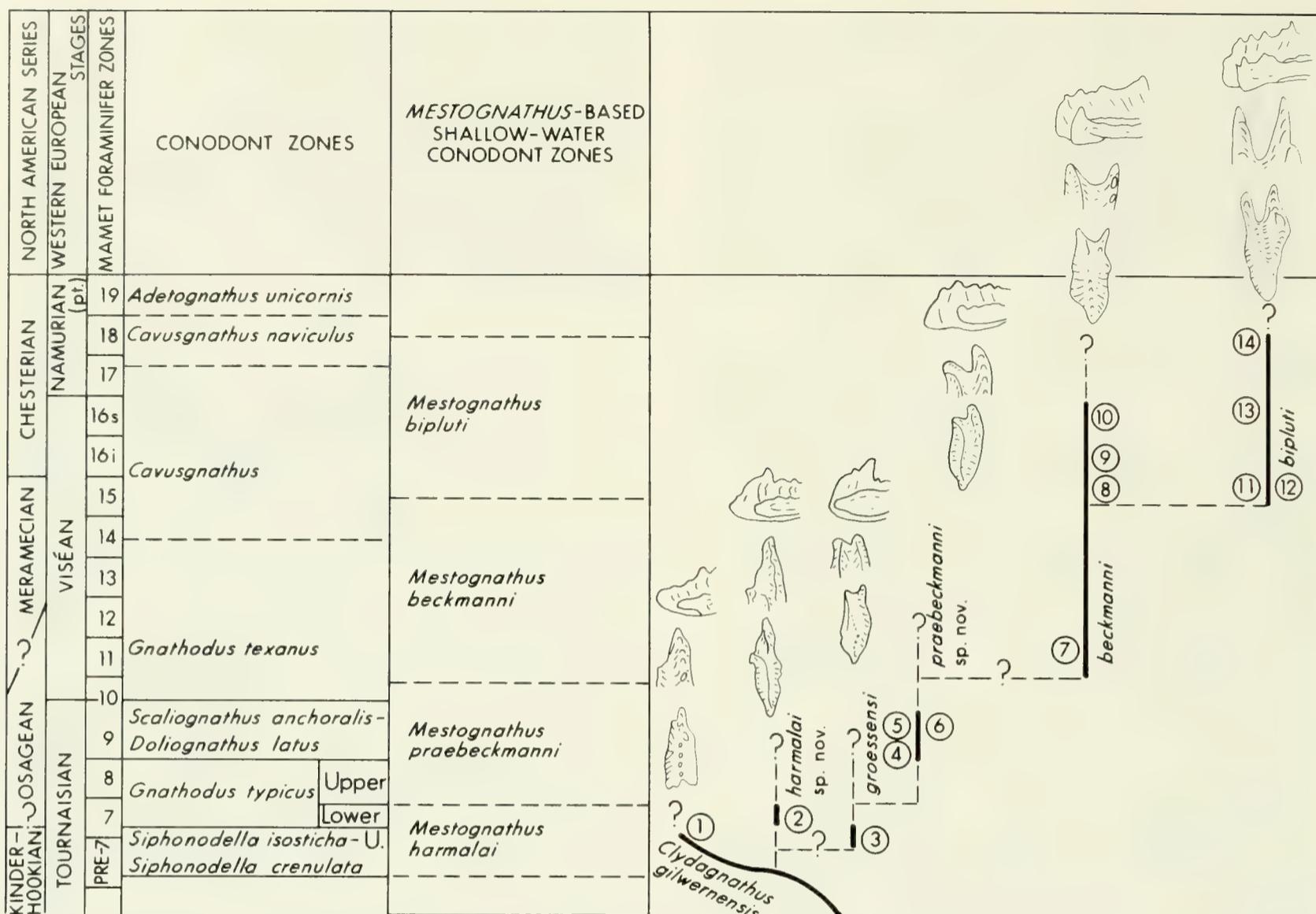
gnathus, a genus that occupied a more nearshore patrognathid-pandorinellinid biofacies. This hypothesis is based on a biofacies model of the Lower *Siphonodella crenulata* Zone (Sandberg and Gutschick, 1983).

d) *Mestognathus* appears to have lived mainly in tidal lagoons in sabkha belts along the coastlines of continents, as well as around islands and atoll lagoons in volcanic areas.

e) The habitat of *Mestognathus* appears to have changed and diversified through time.



Text-fig. 4. *Mestognathus* biofacies in the tidal lagoon and sabkha biotope. Adapted from Sandberg and Gutschick (1984, fig. 14).



Text-fig. 5. Phylogeny and speciation of *Mestognathus* based on biostratigraphically significant occurrences of species of the genus and of transitions within the genus.

1. Canadian occurrence of *Clydagnathus gilwernensis*–*Mestognathus harmalai* sp. nov. evolutionary transition at locality 12 (Appendix), 10 m above an occurrence of *Siphonodella isosticha*. Sketches based on GSC 68885 (Pl. 7, figs. 6,8–10).

2. American occurrence of *M. harmalai* sp. nov. at locality 1 (Appendix), with *Pseudopolygnathus multistriatus* morphotypes 1 and 2 (Lane, Sandberg, and Ziegler, 1980), 18 m below the lowest occurrence of *Pseudopolygnathus oxypageus* which marks the base of the Upper *Gnathodus typicus* Zone. Sketches based on paratype USNM 257754 (Pl. 6, fig. 6) and 257755 (Pl. 6, fig. 3).

3. Polish occurrence of holotype of *M. groessensi* Belka at depth of 125 m in borehole WB-64 near Olkusz, with fauna of *Siphonodella isosticha*–Upper *S. crenulata* Zone and of early form of *M. groessensi* at depth of 165 m (in same hole), with *Gnathodus delicatus*, *G. punctatus*, and *G. typicus* morphotype 1, of Lane, Sandberg, and Ziegler (1980), somewhat below the last occurrence of *Siphonodella isosticha* (Belka, 1983:75). Sketches based on illustrations of holotype of *M. groessensi* (Belka, 1983, pl. 1, figs. 1a–c) (here reproduced as Pl. 1, figs. 26–28).

4. Spanish occurrence (van den Boogaard and Vazquez Guzman, 1981) of early morphotype of *M. praebeckmanni* sp. nov. with *Protognathodus cordiformis* and *Hindeodella segaformis* which range from the highest part of the Upper *Gnathodus typicus* Zone into the *Scaliognathus anchoralis*–*Doliognathus latus* Zone.

5. Belgian occurrence of *M. praebeckmanni* sp. nov. at locality 2 (Appendix) just above *Doliognathus latus* and *Hindeodella segaformis* in the highest Tournaisian (Tn_{3c}). Based on sample BEL-5 which is equivalent to sample 60 of Groessens (1971, log 6).

6. German occurrence of *M. praebeckmanni* sp. nov. at locality 3 (Appendix) with *Scaliognathus anchoralis europensis*. Based on sample GER-80-1 which is equivalent to sample 58 of Stoppel (in Paproth, Stoppel, and Conil, 1973:62–65,135). Sketches based on paratype USNM 257758 (Pl. 8, figs. 5,6).

7. German occurrence of *M. beckmanni* at locality 4 (Appendix) with *Gnathodus* cf. *G. bilineatus*, *G.*

THE VALIDITY OF BIOFACIES INTERPRETATIONS AND HYPOTHESES

Metcalf (1981) recorded what is probably the largest number (271) of mestognathids previously reported in a single study. These collections, from Viséan V_{1a} – V_{3c} (Chadian to Brigantian stages) strata of the Craven Lowlands of northern England, contained 250 and 21 specimens assigned by Metcalfe to *Mestognathus beckmanni* and *M. cf. M. beckmanni*, respectively.

This unusually large collection of mestognathids, from a field area other than our own, allows us to evaluate our palaeoecologic interpretations and hypotheses. Before doing this, however, we need to determine what we are examining, that is, what the species composition is of Metcalfe's mestognathid faunas.

It is difficult to assess whether or not all 21 specimens of *Mestognathus cf. M. beckmanni* (Metcalf, 1981) are assignable to *M. beckmanni*, since Metcalfe (1981:33) differentiated them from *M. beckmanni* mainly because of their slightly larger basal cavities, an ontogenetically variable feature. On his summary range chart (1981, fig. 10), the lowest occurrences of *M. beckmanni* and *M. cf. M. beckmanni* coincide. However, in his tables Metcalfe (1981, tables 14, 15) showed three specimens of *M. cf. M. beckmanni* as occurring below the lowest *M. beckmanni* in the Chadian Thornton Limestone. These three specimens, although not illustrated, may be *M. praebeckmanni*

sp. nov. The single illustrated specimen of *M. cf. M. beckmanni* (Metcalf, 1981, pl. 8, figs. 3a–c) from the upper part of the Thornton Limestone is indeed *M. praebeckmanni* sp. nov. and must represent one of the late occurrences of this species with *M. beckmanni* (Text-fig. 5). Therefore, we assume that only a few specimens (certainly one, and possibly three more) represent *M. praebeckmanni* sp. nov. and consider the remaining 267 specimens to be *M. beckmanni*.

The area studied by Metcalfe (1981) is one of fault-block basins with shallow-water Waulsortian carbonate mounds developed on upthrown blocks in close proximity to moderately deep-water shale basins on downthrown blocks (Miller and Grayson, 1982). This twofold depositional regime makes it possible to separate those mestognathids that were in all probability transported into the deeper basinal areas from those in or close to their inferred original shallow-water habitat on or around Waulsortian mounds.

Examining those occurrences in which mestognathids appear to have been transported, we note first that sample 135 with 60 specimens of *Mestognathus beckmanni* (only 5 per cent of a large fauna of platform conodonts) and sample 138 with 17 specimens (49 per cent of the platform conodonts) are from thin limestone interbeds in the Cephalopod shales (Metcalf, 1981, table 11). Our knowledge of cephalopod shales worldwide suggests that these represent deep-water basinal rocks with introduced limestone beds

pseudosemiglaber, and *G. homopunctatus* in the middle part of the *Scaliognathus anchoralis*–*Gnathodus bilineatus* interregnum (= lower to middle Meramecian). Based on sample GER-80-5, which is equivalent to sample 11 of Stoppel (in Paproth, Stoppel, and Conil, 1973:70,138).

8, 11. Canadian occurrences of *M. beckmanni* and *M. bipluti* at localities 13 and 14 (Appendix) with *Clydagnathus windsorensis*. Based on samples Fisher-2-1 and St. Cr-2-4 from the Fisher and St Croix members, respectively, the megafauna and stratigraphic position of which have caused it to be placed in the B Subzone of Bell (1929), Moore and Ryan (1976), and Moore (in Geldsetzer et al., 1980). Mamet (1970, fig. 4) correlated the B Subzone with foraminiferal zone 15.

9. German occurrence of *M. beckmanni* at locality 3 (Appendix) with unequivocal *Gnathodus bilineatus* and *Cavusgnathus* sp. Based on sample GER-80-8 which is equivalent to sample 22 of Stoppel (in Paproth, Stoppel, and Conil, 1973:70,138). Sketches based on USNM 257759 (Pl. 16, fig. 1) and 257760 (Pl. 16, fig. 9).

10, 13. Canadian occurrences of *M. beckmanni* and *M. bipluti* at locality 17 (Appendix) with *Gnathodus bilineatus*, *G. girtyi*, *Paragnathodus scotiaensis*, *Vogelgnathus? campbelli*, *Apatognathus* sp., *Ozarkodina laevipostica*, and *Cavusgnathus? sp.* Based on sample WaPt-1-3 from the type section of the Wallace Point Member. The megafauna and stratigraphic position of this unit have caused it to be placed in the lowest part of the E Subzone of Bell (1929), Moore and Ryan (1976), and Moore (in Geldsetzer et al., 1980). Mamet (1970, fig. 4) correlated this part of the E Subzone with foraminiferal zone 16s. Sketches based on ROM 43422 (Pl. 18, fig. 10; Pl. 24, fig. 1).

12. German occurrence of *M. bipluti* at locality 4 (Appendix) just below lowest unequivocal *Gnathodus bilineatus*. Sample 19 of Stoppel (in Paproth, Stoppel, and Conil, 1973:70,138) (*Mestognathus* species identification by D. Stoppel).

14. English occurrences of *M. bipluti* morphotype 2, in North Staffordshire, northern England (Higgins, 1961, 1975). Higgins (1975, figs. 3,6) shows the range of *M. bipluti* ending within the range of *Cavusgnathus naviculus*, thus placing its highest occurrence in the *C. naviculus* Zone of our usage.

containing the conodonts. We have thus accounted for the probable origin of 77 *M. beckmanni*, plus 5 others in two smaller samples. Similarly, sample 207, with 17 specimens (19 per cent of the platforms) from another thin limestone in a shale sequence (Metcalf, 1981, table 3), plus an additional 55 specimens from 21 smaller collections, have the same association at the same locality and are regarded by us as transported.

By having considered the samples containing the three largest collections of *Mestognathus beckmanni*, plus lithogenetically similar smaller collections from the same locality, we have reduced the number of potentially indigenous specimens to 113 (267–154). This number can be further reduced to 104 by subtracting 9 more specimens present in three smaller collections (Metcalf, 1981, tables 5, 10). Some of these 104 specimens are widely disseminated in occurrences of one or two per sample and thus are not useful for biofacies analysis.

The only occurrences of apparently untransported *Mestognathus beckmanni* are represented by sample 195 (Thornton Limestone, 21 specimens); sample 374 (Thornton Limestone, 9 specimens); samples 57, 58, 59, and 193 (Butterhaw Limestone, 27 specimens); and samples 100, 140, 141, 142, and 189 (Salt Hill Cap beds, 16 specimens).

The 73 *Mestognathus beckmanni* that we consider to be palaeoecologically important come from only three stratigraphic units—the Thornton and Butterhaw limestones and the Salt Hill Cap beds. These units contain lithologies that we interpret to have been deposited in the original habitat of *M. beckmanni*. Both the Thornton Limestone and Salt Hill Cap beds (Metcalf, 1981, figs. 5,9) appear to be shallow-water carbonate rocks laterally adjacent to or capping bank or reef facies and thus probably associated with Waulsortian mounds. We are unable to interpret the Butterhaw Limestone occurrence from the sparse stratigraphic evidence presented by Metcalf (1981:4).

In summary, we believe the Craven Basin mestognathid occurrences to be in harmony with our own interpretations and hypotheses of the habitat of *Mestognathus*. We consider the *M. beckmanni* faunas recorded by Metcalf (1981) to have lived in shallow-water environments and to have been often transported secondarily downslope into adjacent moderately deep-water basins. To what degree hypersaline environments existed in the Craven Basin is unknown; we do note, however, that Miller and Grayson (1982, fig. 3) in their discussion of this basin show sabkha, evaporite, dolomite, and shallow marine limestone immediately adjacent to a Waulsortian mound complex.

Geographic Distribution

The distribution of the 26 areas of today's world from which species of *Mestognathus* are known is shown in Text-figure 6 (labelled A–Z). In many cases the dots represent many individual samples, in others only one. To some extent the distribution reflects the amount of work done in various parts of the world, and for that reason Europe is well represented. In contrast, the Cordilleran region of North America has only recently been widely sampled for conodonts, and the several locations are a result of this search. Similar attention elsewhere in the world may be expected to reveal new locations for species of *Mestognathus*. For example, the main part of the huge Asian landmass not only has no reported occurrences of *Mestognathus*, but also has only a single reported Carboniferous conodont fauna that might be expected to contain this genus.

An adaptation of the continental reconstruction of Tarling (1980) for the Carboniferous world of *Mestognathus*, excluding only the Asian landmass, is shown in Text-figure 7. This generalized portrayal differs from other reconstructions of the same age in regard to separation of Cordilleran North America. Current theory holds that this region is a collage of crustal fragments (accreted terranes) that originated in a position far removed from their present one (Coney, Jones, and Monger, 1980). The map is a gross

simplification since in Carboniferous time (e.g., Ross and Ross, 1983), and for a long period of time afterwards (e.g., Tozer, 1982), the component parts are envisaged as having been spread over much of the present Pacific region. However, the point is that at least one *Mestognathus* locality in western North America is thought to have been originally far removed from its present docking site. The Toodoggone occurrence of *Mestognathus* (Text-figs. 6 and 7, V) is situated at the eastern edge of Stikinia, a terrane located at 10°–30°S during the Carboniferous (Ross and Ross, 1983:18). Little is known of the Alaskan locality (Text-figs. 6 and 7, W) in terms of its likely origin. The western Utah occurrence (Text-figs. 6 and 7, T) is located near the southern part of two islands on a submarine rise within the Antler foreland trough and thus well on the mid-Mississippian North American continent (Sandberg and Gutschick, 1984, figs. 1,2, locality PC). The other Cordilleran occurrence (the Cariboo localities, Text-figs. 6 and 7, U) is situated at the Carboniferous continental margin, and its original position with respect to cratonic North America is uncertain. Thus the considerable spread in latitude of the four localities along the North American Cordillera is much reduced.

The 26 currently known occurrences of *Mestognathus*, plotted on an Early Carboniferous (Viséan) world map on

which the North American Cordillera is shifted southwards, lie entirely in the southern hemisphere, except for the Cariboo, British Columbia, and northern Alaska occurrences (Text-fig. 7, U and W). Even if these two occurrences are correctly positioned in the northern hemisphere, all known *Mestognathus* occurrences fall within a moderately narrow equatorial belt lying between latitudes 40°S and 25°N. This narrow latitudinal range is in accordance with our observation that all Late Devonian (Sandberg and Poole, 1977) and Early Carboniferous (Mississippian) conodont occurrences are from relatively low (tropical to low temperate) latitudes and contrast with Ordovician occurrences, which extend into boreal latitudes. This early to middle Palaeozoic change in conodont habitat may be only apparent, because during the Early Carboniferous more northerly and more southerly regions of the world were mainly parts of continental landmasses that now contain few, if any, marine deposits. For example, the existence of a southern or Gondwana landmass (Text-fig. 7) explains the apparent absence of *Mestognathus* or any other Mississippian conodont occurrences in more southerly latitudes, including all of South America and most of Africa. Similarly, the postulated existence of a northern landmass (a continuation in time of the Devonian Old Red continent) explains the absence of *Mestognathus* and other Mississippian conodont occurrences from Scandinavia, Greenland, and northern Canada. Focusing on the reconstructed distribution of *Mestognathus*, we see that it occurs in almost all regions where marine Lower Carboniferous (Mississippian) rocks have been studied, with two possible exceptions: the central Asian platform and North American Midcontinent regions. Consequently, *Mestognathus* appears to have a cosmopolitan or widespread distribution rather than an endemic or restricted distribution, as was suggested by Druce (1973:206,207) and Higgins (1981).

On the central Asian platform (not shown on Text-fig. 7 because of lack of palaeomagnetic data, but lying to the right of the mapped area), only one conodont fauna within an age range that might be expected to contain *Mestognathus* has been reported to our knowledge. This fauna from East Kazakhstan, described and illustrated by Aristov and Alekseev (1976), is assignable to the *Scaliognathus anchoralis*-*Doliognathus latus* Zone. The fauna lacks *Mestognathus* but does contain a mestognathid-like cavusgnathoid genus, *Laterignathus*. The two illustrated upper views of *Laterignathus barskovi* (Aristov and Alekseev, 1976, figs. 12a,13a) suggest that this species is close in

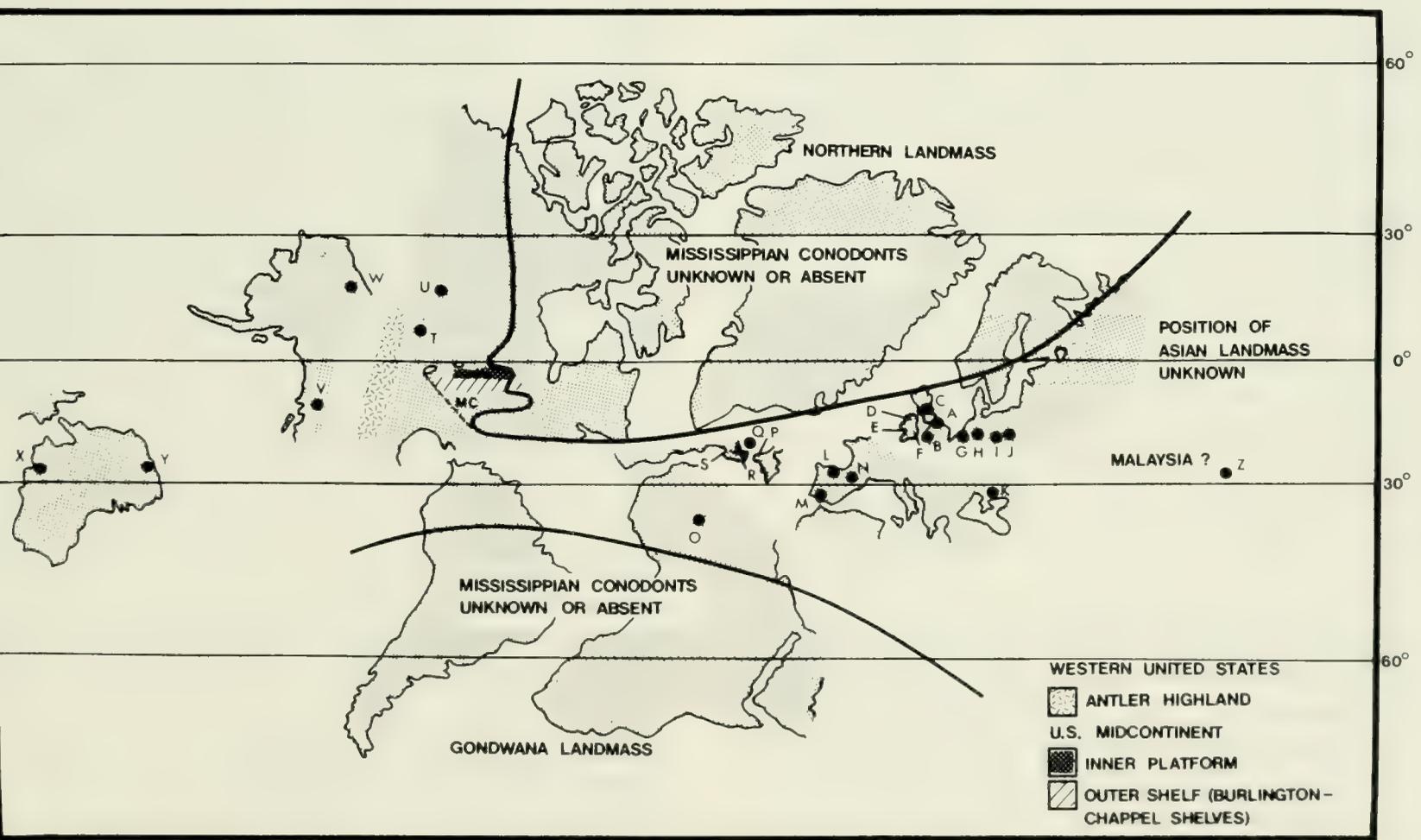
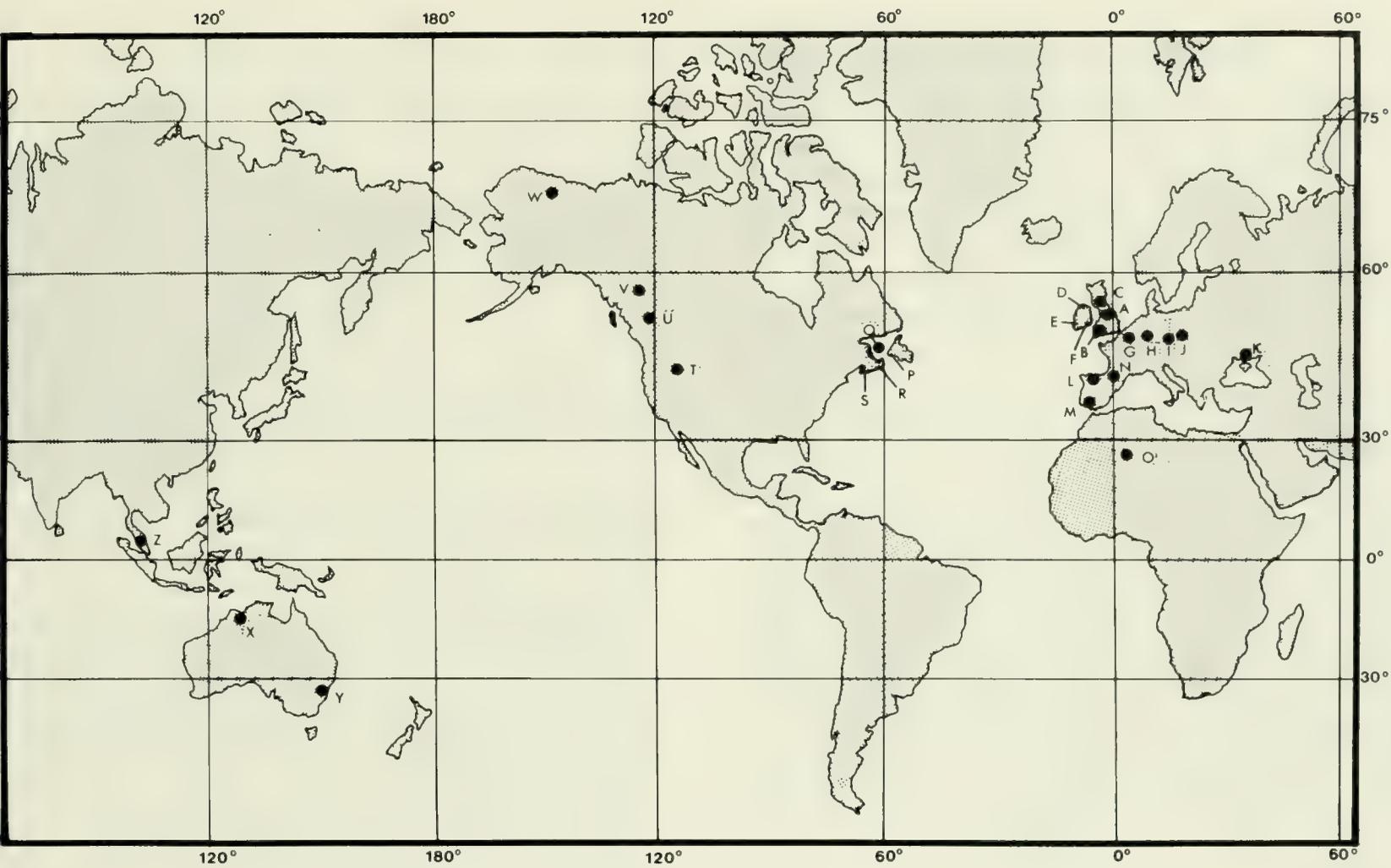
gross morphology to *M. groessensi* or *M. praebeckmanni* sp. nov., except that it has upper-surface ornamentation consisting of nodes or nodose transverse ridges instead of sharp-crested transverse ridges. The illustrations of *L. barskovi* are not of sufficient quality to ascertain whether the carina bends anteriorly to reach the left margin; consequently, possible assignment of this species to *Mestognathus* is equivocal. Thus in central Asia, where only a single information point exists for a vast region, the existence of *Mestognathus* can neither be proved nor disproved.

The apparent absence of *Mestognathus* from the North American Midcontinent region can be explained in two ways, using the bathymetric-palaeocurrent and lithofacies reconstructions of Gutschick and Sandberg (1983, figs. 5,6) for southern North America during the time of the *Scaliognathus anchoralis*-*Doliognathus latus* Zone. The first explanation is that the only area where *Mestognathus* might be expected to occur, on the basis of our palaeoecologic interpretation of its habitat, is on the inner carbonate platform along the south side of the Transcontinental arch. The Midcontinent region (Text-fig. 7, MC) extended only as far west as indicated by the dashed line on Text-figure 7. In the north it was bordered by the peninsula and islands of the Transcontinental arch, whereas in the south its limit was defined by the Appalachian highlands. The area represented an embayment into the Old Red continent and was occupied by only a small part of the world's Early Carboniferous (Mississippian) seas. Mississippian rocks of the inner carbonate platform, shaded in Text-figure 7, are almost entirely in the subsurface, and only a few published reports (e.g., Thompson and Goebel, 1969; Klapper, 1971) deal with Mississippian conodonts from well cores in this area. Hence, data are insufficient to support or deny this possibility. The second explanation is that the Midcontinent region was somewhat, but not completely, isolated and that *Mestognathus* was excluded not by a land bridge (Higgins, 1981, fig. 4.5), but by oceanic current circulation, as suggested by the current patterns shown by Gutschick and Sandberg (1983, fig. 6). We conclude that the apparent absence of *Mestognathus* from the central Asian platform and the American Midcontinent can be attributed either to insufficient sampling (in part of the environment in which *Mestognathus* lived) or to more local palaeoecologic factors. The distribution of the conodont genus *Mestognathus* in the Carboniferous marine world (Text-fig. 7) was probably cosmopolitan rather than provincial in nature.

Text-fig. 6. *Mestognathus* distribution as presently known from published and unpublished sources.

- A. North and west-central England, North Wales, and Isle of Man—Higgins (1961, 1975); Aldridge, Austin, and Husri (1968); Reynolds (1970); Austin and Aldridge (1973); Austin (1974); Metcalfe (1980, 1981).
- B. Southwest England and South Wales—Rhodes, Austin, and Druce (1969); Butler (1973); Austin (1974); Matthews and Thomas (1974); Varker and Sevastopulo (1985).
- C. Central Scotland—Rhodes, Austin, and Druce (1969).
- D. Northern Ireland—Austin (1974); Austin and Mitchell (1975).
- E. Southwest Republic of Ireland—Austin and Husri (1974).
- F. East-central Republic of Ireland—herein, locality 5 (Appendix); I. S. Johnston (ms., 1985).
- G. Belgium—Groessens (1971, 1974); Groessens, Conil, and Lees (1973); Conil, Groessens, and Lys (1973); Groessens and Noel (1974); Bless et al. (1976); herein, locality 2 (Appendix).
- H. Federal Republic of Germany—Bischoff (1957); Voges (1959); Meischner (1970); Witten (1979); Park (1983); herein, localities 3 and 4 (Appendix).
- I. Moravia, Czechoslovakia—Kalvoda (1983).
- J. Poland—Gromczakiewicz-Lomnicka (1974); Chorowska (1978); Matyja and Narkiewicz (1979); Skompski and Sobon-Podgorska (1980); Belka (1983, 1985).
- K. Ukraine—Kozitskaya et al. (1978).
- L. Northern Spain—Marks and Wensink (1970); Higgins (1974); Buchroithner (1979); Higgins and Wagner-Gentis (1982).
- M. Southern Spain and southern Portugal—van den Boogaard (1963); Higgins (1974); van den Boogaard and Vazquez Guzman (1981); Herbig (1984).
- N. Southern France—Perret (1977).
- O. Algeria—Remack-Petitot (1960).
- P. Southwestern Newfoundland, Canada—von Bitter and Plint-Geberl (1982); herein, localities 23 and 24 (Appendix).
- Q. Magdalen Islands, Quebec, Canada—Plint-Geberl (1982); Plint and von Bitter (1986); von Bitter and Plint (in press); herein, locality 22 (Appendix).
- R. Cape Breton Island and northeastern Nova Scotia, Canada—Globensky (1967); von Bitter (1976); herein, localities 19–21 (Appendix).
- S. Southwestern Nova Scotia, Canada—Globensky (1967); von Bitter (1976); von Bitter and Plint-Geberl (1982); herein, localities 13–18 (Appendix).
- T. Utah, United States—herein, locality 1 (Appendix).
- U. East-central British Columbia, Canada—Orchard and Struik (1985); herein, localities 6–8 (Appendix).
- V. Northern British Columbia, Canada—herein, localities 9 and 10 (Appendix).
- W. North-central Alaska, United States—herein, locality 11 (Appendix). [Dr Anita Harris, USGS, Washington (pers. comm., 1985), has indicated the existence of other, additional, occurrences of *Mestognathus* in Alaska.]
- X. Northern Australia—Druce (1969).
- Y. Southeastern Australia—Jenkins (1974).
- Z. Malaysia—Metcalfe (1983).

Text-fig. 7. The Early Carboniferous world showing occurrences of *Mestognathus*. Reconstruction of continents based, in part, on Tarling (1980). Position and configuration of western North America is grossly simplified (e.g., see Ross and Ross, 1983). Note the relatively small size of the American Midcontinent (MC) compared to the European–African and western North American–Asian regions. Palaeogeography of the American Midcontinent is based on Lane (1982), Lane and Ziegler (1983), and Gutschick and Sandberg (1983, fig. 5). Letters A–Z correspond to localities in Text-figure 6.



Late Viséan and Early Namurian Conodont Provincialism?

The absence of *Mestognathus* from the North American Midcontinent region was cited by Higgins (1981) as important evidence for the provincialism of late Viséan to early Namurian conodonts and for their separation into Eurasian faunas, containing *Mestognathus* and Midcontinent faunas lacking *Mestognathus*. We not only doubt that *Mestognathus* was a provincial taxon but are sceptical about some of the evidence, physical and biologic, that has been presented to demonstrate the existence of conodont provincialism during this part of the Carboniferous.

The interpretation of Higgins (1981), following Gordon (1974), was that continuous Appalachian and Llanorian highlands sealed off the Midcontinent region on the south. However, the North American Midcontinent region, mapped and named the Eastern Interior foreland trough by Gutschick and Sandberg (1983, figs. 5,6), was, according to their continental reconstructions, open at its south end. Furthermore, the closing of this trough, by formation of the Ouachita (Llanorian of Higgins, 1981) highlands, as a result of convergence of the South American and North American plates, did not take place, according to Ross

(1979), until latest Pennsylvanian or Permian time.

A second, biologic, basis for the provincialism recognized by Higgins (1981) was the distribution of the gnathodids. For example, in his discussion of *Gnathodus homopunctatus* he stated (1981:40): "Outside Europe it is known only from Japan...and from the St. Genevieve Formation of the Illinois Basin." However, this species is now known to be both abundant and ubiquitous in latest Meramecian to Chesterian faunas of the Great Basin and Rocky Mountain regions of the western United States. For example, Tynan (1980) illustrated *G. homopunctatus* and tabulated its occurrence in his faunas. The widespread distribution of this species in North America may be especially significant because it is apparently an ecologic associate of *Mestognathus* in Belgium.

Although we concede that there is some evidence for endemism between the faunas of the Midcontinent and Cordilleran regions of North America, we conclude that statements concerning geographically separated Eurasian and Midcontinental faunas are attributable, in large part, to biofacies differences.

Phylogeny, Phyletic Gradualism, and Speciation

The morphologic features that define the five recognized species of *Mestognathus* develop through time in an apparently orderly gradualistic manner (Text-fig. 5).

The morphology of the left anterior part of the platform, the parapet area (Sandberg and Ziegler, 1973, 1979), was used by Bischoff (1957:36) in his diagnosis of the genus and continues to be the most important criterion for differentiating species of *Mestognathus*. The gradual morphologic change in the parapet area through time allows us to recognize five species.

The degree of development of the anterior notch, commonly best seen in lower view, is also useful in distinguishing the five species of *Mestognathus*. *M. harmalai* sp. nov. lacks a well-developed anterior notch. This morphologic feature is slightly developed in *M. groessensi* and slightly to moderately well developed in *M. praebeckmanni* sp. nov. The anterior notch is deeper in *M. beckmanni* and reaches its fullest development in *M. bipluti*.

Closely related to the phylogenetic development of an anterior notch is the presence of increasingly fixed and decreasingly free blades in younger *Mestognathus* species. *M. harmalai* sp. nov. has only a short (or no) fixed blade and a long free blade. *M. groessensi* and *M. praebeckmanni* sp. nov. have a mostly fixed anterior blade, with only a very short free blade. *M. beckmanni* and *M. bipluti* have long fixed blades and short free blades.

Also closely related to the development of an anterior notch is the variable development of a secondary keel, containing a basal groove, on the lower surface of mestognathid species. The older pre-Viséan species, *Mestognathus harmalai* sp. nov. and *M. groessensi*, lack a secondary keel and a basal groove. Morphotypes 2 and 3 of *M. praebeckmanni* sp. nov. have a weakly developed secondary keel but lack a basal groove. Viséan and younger mestognathid species possess a well-developed secondary keel, but with a basal groove that is not consistently developed (or at least is not observable in all specimens) and apparently becomes variably "blind" with maturity rather than with phylogeny.

The final morphologic feature useful in differentiating species of *Mestognathus* is the basal cavity, a structure that changes slowly and predictably in size and degree of eversion through the range of the genus. Mature specimens of *M. harmalai* sp. nov., *M. praebeckmanni* sp. nov., and probably *M. groessensi* have noticeably larger, only slightly everted basal cavities, with a large well-defined basal pit. Mature specimens of the younger *M. beckmanni* and *M. bipluti* have strongly everted basal cavities, with only a tiny basal pit remaining.

INTERSPECIFIC AND INTRASPECIFIC VARIATION IN *MESTOGNATHUS*

The degree and subtlety of variation between and within several of the species of *Mestognathus* is noteworthy.

M. praebeckmanni sp. nov., for example, shows evidence of gradual evolutionary change *within* a species. We recognize three successively younger morphotypes of *M. praebeckmanni* sp. nov. (Text-fig. 8). Each succeeding morphotype shows not only a slightly deeper anterior notch, but also successive gradual changes in the detailed morphology of the parapet, including the development of an adcarinal trough exit, the lateral notch, in *M. praebeckmanni* sp. nov. morphotypes 2 and 3.

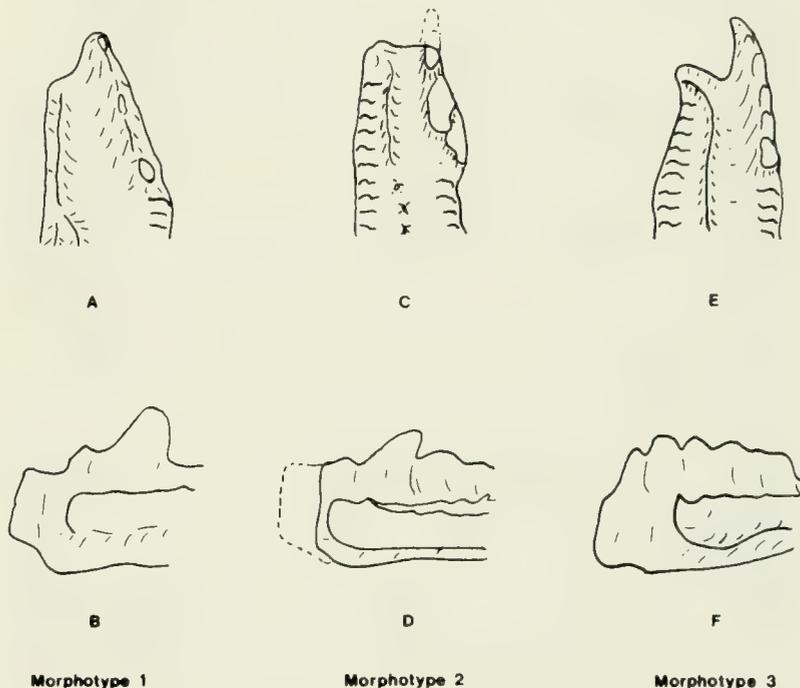
Mestognathus beckmanni transitions with *M. praebeckmanni* sp. nov. occur with *M. beckmanni* and *M. bipluti* in Atlantic Canada and are referred to *M. cf. M. beckmanni* in Table 3 and elsewhere. These transitional specimens, recognized by their low parapets (Pl. 23, figs. 1,2), may, after further study, be assignable to *M. praebeckmanni* sp. nov. Co-occurring populations of *M. praebeckmanni* sp. nov. and *M. beckmanni* are suspected to have been present in the Craven Basin of northern England (Metcalf, 1981) and in Belgium (Conil, Groessens, and Lys, 1973), and we would expect considerable intergradation between these two species in these areas.

Interspecific gradation at the ontogenetic level is well developed in coexisting Viséan *Mestognathus beckmanni* and *M. bipluti* from Atlantic Canada and immature specimens of these two species, shorter than approximately 0.3 mm, cannot be differentiated from one another. The critical parapet structures only begin to differentiate in individuals larger than this—in *M. beckmanni* by the gradual development of a large parapet denticle and in *M. bipluti* by the incremental formation of a spatulate parapet.

Coexisting populations of *Mestognathus beckmanni* and *M. bipluti* from Atlantic Canada also often contain relatively mature specimens whose parapet characteristics are not so clearly defined that one can easily and automatically assign them to one or the other species. Examples of this are the almost mature *M. beckmanni* with a slightly too large denticle anterior to the main parapet denticle or the moderately large *M. bipluti* with a spatulate parapet that is small and not particularly denticulate. The characteristics of such individuals may on one hand be due to ontogeny, in that the specific parapet structure may not yet have developed. Alternatively it may be due in part to phyletic or

evolutionary intergradations of *M. beckmanni* and *M. bipluti* as proposed by Belka (1983:76,79) for Polish Viséan mestognathid populations.

Mestognathus bipluti, like *M. praebeckmanni* sp. nov., shows noticeable intergradation within a species. Viséan populations of *M. bipluti* from Atlantic Canada, Poland, Belgium, and elsewhere are smaller and have a less massive and less denticulated parapet (morphotype 1) than does their Namurian descendant, *M. bipluti* morphotype 2, presently known only from North Staffordshire, England.



Text-fig. 8. Upper and left lateral views of the three successively younger morphotypes of *M. praebeckmanni* sp. nov. Note gradual deepening of the anterior notch and the development of an adcarinal trough exit. Presently unknown if the gradual suppression of the anterior blade cusp from morphotype 1 to morphotype 3 is consistent.

A,B. TCD 23164 and 23162, respectively, locality 5 (Appendix). Sketches based on Pl. 9, figs. 6,10.

C,D. Holotype, USNM 257757, locality 2 (Appendix). Sketches based on Pl. 8, figs. 1,4,10.

E,F. Paratype, USNM 257758, locality 3 (Appendix). Sketches based on Pl. 8, figs. 5,6.

Phylogenetic Relationships

Mestognathus probably evolved from *Clydagnathus gilwernensis* (Rhodes, Austin, and Druce, 1969, pl. 2, fig. 1), a species that had a completely right-sided blade, a posterior carina extending anteriorly at least past midlength of the platform, and a rounded parapet area (Druce, 1969, pl. 4, figs. 2–4; Savage, 1982, pl. 1, figs. 17–28). The change from *C. gilwernensis* to *M. harmalai* sp. nov. was

accomplished by the bending of the carina towards the left margin anteriorly and by slight eversion of the basal cavity. In fact, we have observed specimens transitional between the two species (Pl. 7, figs. 6–10) that closely approach *M. harmalai* sp. nov. (Pl. 6, fig. 7).

Aristov and Alekseev (1976) stated that *Mestognathus* “is related, through a number of intermediate forms, to the

Table 3. *Mestognathus* species composition and abundances, Atlantic Canada.

	<i>M. bipluti</i>	<i>M. beckmanni</i>	<i>M. spp.</i> (juveniles)	<i>M. spp.</i>	
Locality 13					
Fisher-2-1	3*	5	0	5	
Bel-2-3	2*	0	0	2	
Locality 14					
Went-1-1	0	0	0	1	
St.Cr-2-4	2	1†	0	0	
St.Cr-2-5	0	2(1†)	0	1	
Locality 15					
Hb-1-5	2	0	0	0	
Hb-1-6	1	0	1	1	
Hb-1-7	8	3	2	4	
Hb-1-8	0	0	0	2	
Locality 16					
Avn-1-4	6*	0	0	0	
Avn-1-5	6*	0	0	0	
Locality 17					
WaPt-1-1	0	1	0	0	
WaPt-1-2	4	0	1	5	
WaPt-1-3	21	5	6	8	
Locality 18					
Mosh-15-1	0	0	1	0	
Clov-13-4	0	1‡	0	0	
HerbR-8-4	0	1	0	0	
HerbR-8-5	2	2‡	0	0	
HerbR-7-7	7	42(10‡)	4	14	
Avn-5-1	14	6(3†, 2‡)	5	1	
MeaR-4-1	0	0	0	1	
MeaR-4-3	0	0	0	2	
WaPt-3-2	3	3(1‡)	0	0	
WaPt-3-3	7	3	1	0	
Locality 19					
Ard-1-1	0	1‡	0	0	
Locality 20					
PHI-C ₃ -4	1	1	0	4	
Locality 21					
PHI-D ₁ -2	6	2	2	10	
PHI-D ₁ -3	2	0	1	4	
Locality 22					
IDM-3-21	5	0	1	3	
Locality 23					
Cod-1-9	2	0	0	2	
Locality 24					
Cod-1-15	0	2(1‡)	0	4	
	104	82	24	74	Total
					284

*60%–70% convincing *M. bipluti*.

†Intermediate between *M. beckmanni* and *M. bipluti*.

‡*M. cf. M. beckmanni* transitional with *M. praebeckmanni*.

genus *Siphonodella*". These authors failed to show intermediate forms and we believe that they placed too large a significance on the size of the basal cavity, because they were unaware that morphologically distinct species of *Mestognathus* (a genus then not known from the USSR) are being found increasingly in rocks of Tournaisian age elsewhere in the world. We reject any relationship between *Siphonodella* and *Mestognathus* on the basis of dissimilar phylogeny, morphology, and palaeoecology.

The longest surviving individuals of the genus *Siphonodella* are representatives of the *S. isosticha* group of species and morphotypes, which show early or juvenile characteristics of the genus and which died out without leaving any remotely similar descendants (Sandberg et al., 1978). Not only this group but all other species of the genus *Siphonodella* lack a parapet area (having instead a rostrum in all but the two oldest species), have a relatively thin platform, and show no tendency for the blade to occupy other than a central position. *Siphonodella* is most common in sediments indicative of offshore, deeper-water conditions (Sandberg and Gutschick, 1983). On the other hand, *Mestognathus* and *Clydagnathus* have a similar palaeoecology (near-shore, shallow-water) and morphology (right-sided blade), as well as an observed phylogenetic link.

Austin (1976:212) hypothesized that *Mestognathus* probably developed from *Pseudopolygnathus triangulus*. This species, originally described by Voges (1959), was recently transferred to *Polygnathus* (Lane, Sandberg, and Ziegler, 1980:135). We reject the hypothesis that *Mestognathus* and *Polygnathus triangulus* (Voges) are closely related, because the morphology of *P. triangulus* is as dissimilar to that of *Mestognathus* as the morphology of *Mestognathus* is to that of *Siphonodella*. As further proof of this lack of relationship, we offer the fact that *Polygnathus triangulus*, showing no morphologic change over older occurrences of

the same species, is found together with *Mestognathus beckmanni*, the second youngest species of *Mestognathus*, in sample GER-80-5 (Appendix, locality 4), and that the two species are morphologically quite distinct. These phylogenetically late *Polygnathus triangulus*, like their Tournaisian ancestors that lived with the earliest mestognathids, possess a relatively thin platform that is totally different in cross-section from that of *Mestognathus*. They also have a central blade and a small rimmed basal cavity that is present in juveniles and does not evert ontogenetically.

Park (1983:111,118) concluded that *Mestognathus* developed from *Polygnathus mehli* at the lower boundary of the *Gnathodus texanus* Zone. *P. mehli*, like *P. triangulus*, possesses a central blade, again making it an unlikely ancestor. Furthermore, it can be seen that *Mestognathus harmalai* sp. nov., *M. groessensi*, and *M. praebeckmanni* sp. nov. all evolve earlier (Text-fig. 5) than does *P. mehli*, a species that first appears high in the *Scaliognathus anchoralis*-*Doliognathus latus* Zone (Lane, Sandberg, and Ziegler, 1980, table 2).

Rhodes, Austin, and Druce (1969:150) and Metcalfe (1981:33) suggested that *Mestognathus* and *Cavusgnathus* may be closely related. Both genera are cavusgnathoids, having in common a similarly shaped platform, an eccentric blade, and, at least in juvenile stages of *Mestognathus*, an open, unevverted basal cavity. *Cavusgnathus* most closely resembles *M. praebeckmanni* sp. nov. morphotypes 1 or 2, which differ mainly in having an elongate carina and a divided trough. *Cavusgnathus* is not likely to have evolved from *M. praebeckmanni* sp. nov. however, because of the gap in their ranges. At the time when *Cavusgnathus* evolved, the only extant species of *Mestognathus* were *M. beckmanni* and *M. bipluti* (Text-fig. 5), both of which possess a parapet—a morphologic feature not found in *Cavusgnathus*.

Previous Biostratigraphic Applications of *Mestognathus*

Mestognathus beckmanni was for many years recognized to be the geologically oldest and geographically most widely distributed species of the genus. Austin (1973) and Groessens (1974) interpreted that the appearance of this species coincided with the base of the Viséan, and most later authors accepted this. The recognition of the existence of species of *Mestognathus* older than *M. beckmanni* causes us to point out several discrepancies in the formulation of this interpretation.

Groessens (1971, unnumbered upper Tournaisian conodont range chart and log 6) showed that *Mestognathus beckmanni* occurred in the upper part of Tournaisian Tn_{3c}, on the basis of its occurrence in bed 60 at our locality 2 (Appendix), the Route de Salet section. However, we recog-

nize his illustrated specimen of *M. beckmanni* (Groessens, 1971, pl. 2, fig. 8) to be *M. praebeckmanni* sp. nov. This is corroborated by the fact that the holotype of this species (Pl. 8, figs. 1-4, 8, 10) is from the very same bed and was found in a sample collected by Sandberg in 1971 under the guidance of Eric Groessens. Thus, when Austin (1973) and Groessens (1974:45,46, fig. 46) followed Austin, Conil, and Rhodes (1973) in raising the base of the Viséan, they made it coincide with what they regarded to be the first occurrence of *M. beckmanni*. Unfortunately, they were actually making the conodont definition of the Tournaisian-Viséan boundary coincide with what we now know is the lowest biofacies occurrence of *M. praebeckmanni* sp. nov. in Belgium. This is an occurrence that is probably high in

the total range of that species (Text-fig. 5).

If we discount the specimen illustrated by Groessens (1971), one of the few unquestionable documented specimens of *Mestognathus beckmanni* from Belgium of which we are aware is the one illustrated by Groessens and Noel (1974, pl. 7, fig. 22).

Apart from a questionable specimen illustrated by Groessens and Noel (1974, pl. 7, fig. 21), only two other, poorly illustrated, Belgian specimens of *M. beckmanni* have been published. One is from bed 57 (assigned to the base of V_{1a}) at the Maredsous railroad tunnel (Groessens, Conil, and Lees, 1973, pl. 3, fig. 19). The other is from bed 181 (assigned to V_{1b}) in the Yves-Gomezée section (Conil, Groessens, and Lys, 1973, pl. 6, fig. 30). This paper also shows as *M. beckmanni* three very poorly illustrated, and hence specifically indeterminable, specimens of *Mestognathus* (pl. 6, figs. 27–29) and one specimen of an apparent *M. praebeckmanni* sp. nov. (pl. 6, fig. 26). This specimen from Rocher du Bastion, the stratotype of the Dinantian, is from bed 157, about 3 to 4 m above the base of the Viséan, a boundary they show at the base of bed 141. A biostratigraphic interval of 10 m separates their highest reported occurrence of *Scaliognathus anchoralis* in bed 122 and the lowest occurrence of *M. beckmanni*. It is within this gap that they not only place the base of the Viséan, but they also

report the occurrence of *Gnathodus homopunctatus* from just above its base in bed 143. This species generally does not occur below the base of the *Cavusgnathus* Zone (Text-fig. 5) elsewhere in the world. Thus, if their identification of *G. homopunctatus* were correct, then *M. beckmanni* in bed 157 could represent a position well above the base of the Viséan. However, their illustration of *G. homopunctatus* from bed 143 (Groessens and Noel, 1974, pl. 7, fig. 16) bears little resemblance to that species. More significant, the specimen illustrated as *Gnathodus* cf. *G. homopunctatus* by Groessens (1971, pl. 2, fig. 9) is *G. homopunctatus*. Unfortunately, its stratigraphic position in the section at the Yves-Gomezée railroad cut is not given, and so it could have come either from upper V_{1a} or basal V_{1b} (Groessens, 1971, log 7, bed 133 or 150).

In summary, published evidence from Belgium documents only that *Mestognathus beckmanni* first appears somewhat above the base of the type Viséan, but below the first appearance of typical *Gnathodus homopunctatus*. Consequently, the custom of equating the first appearance of either the genus *Mestognathus* or the species *M. beckmanni* with the base of the Viséan in other parts of the world has no basis in the type Viséan of Belgium (see also Lane and Ziegler, 1983:210 for similar conclusions).

Proposed *Mestognathus*-based Shallow-Water Zonation

On the basis of the newly recognized species of *Mestognathus* and the documented ranges of all species, we propose a *Mestognathus*-based zonation based on four time zones that is applicable to sediments deposited in shallow water (Text-fig. 5). The standard conodont zones employed at the left of Text-figure 5 are those of Sandberg (Sando, Sandberg, and Gutschick, 1981). The limits of these zones are unchanged from previous usage except that those of the *Cavusgnathus* Zone have been constricted somewhat, based on new biostratigraphic data. In terms of the foraminifer zones of Mamet (see Sando, Sandberg, and Gutschick, 1981) the lower limit of the *Cavusgnathus* Zone has been raised from the base of 13 to mid-14 and the upper limit has been lowered from the base of 18 into the upper part of 17. Using this combined standard and provisional conodont zonation and the Mamet foraminifer zonation as a "standard" against which to plot, we show the limits of four zones of a proposed *Mestognathus*-based conodont zonation. This new zonation is applicable to several of the more nearshore Lower Carboniferous (Mississippian) environments as modelled by Sandberg and Gutschick (1984, fig. 14). In constructing this parallel zonation, we have applied the rationale and techniques of Sandberg and Dreesen (1984) in proposing an icriodontid-based shallow-water

zonation as an alternative, parallel zonation to the *Palmatolepis*-based deep-water standard Late Devonian zonation (Ziegler and Sandberg, 1984). The proposed zonation comprises, in ascending order, the *Mestognathus harmalai*, *M. praebeckmanni*, and *M. beckmanni* First Occurrence zones and the *M. bipluti* Range Zone. The reason that the highest zone is defined in a different manner is that there is no known descendant of *M. bipluti*, the first occurrence of which can be used as an upper limit to the *M. bipluti* Range Zone. The major tool for establishing these zones, the limits of which are firmly fixed conceptually (but are tentatively aligned in terms of the "standard"), is the phylogeny and range chart depicted on the right half of Text-figure 5.

Mestognathus harmalai First Occurrence Zone

Lower limit defined by the first appearance of the name bearer. Upper limit defined by the first appearance of *M. praebeckmanni* sp. nov.

ASSOCIATED FAUNA

Polygnathus communis communis, *P. communis carina*; *Bispathodus utahensis*; *Hindeodus* spp.; *Pseudopolygnathus multistriatus* morphotypes 1 and 2; *Bactrognathus* sp. nov. Lane, Sandberg, and Ziegler; *Gnathodus delicatus*,

G. punctatus, *G. typicus* morphotype 1; *Mestognathus groessensi*, and forms transitional from *Clydagnathus gilwernensis* to the name bearer of the zone.

AGE

Siphonodella isosticha—Upper *S. crenulata* and Lower *Gnathodus typicus* zones.

GEOGRAPHIC DISTRIBUTION

Presently recognized at locality 1 (Appendix) in Utah, USA, and in southern Poland (Belka, 1983, borehole WB-64).

Mestognathus praebeckmanni First Occurrence Zone

Lower limit defined by the first appearance of the name bearer. Upper limit defined by the first appearance of *M. beckmanni*.

ASSOCIATED FAUNA

Bactrognathus sp. nov. Lane, Sandberg, and Ziegler; *Bispathodus utahensis*; *Doliognathus latus* morphotype 2; *Dollymae bouckaerti*; *Eotaphrus burlingtonensis*; *Gnathodus cuneiformis*, *G. pseudosemiglaber*?, *G. semiglaber*, *G. typicus*; *Hindeodella segaformis*; *Hindeodus* cf. *H. cristulus*; *Mestognathus harmalai* sp. nov.; *Polygnathus bischoffi*, *P. communis communis*, *P. symmetricus*?, *P. triangulus*; *Protognathodus cordiformis*; *Pseudopolygnathus nudus*, *Ps. oxypageus* morphotype 2, *Ps. pinnatus*; *Scaliognathus dockali*, *S. anchoralis europensis*; probably *Eotaphrus bultyncki*, *Mestognathus groessensi*, and *Pseudopolygnathus multistriatus* morphotype 2.

AGE

Upper *Gnathodus typicus* and *Scaliognathus anchoralis*—*Doliognathus latus* zones.

GEOGRAPHIC DISTRIBUTION

Western North America (British Columbia and Alaska) and most of western Europe (Northern Ireland, Republic of Ireland, Belgium, Federal Republic of Germany, Poland, Czechoslovakia, Spain).

Mestognathus beckmanni First Occurrence Zone

Lower limit defined by the first appearance of the name bearer. Upper limit defined by the first appearance of *M. bipluti*.

partim 1969 *Mestognathus beckmanni*—*Polygnathus bischoffi* Assemblage Zone; Rhodes, Austin, and Druce, p. 42 and fig. 12; see also Austin and Aldridge (1969:235 and fig. 1); Rhodes and Austin (1971:333 and fig. 2); Austin (1974, fig. 3); Great Britain; “Lower limit defined by the oldest stratigraphic occurrence of *Mestognathus beckmanni*. The upper limit probably coincides with the zone of maximum abundance of *Gnathodus texanus*

(Roundy)” (Rhodes, Austin, and Druce, 1969:42). (Comments: the base of this zone is coincident with ours, but the top is not.)

non 1969 *Mestognathus beckmanni*—*Gnathodus bilineatus* Assemblage Zone; Rhodes, Austin, and Druce, p. 44 and fig. 12; see also Austin (1973, chart) and Varker and Sevastopulo (1985:180 and fig. 5.5); Great Britain; the upper and lower limits of this zone are defined by species of *Gnathodus*, *G. bilineatus*, and *G. mononodosus*, respectively. (Comments: latter species of *Gnathodus* would be placed in *Paragnathodus* by us; *Mestognathus beckmanni* is present and characteristic of the zone but is not used in defining its limits.)

partim 1973 *Gnathodus homopunctatus*—*Mestognathus beckmanni* Zone; Austin, p. 528 and chart; Belgium and Germany; base of zone (and of the Viséan) defined by the first appearance of *Gnathodus homopunctatus* and/or *Mestognathus beckmanni* (Austin, 1973:528). Top of zone defined by first occurrence of *Gnathodus commutatus*. (Comments: latter species of *Gnathodus* would be placed in *Paragnathodus* by us; the base of this zone is, in part, coincident with that of our zone (see discussion at beginning of this section)—top of this zone is not.)

partim 1973 *Mestognathus beckmanni* Zone; Groessens, Conil, and Lees, p. 38 (fig. 12) and unnumbered chart; also in Groessens (1974:167 and pl. 46), Conil; Groessens, and Pirlet (1976:366, tables 1 and 2), and Paproth et al. (1983:192 and enclosure); Belgium. Shown by Groessens (1974, pls. 16,17) as an acrozone, that is, range zone (Hedberg, 1976). Groessens (1974:167) stated that this zone is characterized by the presence of *Mestognathus beckmanni*, that for practical purposes the base of the zone at Dinant coincides with the base of the Viséan, and that its upper limit (i.e., relationship with the *Gnathodus bilineatus* Zone) cannot be determined. A tentative threefold subdivision of this zone was presented by Paproth et al. (1983:192, table 2 and enclosure). (Comments: the base of this zone is coincident with that of ours if “presence” means first appearance; the top is not. See discussion at beginning of section.)

partim 1974 *Mestognathus beckmanni*—*Polygnathus lacinatedus* Zone; Austin, fig. 3; Great Britain; definition, limits, and distribution not given by Austin (1974). (Comments: Austin (1974) inadvertently? applied this name to former *M. beckmanni*—*P. bischoffi* Zone and the latter name to next higher zone.)

partim 1981 *Mestognathus beckmanni*—*Polygnathus bischoffi* Local Range Zone; Metcalfe, p. 7 and fig. 12; see also Varker and Sevastopulo (1985:181); Great Britain; lower limit defined by the “first appearance of *Mestognathus beckmanni*”; the upper limit defined by the “first appearance of *Gnathodus homopunctatus*”. (Comments: the base of this zone is coincident with ours, but the top is not.)

ASSOCIATED FAUNA

Geniculatus cf. *G. glottoides*; *Gnathodus bilineatus*?, *G. cf. G. bilineatus*, *G. cuneiformis*, *G. girtyi girtyi*, *G. pseudo-semiglaber*, *G. semiglaber*, *G. texanus*; *Mestognathus praebeckmanni* sp. nov. morphotypes 2 and 3; *Paragnathodus commutatus*; *Polygnathus bischoffi*, *P. triangulus*.

AGE

From slightly above base of *Gnathodus texanus* Zone into lower part of *Cavusgnathus* Zone.

GEOGRAPHIC DISTRIBUTION

Federal Republic of Germany, Belgium, Wales, England, Poland?, Australia?.

Mestognathus bipluti Range Zone

Lower limit defined by the first appearance of the name bearer. Upper limit defined by the highest occurrence of the name bearer.

ASSOCIATED FAUNA

Cavusgnathus naviculus, *C. unicornis*; *Clydagnathus windsorensis*; *Geniculatus claviger*; *Gnathodus bilineatus*, *G. girtyi girtyi*, *G. girtyi intermedius*, *G. girtyi simplex*, *G. homopunctatus*; *Hindeodus? scitulus*; *Apatognathus* spp.; *Paragnathodus commutatus*, *P. cruciformis*, *P. monodosus*, *P. nodosus*, *P. scotiaensis*; in lower part of zone, *Mestognathus beckmanni*.

AGE

Upper part of *Cavusgnathus* Zone and *C. naviculus* Zone. Mamet foraminifer zones 15 at least through 16, probable; co-occurrence with zones 17 and 18 not documented.

GEOGRAPHIC DISTRIBUTION

Republic of Ireland, Wales, Scotland, England, Federal Republic of Germany?, Belgium, Poland, Spain, Atlantic Canada (Appendix, localities 13–24).

REMARKS

The highest known occurrence of *Mestognathus bipluti* is the top of the *Kladognathus–Gnathodus girtyi simplex* Zone of the Pendleian Stage (Higgins, 1975:13, table 2; A. C. Higgins, pers. comm., 1985).

Although Higgins (1975:13, table 2) did not consider *Cavusgnathus naviculus* a characteristic species of the *Kladognathus–Gnathodus girtyi simplex* Zone, this species was abundant in the only three Pendleian samples (CH 3, 4, and 5) in which *Mestognathus bipluti* was common. Because *C. naviculus* is moderately abundant in the Pendleian, it ranges well below the *Gnathodus bilineatus bollandensis–Cavusgnathus naviculus* Zone. Higgins (1975:fig. 3) did not record *C. naviculus* from below the Pendleian. We conclude that the *C. naviculus* Zone of our usage lies directly below Higgins's *Gnathodus bilineatus bollandensis–C. naviculus* Zone, which we equate in part, if not entirely, with the *Adetognathus unicornis* Zone of our usage.

Systematic Palaeontology

Phylum Conodonta Pander, 1856

Class Conodontata Pander, 1856

Order Conodontophorida Eichenberg, 1930

Family Mestognathidae Austin and Rhodes in Robison, 1981

Genus *Mestognathus* Bischoff, 1957

TYPE SPECIES

Mestognathus beckmanni Bischoff, 1957, by original designation.

ORIGINAL DIAGNOSIS (Translated from German)

Ornamented trough-shaped platform with a short, abruptly ending blade on the anterior outer edge—a blade that does not project over the platform (or does so only slightly) and that increases in height posteriorly. A more or less parapetlike anterior inner edge and a convex aboral surface (seen in cross-section) with a small basal pit in the middle part.

REVISED DIAGNOSIS

A genus based on platform elements (Pa, P, or Sp,

according to different notation systems) that have a Class IIIa symmetry. In upper view the genus has a moderately high anterior blade along the right side of the platform; transverse ridges; and a long, slightly sigmoidal, posteriorly nodose carina. The carina dies out or is deflected sharply to the left near the anterior end of the platform, so that it reaches the left side of the platform or climbs the parapet. In lower view the genus shows a basal opening that everts ontogenetically from an open basal cavity to an eversion strip or pseudokeel containing a basal pit.

EFFECTS OF ONTOGENY

Diagnoses of the five species recognized by us are based on mature specimens (all greater than 1 mm and many greater than 1.5 mm [see Text-fig. 2]), a practice that we recommend strongly. Juveniles of all five have open basal cavities which evert ontogenetically to different degrees.

PHYLOGENY

A complete phyletic lineage from *M. harmalai* sp. nov. to *M. groessensi* Belka to *M. praebeckmanni* sp. nov. to *M. beckmanni* Bischoff to *M. bipluti* Higgins exists within *Mestognathus*. Transitional specimens are often difficult to assign unequivocally to the ancestral or the descendant species.

SPECIATION

This genus is differentiated mainly by the morphology of the parapet area (left anterior part of platform) into five species: *Mestognathus harmalai* sp. nov., *M. groessensi* Belka, *M. praebeckmanni* sp. nov., *M. beckmanni* Bischoff, and *M. bipluti* Higgins. We demonstrate that the two other named species, *M. dhuensis* Globensky and *M. neddensis* Rhodes, Austin, and Druce, are synonyms of *M. beckmanni*, *M. bipluti*, and *Mestognathus* spp.

COMPARISONS

Mestognathus, because of its right-sided anterior blade, resembles four other genera: *Cavusgnathus* Harris and Hollingsworth, 1933; *Cloghergnathus* Austin and Mitchell, 1975; *Laterignathus* Aristov and Alekseev, 1976; and *Scaphignathus* Helms, 1959. It is readily distinguished from *Cavusgnathus* and right forms of *Cloghergnathus*, because these genera have a large, open basal cavity, which never becomes more than slightly everted ontogenetically. Moreover, left forms of *Cloghergnathus* have a left, central, or right-central anterior blade. *Mestognathus* is readily distinguished from *Laterignathus*, which has nodose platform ornamentation instead of transverse ridges and a carina that is apparently not deflected to the left so as to climb the parapet. *Mestognathus* is readily distinguished from *Scaphignathus* by criteria discussed under the heading Generic Concept (p. 2).

STRATIGRAPHIC RANGE

Siphonodella isosticha–Upper *Siphonodella crenulata* Zone into the *Cavusgnathus naviculus* Zone.

Mestognathus harmalai Sandberg and von Bitter, sp. nov.

Pl. 5, figs. 1–7; Pl. 6, figs. 1–10; Pl. 10, figs. 8,9; Pl. 11, figs. 11,12

HOLOTYPE

USNM 257751 from sample PC-2B(R); illustrated in Pl. 5, figs. 1,2,5,6.

Derivatio nominis—The species is named to honour John Harmala, who recovered the first known specimens of this species (Harmala, 1982).

Stratum typicum—Joana Limestone, 14 m below top of

formation. Collection made as sample PC-2B(R) in measured and marked section (Appendix, locality 1).

Locus typicus—Pool Canyon, Deep Creek Mountains, north of Gold Hill, Utah, USA (Appendix, locality 1).

DIAGNOSIS

A species of *Mestognathus* characterized by a narrow, elongate platform, a carina that is strongly deflected to the left margin of the platform in the low parapet area, and a convex termination of the inner anterior platform.

STRATIGRAPHIC RANGE

Lower to Upper *Gnathodus typicus* Zone, based on our collections. Inferred to range low into *Siphonodella isosticha*–Upper *Siphonodella crenulata* Zone, because its descendant *M. groessensi* was reported by Belka (1983) to occur within that zone.

GEOGRAPHIC DISTRIBUTION

Western North America (Utah, USA, and British Columbia, Canada).

MATERIAL

Eleven specimens from locality 1 (Appendix) in Utah (three recovered by Harmala (1982), eight subsequently recovered by Sandberg); one specimen from British Columbia.

REMARKS

An anterior notch and a secondary keel are not developed. Juvenile specimens have a large basal cavity (Pl. 5, figs. 3,4). With an increase in size this everts to become slightly smaller, so that in mature specimens it is a well-defined large basal pit (Pl. 2, figs. 5,8–10; Pl. 5, figs. 2,6,7).

In some specimens the narrow platform does not reach the posterior end of the element. Instead it forms a bladelike posterior process with a rounded cross-section (Pl. 5, figs. 1,2,5), much like that of the holotype of *Clydagnathus gilwernensis* of Rhodes, Austin, and Druce (1969, pl. 2, figs. 1a–d). The origin of *Mestognathus harmalai* sp. nov. from *C. gilwernensis* is documented by specimens transitional between the two species (e.g., Pl. 7, figs. 6–10; Rhodes, Austin, and Druce, 1969, pl. 2, figs. 13a–c) as well as by specimens of *M. harmalai* sp. nov. that retain some ancestral characteristics (e.g., Pl. 6, figs. 1,4,5). Specimens of *M. harmalai* sp. nov. in which the high denticles of the posterior process are preserved can be readily distinguished from the other species of *Mestognathus*, none of which has high denticles on the posterior carina. Our smallest specimen from Utah (Text-fig. 2, no. 17; USNM 257752), with a total (as opposed to platform) length of 1.6 mm, has a relatively large basal cavity (Pl. 5, figs. 3,4), because eversion to a pit apparently does not take place until an even later ontogenetic stage than in the other species of *Mestognathus*.

***Mestognathus groessensi* Belka, 1983**

Pl. 1, figs. 26–31

?*Scaphignathus*? sp. B Rhodes, Austin, and Druce, 1969, pl. 2, figs. 12a–c

Mestognathus groessensi Belka, 1983, pl. 1, figs. 1a–c, 2; pl. 2, figs. 1a, b [only]

Mestognathus groessensi—Belka, 1985, pl. 10, figs. 1a, b, 2, 3

?*Mestognathus groessensi*—Varker and Sevastopulo, 1985, pl. 55, figs. 7, 9

ORIGINAL DIAGNOSIS

A species of *Mestognathus* characterized by a bluntly pointed and rounded inner parapet. The carina is developed in the posterior part of the unit; it extends to the midpoint of the platform or, in adult specimens, a little away where it curves inwards to meet the inner lateral margin. The basal cavity is large and asymmetrical being expanded on the inner side; it is never as wide as the platform (from Belka, 1983:78).

SUBSEQUENT DIAGNOSIS

A species of *Mestognathus* with a median carina and an unusually large aboral cavity (from Varker and Sevastopulo, 1985:200).

REVISED DIAGNOSIS

A species of *Mestognathus* characterized by a strong carina that bends beginning at midlength of the element to meet the platform margin approximately opposite the cusp, a parapet area that is horizontal or anteriorly inclined and featureless, a lower margin that bends upwards beneath the parapet area, and a large asymmetric basal cavity that is presently not known to evert ontogenetically to a pit.

STRATIGRAPHIC RANGE

According to Belka (1983:78) *Siphonodella isosticha*—Upper *Siphonodella crenulata* Zone into *Scaliognathus anchoralis*—*Doliognathus latus* Zone, but according to our interpretation only as high as Upper *Gnathodus typicus* Zone (Text-fig. 5).

GEOGRAPHIC DISTRIBUTION

Olkusz area, Poland (Belka, 1983:74). Known only from a single borehole.

REMARKS

The specimen (BMNH X 533) referred by Rhodes, Austin, and Druce (1969, pl. 2, figs. 12a–c) to *Scaphignathus*? sp. B, and by Belka (1983) and Varker and Sevastopulo (1985, pl. 5.5, figs. 7, 9) to *Mestognathus groessensi* strongly resembles *M. groessensi* but cannot be assigned with certainty to that species. Reasons for this include the fact

that the posterior part of the platform is not preserved, shadows in the published photographs make it impossible to determine if the carina bends towards the left margin, and the blade denticles are of equal height.

This species is apparently between *Mestognathus harmalai* sp. nov. and *M. praebeckmanni* sp. nov. in phylogenetic development. It has two characteristics—more posteriorward deflection of carina and a low parapet area—that ally it to *M. harmalai* sp. nov. and one characteristic—a shallow anterior notch—that allies it to *M. praebeckmanni* sp. nov.

It is not known to what degree the large basal cavity of *M. groessensi*, like that of *M. harmalai* sp. nov. and *M. praebeckmanni* sp. nov., everts with maturity to form a large basal pit. The holotype of the species (Text-fig. 2, no. 15) is a relatively immature specimen that cannot be used to answer this question (as is probably true of the only two other specimens accepted by us as belonging to *M. groessensi*). The upward bend of the lower surface of the platform beneath the parapet area, as characterized by the holotype (Pl. 1, fig. 26), is a feature that has not been found in any other species of *Mestognathus*.

***Mestognathus praebeckmanni* Sandberg, Johnston, Orchard, and von Bitter, sp. nov.**

Pl. 1, figs. 32–34; Pl. 7, figs. 1–5; Pl. 8, figs. 1–11; Pl. 9, figs. 1–11; Pl. 10, figs. 1–7, 10, 11; Pl. 11, figs. 1–10

?*Mestognathus beckmanni* Bischoff—Kronberg et al., 1960, pl. 3, figs. 1a, b

Mestognathus beckmanni—Groessens, 1971, pl. 2, figs. 8a, b

Mestognathus beckmanni—Conil, Groessens, and Lys, 1973, pl. 6, fig. 26 [only]

Mestognathus beckmanni—Austin and Mitchell, 1975, pl. 1, fig. 21 (here refigured as Pl. 11, figs. 1–3, 5, 6)

?*Mestognathus* sp.—Matyja and Narkiewicz, 1979, pl. 8, figs. 3, 6, 8

Mestognathus cf. *M. beckmanni*—Metcalf, 1981, pl. 8, figs. 3a–c

Mestognathus beckmanni—van den Boogaard and Vazquez Guzman, 1981, fig. 3A

Mestognathus groessensi Belka, 1983, pl. 2, figs. 2a, b, 6 [only]

?*Cavusgnathus unicornis* Youngquist and Miller—Kalvoda, 1983, pl. 1, fig. 7

Mestognathus n. sp. A—Park, 1983, pl. 1, figs. 6, 7

Mestognathus n. sp.—Orchard and Struik, 1985, pl. 1, figs. 7, 8

Mestognathus sp. nov. A—I. S. Johnston (ms., 1985), figs. 3.20–3.30, 4.1 (here figured as Pl. 9, figs. 1–11; Pl. 10, figs. 1–3)

Mestognathus groessensi—Belka, 1985, pl. 10, figs. 5a,b,6 [only]

HOLOTYPE

USNM 257757 from sample BEL-5 illustrated in Pl. 8, figs. 1–4,8,10.

Derivatio nominis—With reference to its role as the ancestor of *Mestognathus beckmanni* Bischoff.

Stratum typicum—Facies de Leffe, Banc 60 of Groessens (1971, log 6, section 8).

Locus typicus—Route between Salet and Bioul, 8 km northwest of Dinant, Belgium (Appendix, locality 2).

DIAGNOSIS

A species of *Mestognathus* characterized by a shallow to moderately deep anterior notch, a low or slightly raised parapet area, a partly everted basal cavity, and a moderately large basal pit.

STRATIGRAPHIC RANGE

Upper *Gnathodus typicus* Zone to *Scaliognathus anchoralis*–*Doliognathus latus* Zone.

GEOGRAPHIC DISTRIBUTION

Western North America (British Columbia and Alaska) and Europe (England?, Republic of Ireland, Northern Ireland, Federal Republic of Germany, Belgium, Poland, Czechoslovakia?, and Spain).

MATERIAL EXAMINED

Holotype, plus 1 specimen, from Belgium; paratype, plus 4 specimens, from the Federal Republic of Germany; 1 specimen from Northern Ireland; 20 specimens from the Republic of Ireland; 22 specimens from British Columbia; 1 specimen from Alaska.

REMARKS

The species possesses a slightly developed secondary keel that lacks a basal groove. *Mestognathus praebeckmanni* sp. nov. is distinguished from *M. groessensi* Belka in that adult specimens of the former have a pit, a low to moderately low structured parapet area, and a deflection of the carina that is at a position anterior to the cusp. As noted in the section dealing with interspecific and intraspecific variation (p. 26), specimens transitional between *M. praebeckmanni* sp. nov. and *M. beckmanni* are known from Atlantic Canada (Table 3). These are illustrated under *M. beckmanni* as *M. cf. M. beckmanni*.

Three morphotypes appear to demonstrate the existence of phyletic gradualism within this species (Text-fig. 8). The early morphotype, here designated morphotype 1 and illustrated by specimens from the Republic of Ireland and British Columbia (Text-figs. 8A,B; Pl. 9, figs. 2,6,9; Pl.

10, figs. 1,2; Pl. 11, figs. 4,7), has a shallow anterior notch and a flat parapet area. The intermediate, slightly younger morphotype 2, exemplified by the holotype of *M. praebeckmanni* sp. nov. (Text-figs. 8C,D; Pl. 8, figs. 1,4,10), has a shallow anterior notch and a slightly raised parapet area. The advanced morphotype, morphotype 3, illustrated by a specimen from the Federal Republic of Germany (Text-figs. 8E,F; Pl. 8, figs. 5,6), has a deep anterior notch and a slightly raised parapet area. Some specimens of morphotype 2 (Text-figs. 8C,D; Pl. 8, fig. 10) and morphotype 3 (Text-figs. 8E,F; Pl. 8, fig. 11) show the exit of a branch of the main trough through the lateral notch of the parapet area. The effect of this notch is to produce a low parapet at the anterior end of the platform.

The three morphotypes illustrated in Text-figure 8 show, from left to right, a gradual suppression of the cusp of the anterior blade, similar to that recognized by Rexroad (1981:8) in *Cavusgnathus unicornis*. We are presently unable to demonstrate the morphologic constancy of this feature for each of the three morphotypes.

Most specimens of *Mestognathus praebeckmanni* sp. nov. morphotypes 1 and 2 are narrow or lanceolate and have more or less parallel platform margins in upper view (Pl. 8, figs. 1,2). Some specimens of morphotype 3 have a broader platform that is widest at midlength and tapers anteriorly and posteriorly (Pl. 8, figs. 6,7).

Juvenile specimens of *M. praebeckmanni* sp. nov. have large, open basal cavities (Pl. 9, figs. 3,4,7), whereas adult specimens have a partly everted basal cavity, and commonly possess a pseudokeel and a moderately large basal pit (Pl. 9, fig. 11). A weakly developed secondary keel lacking a basal groove is present on the lower surface of *M. praebeckmanni* sp. nov.

Both the holotype and the other specimen of this species recovered by Sandberg from locality 2 (Appendix), Belgium, have a total length greater than 1.6 mm (see Text-fig. 2, no. 21 for holotype).

Mestognathus beckmanni Bischoff, 1957

Pl. 1, figs. 1–8,23; Pl. 2, figs. 1–5,9; Pl. 3, figs. 1–5,9; Pl. 4, figs. 1–5,9; Pl. 12, figs. 1–6; Pl. 13, figs. 1–9; Pl. 14, figs. 1–12; Pl. 15, figs. 1–12; Pl. 16; Pl. 17, figs. 1–13; Pl. 19, figs. 1–5; Pl. 20, figs. 3,6,10, 12; Pl. 23, figs. 1–3; Pl. 25, figs. 7–9; Pl. 26, fig. 4; Pl. 27, figs. 3,4,7

Mestognathus beckmanni Bischoff, 1957, pl. 2, figs. 4a–d,9

?*Mestognathus beckmanni* Bischoff, 1957, pl. 2, figs. 5,6,8

Mestognathus beckmanni—Bartenstein and Bischoff, 1962, pl. 6, figs. 38a–d

Mestognathus dhuensis Globensky, 1967, pl. 57, fig. 22 [only]

Mestognathus beckmanni—Rhodes, Austin, and Druce, 1969, pl. 15, figs. 7a–d
Mestognathus beckmanni—Druce, 1969, pl. 13, figs. 4a,b; 5a,b
 ?*Mestognathus neddensis* Rhodes, Austin, and Druce—Druce, 1969, pl. 13, figs. 2a–c,3
 ?*Mestognathus beckmanni*—Reynolds, 1970, pl. 11, fig. 1
 ?*Mestognathus beckmanni*—Austin and Aldridge, 1973, pl. 2, fig. 12
Mestognathus beckmanni—Groessens, Conil, and Lees, 1973, pl. 3, fig. 19
Mestognathus beckmanni—Conil, Groessens, and Lys, 1973, pl. 6, fig. 30 [only]
 ?*Mestognathus beckmanni*—Conil, Groessens, and Lys, 1973, pl. 6, figs. 27–29
 ?*Mestognathus beckmanni*—Butler, 1973, pl. 58, figs. 1,2
Mestognathus beckmanni—Austin and Husri, 1974, pl. 5, figs. 8a–d
Mestognathus neddensis—Austin and Husri, 1974, pl. 5, figs. 2a–c [only] (Negative for 2c reversed.)
Mestognathus bipluti Higgins—Gromczakiewicz-Lomnicka, 1974, pl. 2, figs. 2a–d
 ?*Mestognathus beckmanni*—Groessens and Noel, 1974, pl. 7, fig. 21 [only]
Mestognathus beckmanni—Groessens and Noel, 1974, pl. 7, fig. 22 [only]
Mestognathus beckmanni—Matthews and Thomas, 1974, pl. 50, figs. 27,28
 ?*Mestognathus beckmanni*—Perret, 1977, pl. 51, figs. 15a,b
 ?*Mestognathus* cf. [*M.*] *beckmanni*—Perret, 1977, pl. 51, figs. 19a,b
 ?*Mestognathus beckmanni*—Chorowska, 1978, pl. 5, figs. 3a,b
 ?*Mestognathus* cf. *M. beckmanni*—Chorowska, 1978, pl. 6, fig. 1
 ?*Mestognathus* sp.—Chorowska, 1978, pl. 5, figs. 4a,b; pl. 6, fig. 2
 ?*Mestognathus* sp.—Kozitskaya et al., 1978, pl. 11, fig. 8
Mestognathus beckmanni—Metcalf, 1980, pl. 13, fig. 11
Mestognathus beckmanni—Metcalf, 1981, pl. 8, figs. 1a,b,2
Mestognathus sp.—von Bitter and Plint-Geberl, 1982, pl. 4, fig. 2 [only]
 ?*Mestognathus beckmanni*—Higgins and Wagner-Gentis, 1982, pl. 34, figs. 16,17
Mestognathus beckmanni—Belka, 1983, pl. 1, figs. 3,4
 ?*Mestognathus beckmanni*—Belka, 1983, pl. 2, fig. 5 [only]
Mestognathus bipluti—Belka, 1983, pl. 2, fig. 7 [only]
 ?*Mestognathus beckmanni*—Kalvoda, 1983, pl. 1, fig. 3 (Negative reversed?)
 ?*Mestognathus beckmanni*—Metcalf, 1983, pl. 2, figs. 5,6

?*Mestognathus beckmanni*—Park, 1983, pl. 1, figs. 8,9
Mestognathus beckmanni—Varker and Sevastopulo, 1985, pl. 5.5, figs. 1,3,5
 ?*Mestognathus beckmanni*—Belka, 1985, pl. 10, figs. 4a, b,7a–c

Translation from German of original documentation, diagnosis, and description of Bischoff (1957:37):

Derivatio nominis—After Dr H. Beckmann, who let me have, among others, the beautiful fauna from the locality at the Waldcafé.

HOLOTYPE

The example illustrated on pl. 2, figs. 4a–d (Bi 1957/35) [here reproduced as Pl. 1, figs. 1–4].

Locus typicus—Small quarry 1 km north of Lethmathe immediately north of the Waldcafé, on the road between Lethmathe and Schwerte, Topographic Sheet Hohenlimburg.

Stratum typicum—Lower *Goniatites* Stufe, cu III α .

MATERIAL PRESENT

About 50 examples.

DIAGNOSIS

A species of the genus *Mestognathus* with the following characteristics: strong, approximately triangular platform with more or less coarse cross-ribbing on the oral surface; a high blade with a sharp anterior termination, the blade projecting slightly over the platform; and a deep trough on the inner side of the blade.

DESCRIPTION

The platform, which is approximately triangular in outline, is thick and slightly arched in lateral view. The oral surface is only weakly troughlike at the posterior end—at the anterior end it is strongly so. A row of more or less strongly fused small nodes extends from the posterior end to the anterior end of the inner edge. With the exception of the anterior outermost part, the oral surface bears more or less strong cross-ribs, which occasionally dissolve into elongated nodes. The anterior inner border or margin of the platform is parapetlike and in adult examples bears a strong denticle with a flat-oval cross-section. The anterior outer margin bears a high blade that projects anteriorly slightly over the platform, ends in a point anteriorly, and is formed by 6 to 12 denticles having a flat-oval cross-section. The denticles are fused with one another up to their triangular tips and are inclined anteriorly on the anterior part and posteriorly on the posterior part of the blade, respectively.

Posteriorly the denticles increase in size more or less evenly. Except in one adult example, the last denticle of the blade is especially long and robust and is inclined posteriorly

to a greater degree than are the remaining denticles. The aboral surface of the platform is strongly convex in cross-section. At the end of the anterior one-third a small elongated basal pit is present. From this pit a more or less sharp keel, which becomes higher posteriorly, and a second sharp keel extend to the posterior end of the platform and to the anterior end of the blade, respectively. Both keels are traversed by a narrow groove that cannot be observed in adult examples. Weakly developed stripes of growth lines can be recognized on the aboral surface of some specimens, on each side of the keels.

SUBSEQUENT DIAGNOSIS

A species of *Mestognathus* with one high anterior blade with 6 to 12 denticles, a prominent medial trough, and a restricted basal cavity which is shallow and occupies the anterior half of the platform (from Varker and Sevastopulo, 1985:200).

REVISED DIAGNOSIS

A species of *Mestognathus* characterized by a deep anterior notch, a pillarlike parapet having a vertical or near-vertical anterior margin, and an almost completely everted basal cavity with a small pit. The parapet of adults bears a single large denticle, anterior to which a single smaller denticle may be present.

STRATIGRAPHIC RANGE

From just above the base of the *Gnathodus texanus* Zone into the upper part of the *Cavusgnathus* Zone.

GEOGRAPHIC DISTRIBUTION

Western North America (British Columbia), eastern North America (Nova Scotia and Newfoundland), Europe (Republic of Ireland, Scotland?, Wales?, England, Federal Republic of Germany, France?, Belgium, Czechoslovakia?, Poland, Ukraine?, Spain?), North Africa (Algeria?), Asia (Malaysia?), Australia.

MATERIAL EXAMINED

Five primary types from near Lethmathe and 13 specimens from locality 4 (Appendix) at Zippenhaus, Federal Republic of Germany; figured specimen BMNH X 245 of Rhodes, Austin, and Druce (1969), according to label on slide, from near Pittenweem, Scotland, elsewhere (Rhodes, Austin, and Druce, 1969:293, 298) given as from Fall Bay, Gower, South Wales; figured specimens Z.1.42 and Z.1.45, and 5 unfigured specimens (2 from sample L9 from County Limerick, 3 from sample CI 12A from County Clare) of Austin and Husri (1974) from the Republic of Ireland.

Paratype UNB 64-F-215 (KD-6) of Globensky (1967) from Nova Scotia; 10 specimens from British Columbia; 82 specimens from Atlantic Canada, including specimen ROM

38492 of von Bitter and Plint-Geberl (1982) from Newfoundland (Table 3).

Transitional specimens between *Mestognathus beckmanni* and *M. praebeckmanni* sp. nov. from Atlantic Canada are assigned to *M. cf. M. beckmanni* (Table 3 and section on interspecific and intraspecific variation, p. 26).

REMARKS

The revised diagnosis emphasizes the pillarlike parapet having a vertical or near-vertical anterior margin, an important characteristic not mentioned in Bischoff's diagnosis.

Re-examination and photographic documentation (Pl. 2, figs. 1-5; Pl. 3, figs. 1-5; Pl. 4, figs. 1-5; Pl. 12, figs. 1-6; Pl. 13, figs. 1-9; Pl. 14, figs. 1-12; Pl. 15, figs. 1-12) of the types of *Mestognathus beckmanni*, using the scanning electron microscope, and comparison with the illustrations of Bischoff (1957, pl. 2, figs. 4-6,8,9; here reproduced as Pl. 1, figs. 1-8) demonstrates the following:

a) The specimens are still in the same state of preservation as they were when Bischoff (1957) designated them types, except that paratype PUM Bi 1957/39 has broken across an existing crack (Pl. 1, fig. 8; Pl. 3, fig. 5; Pl. 13, fig. 7), a break that has allowed us to document a cross-sectional view of the platform (Pl. 20, fig. 6).

b) The preservation of these five specimens varies greatly. Three of the five have broken parapets and do not show this key feature (Pl. 4, figs. 2-4; Pl. 13, figs. 4-8). Only two of the five specimens, the holotype PUM Bi 1957/35 (Pl. 4, fig. 1; Pl. 13, fig. 3) and paratype PUM Bi 1957/39 (Pl. 4, fig. 5; Pl. 13, fig. 9) have the diagnostic pillarlike parapet preserved. Paratype PUM Bi 1957/37 is badly corroded and not taxonomically useful (Pl. 2, fig. 3; Pl. 3, fig. 3; Pl. 4, fig. 3; Pl. 12, figs. 3,6; Pl. 13, fig. 5). The lack of a preserved parapet on paratypes PUM Bi 1957/36 to 38, inclusive, means that we can never be certain of the specific identity of these three paratypes.

c) The five type specimens vary noticeably in size (and thus in maturity) from a length of 0.9 mm (paratype PUM Bi 1957/38) to 1.14 mm (holotype PUM Bi 1957/35) to 1.92 mm (paratype PUM Bi 1957/39).

d) There is considerable ontogenetic variation in these five type specimens. For example, the holotype (PUM Bi 1957/35) shows two denticles, a smaller one immediately anterior to a larger one, on the pillarlike parapet (Pl. 4, fig. 1; Pl. 13, fig. 3), whereas paratype PUM Bi 1957/39, a very large platform element, shows only the single large pillarlike denticle of the parapet (Pl. 4, fig. 5; Pl. 13, fig. 9), a feature that has come to be regarded as the defining characteristic of the species.

Mestognathus bipluti Higgins, 1961

Pl. 1, figs. 9,10,13-15,24,25; Pl. 2, figs. 6,7,10-12; Pl. 3, figs. 6,7,10-12; Pl. 4, figs. 6,7,10-12; Pl. 19, figs. 6-10;

Pl. 20, figs. 1,2,4,7-10,13; Pl. 21, figs. 1-10; Pl. 22, figs. 1-8; Pl. 23, figs. 4-10; Pl. 24, figs. 1-13; Pl. 25, fig. 10; Pl. 26, figs. 1,2,5-8; Pl. 27, figs. 1,2,5,6,8,9; Pl. 28, figs. 1,4,6; Pl. 29, figs. 1-4,7,8

Mestognathus bipluti Higgins, 1961, pl. X, figs. 1, 2, text-fig. 4 (Negative for fig. 1 reversed.)

Mestognathus dhuensis Globensky, 1967, pl. 57, figs. 23, 24 [only]

Mestognathus bipluti—Rhodes, Austin, and Druce, 1969, pl. 15, figs. 1a-c,2a-c,3a-c,8a,b

Mestognathus neddensis Rhodes, Austin, and Druce, 1969, pl. 15, figs. 6a-c [only]

?*Mestognathus bipluti*—Marks and Wensink, 1970, pl. 1, figs. 7a,b, 8a,b

Mestognathus bipluti—Reynolds, 1970, pl. 2, fig. 2

Mestognathus bipluti—Rhodes and Austin, 1971, pl. 2, fig. 7

Mestognathus neddensis—Austin and Aldridge, 1973, pl. 1, fig. 12

Mestognathus neddensis—Gromczakiewicz-Lomnicka, 1974, pl. 2, figs. 4a-d (Negatives for 4a,b reversed.)

Mestognathus bipluti—Austin, 1974, pl. 1, fig. 22

Mestognathus bipluti—Austin and Husri, 1974, pl. 5, figs. 9a-c,10a,b

Mestognathus neddensis—Austin and Husri, 1974, pl. 5, figs. 7a-c [only] (Negative for 7c reversed.)

Mestognathus bipluti—Higgins, 1975, pl. 8, figs. 8,10

Mestognathus sp.—Higgins, 1975, pl. 10, figs. 12,13

Mestognathus bipluti—Bless et al., 1976, pl. 14, fig. 14 (Negative reversed.)

Mestognathus bipluti—Skompski and Sobon-Podgorska, 1980, pl. 5, figs. 11,13,14

?*Mestognathus bipluti*—Park, 1983, pl. 1, figs. 10-12

Mestognathus bipluti—Belka, 1983, pl. 1, figs. 5-8; pl. 2, figs. 3a,b,4,8a,b

Mestognathus bipluti—Herbig, 1984, pl. 8, figs. 10,11

Mestognathus bipluti—Varker and Sevastopulo, 1985, pl. 5.4, figs. 17,18

ORIGINAL DIAGNOSIS

A *Mestognathus* with two denticulate parapets, inner and outer, at the anterior end of the unit (from Higgins, 1961:216).

SUBSEQUENT DIAGNOSIS

A species of *Mestognathus* distinguished by its two denticulated anterior parapets (from Varker and Sevastopulo, 1985:198).

REVISED DIAGNOSIS

A species of *Mestognathus* that has a deep anterior notch; a long anterior blade; and a subparallel, denticulate spatulate parapet, which in adults bears three or more denticles.

STRATIGRAPHIC RANGE

Lower part of *Cavusgnathus* Zone to *C. naviculus* Zone.

GEOGRAPHIC DISTRIBUTION

Eastern North America (Nova Scotia, Quebec, and Newfoundland) and Europe (Republic of Ireland, Wales, Scotland, England, Federal Republic of Germany?, Poland, Belgium, and Spain).

MATERIAL EXAMINED

Two primary types and four topotypes from North Staffordshire; paratypes UNB 64-F-217 (MV-1) and UNB 64-F-214 (KD-6) of Globensky (1967) from Nova Scotia; holotype BMNH X 250 and figured specimens BMNH X 248 and X 249 of Rhodes, Austin, and Druce (1969) and figured specimen CQ 139 of Austin (1974), all from Wales; figured specimens BMNH X 246 and X 247 of Rhodes, Austin, and Druce (1969) from Scotland; figured specimens Z.1.43, Z.1.44, and Z.1.46 of Austin and Husri (1974) from the Republic of Ireland; 104 specimens from Atlantic Canada (Table 3).

REMARKS

Our revised diagnosis emphasizes the denticulate, spatulate parapet and differentiates this structure from the anterior blade. Of the three or more parapet denticles, at least two are situated anterior to the denticle that forms the high point of the parapet. The parapet slopes gently anteriorwards from this high point.

Marks and Wensink (1970:266) believed that this species differed from *Mestognathus beckmanni* in having a median carina. Our observations suggest that the two species are identical in this respect.

Re-examination and photographic documentation using the scanning electron microscope (Pl. 2, figs. 6,7; Pl. 3, figs. 6,7; Pl. 4, figs. 6,7; Pls. 21,22) of the types of *M. bipluti* Higgins (Pl. 1, figs. 9,10) and of topotype specimens (Pl. 23, figs. 5-10) demonstrate the following:

a) The holotype and paratype of *M. bipluti* are poorly preserved. The upper surface of the holotype is covered with an organic coating that we were unable to remove with common organic solvents (Pl. 2, fig. 6; Pl. 4, fig. 6; Pl. 21, figs. 1,3,6). Attempts at physical removal with a fine needle caused some scratches on the holotype (Pl. 22, fig. 6). At least one of the topotypes had the same coating (Pl. 23, figs. 5,6). In both cases the quality and resolution of the SEM pictures were adversely affected. The paratype, although lacking the problematic organic coating, is heavily corroded (Pl. 2, fig. 7; Pl. 3, fig. 7; Pl. 4, fig. 7; Pl. 21, figs. 2,7,9; Pl. 22, figs. 3,5,8).

b) The elongate, denticulate spatulate parapet, a feature idealized by Higgins (1961) in his text-figure 4 and in his description of the left lateral view (rather than in his photographic illustrations), was and continues to be the

most useful characteristic in recognizing and defining the species.

c) For reasons of nondevelopment, poor preservation, and breakage, as well as of ontogenetic variation, the presence of a fixed number of parapet denticles (given as "usually 6" by Higgins, 1961, but shown as five in his text-figure 4) is often difficult or impossible to document in this species. For example, although we are able to document the large spatulate parapet (Pl. 4, figs. 4,7; Pl. 21, figs. 3,7; Pl. 23, figs. 5-10) we are unable to determine the number of denticles on the holotype and paratype of *M.*

bipluti (Pl. 4, figs. 4,7; Pl. 21, figs. 3,7). A. C. Higgins has indicated (pers. comm., 1985) that, although the parapet denticles of the holotype of *M. bipluti* are not complete, he was able, in his doctoral dissertation, to document photographically five or six parapet denticles on this specimen. A second, more complete, specimen was shown by him, in the same work, to have had five parapet denticles. A large topotype specimen of this species from North Staffordshire, examined by us, does show six parapet denticles (Pl. 23, figs. 5,6).

Synonymized Species

Mestognathus dhuensis Globensky, 1967—Junior synonym of *M. bipluti*, *M. beckmanni*, and *Mestognathus* sp.

The presence of moderately abundant mestognathids in conodont faunas of Early Carboniferous age of Atlantic Canada (Globensky, 1967; von Bitter, 1976; von Bitter and Plint-Geberl, 1982), the uncertain taxonomic status of *M. dhuensis* Globensky, 1967 (the first mestognathid known and named from North America), and the blurred illustrations of that species (Globensky, 1967, pl. 57; here reproduced as Pl. 1, figs. 22-25) prompted P. H. von Bitter to begin his evaluation of the taxonomic validity of species of *Mestognathus*.

Detailed examination and redocumentation of the types of *M. dhuensis* (Pl. 2, figs. 8-11; Pl. 3, figs. 8-11; Pl. 4, figs. 8-11; Pls. 25-27) have shown the following:

a) Although the anterior blade of the holotype has probably been broken since 1967 (Pl. 3, fig. 8; Pl. 4, fig. 8; Pl. 25, fig. 2; Pl. 26, fig. 3), the other specimens are still in the same state of preservation as when Globensky (1967) designated them types.

b) Two of the four type specimens, including the holotype, are poorly preserved, having a damaged parapet area (Pl. 4, figs. 8-11; Pl. 26, figs. 3,4,7,8). Although Globensky (1967:443) characterized this species as possessing a "short inner parapet bearing two to three small pointed denticles", only one of the type specimens, paratype UNB 64-F-217 (MV-1), showed (Globensky, 1967, pl. 57, fig. 23) or shows (Pl. 4, fig. 10; Pl. 26, fig. 7) any trace of these. Although the anterior end of the parapet is damaged in this specimen, a spatulate parapet bearing two denticles is preserved (Pl. 4, fig. 10; Pl. 26, fig. 7). This specimen is a mature specimen and the only one of the four types that fits Globensky's characterization of the species. Of interest is the fact that although UNB 64-F-216 (MH-2-19), an immature damaged specimen, was designated as holotype (Globensky, 1967:243, pl. 57, fig. 21), specimen UNB 64-F-217 (MV-1), which more accurately

displays the features described by Globensky (1967) for this species, was labelled holotype on the slide housing it.

c) Two of the four type specimens are juvenile specimens (the holotype UNB 64-F-216 (MH-2-19) and paratype UNB 64-F-214 (KD-6)). The relative size (and hence the maturity) of these four specimens is best seen on Plate 1 (figs. 22-25) and Text-figure 2.

d) Of the five specimens studied by Globensky (1967:443), four were figured and designated as types by him. The disposition of the fifth specimen is unknown.

These observations, as well as additional ones based on abundant new material from Atlantic Canada, cause us to conclude the following:

a) The taxonomic identity of the holotype can never be determined with any degree of certainty and the holotype can be identified only as *Mestognathus* sp. The parapet of this specimen was damaged when figured by Globensky (1967, pl. 57, fig. 21; reproduced in this study as Pl. 1, fig. 22)—damage that is documented by us (Pl. 4, fig. 8; Pl. 26, fig. 3; Pl. 27, figs. 10,11).

b) Paratype UNB 64-F-215 (KD-6) has an undamaged parapet (Pl. 27, figs. 4,7) and displays the single large parapet denticle characteristic of *M. beckmanni* (Pl. 1, fig. 23; Pl. 4, fig. 9; Pl. 26, fig. 4). This, taken in conjunction with its relatively large size (Pl. 1, figs. 23-25 and Text-fig. 2), and the fact that it can easily be accommodated in the ontogenetic growth series of *M. beckmanni* (Pl. 17, figs. 1-13; Pl. 19, figs. 1-5) from the upper Windsor Group of Atlantic Canada (the same stratigraphic interval and geographic area from which Globensky, 1967, obtained the five specimens used to describe *M. dhuensis*), causes us to conclude that this paratype is a specimen of *M. beckmanni*.

c) Paratype UNB 64-F-217 (MV-1) agrees most closely with Globensky's concept of *M. dhuensis* and it was apparently intended to be the holotype; nevertheless, we are able to accommodate this specimen easily in the ontogenetic growth series of *M. bipluti* from Atlantic

Canada (Pl. 19, figs. 6–10; Pl. 24, figs. 1–13). We conclude that this specimen is a mature specimen of *M. bipluti*.

d) Paratype UNB 64-F-214 (KD-6) is the smallest of the four types (Pl. 1, fig. 25), does not appear to have a damaged parapet (Pl. 4, fig. 11; Pl. 26, fig. 8), and has a single moderately large parapet denticle anterior to which there is the suggestion of a spatulate enlargement. This specimen can be accommodated without too much difficulty in the lower end of the ontogenetic growth series of *M. bipluti* (Pl. 19, figs. 6–10; Pl. 24, figs. 1–13) from the same stratigraphic interval and geographic region as this paratype. We conclude that it is an immature specimen of *M. bipluti*.

Our conclusion that Globensky (1967) included two existing taxa (*M. beckmanni* and *M. bipluti*) in his new species and that the holotype of *M. dhuensis* is indeterminable and can be identified only generically as a representative of *Mestognathus* agrees only partly with Belka (1983:76) and Park (1983:116). These authors placed *M. dhuensis* in synonymy with *M. beckmanni* and *M. bipluti*, respectively, without having examined the type specimens.

The five *mestognathids* recovered by Globensky (1967) from Atlantic Canada are part of a mixed population of *M. bipluti* and *M. beckmanni* that existed during Viséan time. These mixed populations resulted in the subsequent stratigraphic overlap of these two species, a condition that is the rule in Atlantic Canada (Table 3) and is evident elsewhere. For example, both species co-occur in sample CYD 7 from the Avonian of the North Crop of Wales (Rhodes, Austin, and Druce, 1969:150,152). The Avonian of Great Britain has been correlated with the Windsor (and by extension with the Codroy) Group of Atlantic Canada for many years (Bell, 1929; von Bitter and Austin, 1984).

***Mestognathus neddensis* Rhodes, Austin, and Druce,
1969—Junior synonym of *M. bipluti* and
Mestognathus spp.**

Examination and redocumentation of the types of *M. neddensis* Rhodes, Austin, and Druce (Pl. 1, figs. 13–21) has shown (Pl. 2, figs. 12–14; Pl. 3, figs. 12–14; Pl. 4, figs. 12–14; Pl. 28, figs. 1–9; Pl. 29, figs. 1–10) the following:

a) The types are in the same state of preservation as when originally described by Rhodes, Austin, and Druce (1969).

b) The holotype, specimen BMNH X 250 (Rhodes, Austin, and Druce, 1969, pl. 15, figs. 6a–c), a mature specimen, although corroded, is moderately well preserved, and has a spatulate parapet anterior to two well-defined denticles (Pl. 4, fig. 12; Pl. 28, fig. 6).

c) The two paratypes are so damaged or so poorly preserved that certain specific assignment is impossible. Al-

though in paratype BMNH X 251 (Rhodes, Austin, and Druce, 1969, pl. 15, figs. 4a–c; their figures here reproduced as Pl. 1, figs. 16–18) the parapet is preserved, it is badly twisted, and the specimen is heavily corroded (Pl. 4, fig. 13; Pl. 28, fig. 9). Paratype BMNH X 252 has a broken parapet (Rhodes, Austin, and Druce, 1969, pl. 15, figs. 5a–c; their figures here reproduced as Pl. 1, figs. 19–21) and shows only a single parapet denticle (Pl. 4, fig. 14; Pl. 28, fig. 9).

d) The two paratypes are both juvenile specimens (Pl. 1, figs. 13–21 and Text-fig. 2).

We have been unable to locate the two unfigured specimens used by Rhodes, Austin, and Druce (1969:153) in their definition of this species.

The preceding observations suggest the following:

a) The taxonomic identity of the two paratypes cannot be established because of poor preservation. Additionally, because parapet size, configuration, and denticle number are a function of element size, these two juvenile specimens should not have been used by Rhodes, Austin, and Druce (1969) to characterize a new species of *Mestognathus*.

b) It was probably the holotype that was the basis of the claim (Rhodes, Austin, and Druce, 1969:154) that “the anterior inner edge is *frequently* [our italics] developed into one or two rather conspicuous denticles.” The holotype of *M. neddensis*, a mature well-preserved specimen, possesses a spatulate parapet anterior to the two denticles (Pl. 4, fig. 12; Pl. 28, fig. 6). It lacks the abrupt vertical or even overhanging parapet termination and the single strong parapet denticle characteristic of *M. beckmanni* (Pl. 4, figs. 1,5; Pl. 13, figs. 2,9; Pl. 16, figs. 1,9,11). Higgins (1961:217) described *M. bipluti* as having “a well-developed inner parapet”. Our revised diagnosis of *M. bipluti* and the morphology of the holotype of *M. neddensis* fully meet the requirement for *M. bipluti* of possessing such a well-developed inner parapet. We conclude that the holotype of *M. neddensis* is reasonably included in *M. bipluti*.

In addition to fulfilling this basic criterion the holotype of *M. neddensis* meets other criteria for inclusion in *M. bipluti*. We interpret the holotype of *M. neddensis* to have borne two, possibly three, parapet denticles (since there appears to be a small broken-off denticle anterior to the highest denticle (Pl. 4, fig. 12; Pl. 28, fig. 6)) and to fit into the ontogenetic growth series of *M. bipluti* documented by us from rocks of the same age from Atlantic Canada (Pl. 24).

Although the paratypes of *M. neddensis* cannot be utilized for clarifying the validity of this species, other lines of evidence possibly can. The five specimens used to describe *M. neddensis* apparently all came from samples CYD 6 and CYD 7 from the North Crop of Wales (Rhodes, Austin, and Druce, 1969:153,298). Of the four intermediate-sized specimens of *M. bipluti* illustrated by Rhodes, Austin, and Druce (1969:152; our Pl. 15, figs. 1–3,8), two (BMNH X 248 and X 249) apparently came from the same Welsh

locality and samples as the types of *M. neddensis* (Rhodes, Austin, and Druce, 1969:153).

We have already discussed the existence, in strata of late Viséan age from Atlantic Canada, of mixed mestognathid populations consisting of *M. bipluti* and *M. beckmanni*. There is no evidence, other than specimens transitional between *M. beckmanni* and *M. praebeckmanni* (Table 3 and Pl. 23, figs. 1,2), of another species in these populations—in fact, we were able to synonymize *M. dhuensis* with *M. bipluti*, *M. beckmanni*, and *Mestognathus* sp. We suggest that exactly the same situation, that is, populations of *M. bipluti* and *M. beckmanni* without any other mestognathid species, existed in the carbonate-depositing environments of the North Crop of Wales. This interpretation is particularly convincing because the faunas of both the North Crop and eastern Canada (the upper Windsor and Codroy groups) that most commonly contain mestognathids (Appendix) have been correlated with the D₂ Subzone of the Avon Gorge, near Bristol (Rhodes, Austin, and Druce, 1969, fig. 12; and Bell, 1929:71, respectively).

In summary, our placement of *M. neddensis* in synonymy with *M. bipluti* is based largely on the parapat

morphology of the holotype and to a lesser degree on our comparison of the mixed species composition of the mestognathid populations, of apparently identical age, from the North Crop of Wales and Atlantic Canada. Similar populations probably existed during the Viséan in Scotland (Rhodes, Austin, and Druce, 1969; specimens BMNH X 245, X 246, X 247), in Flintshire, North Wales (Aldridge, Austin, and Husri, 1968, table 1), and in the Federal Republic of Germany (Paproth, Stoppel, and Conil, 1973, tables 1–3). They may also have existed in Poland (Skompski and Sobon-Podgorska, 1980; Belka, 1983), in the Republic of Ireland (Austin and Husri, 1974, fig. 18), and elsewhere.

Our assessment of the holotype of *M. neddensis* agrees with that of Belka (1983:77), who reached the same conclusion without having examined the types of *M. neddensis*. We cannot, however, agree with his placement (1983:76) of the two paratypes in *M. beckmanni*. Although they may have belonged to *M. beckmanni*, their preservation makes it impossible to determine their original identity.

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Appendix: Locality Register

Locality information for the 24 localities was obtained from a variety of published and unpublished sources. The accuracy with which measurements such as latitude and longitude were given varied, as did directions for the relocation of specific localities. We have been unable to impose one "standard" on this diverse information, and we invite interested readers to consult the references we have cited.

LOCALITY 1

NW SW NW sec. 23 T. 7 S. R. 18 W. Tooele Co., Utah, United States.

Gold Hill Map Sheet 1:24 000 quadrangle.

Samples taken in Joana Limestone in medium grey, very coarse recrystallized crinoidal (= encrinitic) wackestone, interpreted as being a debris flow.

Original sample, PCM-35, collected in 1981 by John Harmala from unknown position below top of Joana Limestone. This sample yielded three specimens of *Mestognathus harmalai* sp. nov., a species referred to *Clydagnathus* cf. *C. cavusformis* Rhodes, Austin, and Druce (1969), by Harmala (1982).

Seven samples were collected subsequently by Sandberg in an attempt to locate the exact position of Harmala's sample PCM-35. Of these the following three collected in 1982 produced eight additional specimens of *M. harmalai* sp. nov.:

Sample PC-2A from 14 m below the top of the Joana Limestone;

Samples PC-2B and PC-2B(R) from 14.8 m below the top of the Joana Limestone.

Fauna recovered from 29 kg of seven combined samples

(partial list of Pa elements in 1851 platform and ramiform conodonts recovered by Sandberg)

Mestognathus harmalai sp. nov. (8); *Polygnathus communis communis* (1016), *P. communis carina* (3); *Bispathodus utahensis* (99); *Hindeodus* spp. (4); *Pseudopolygnathus multistriatus* morphotypes 1 and 2 (81, combined); and *Bactrognathus* sp. nov. Lane, Sandberg, and Ziegler (2).

Zone determination

Mestognathus harmalai Zone of *Mestognathus*-based shallow-water zonation; Lower *Gnathodus typicus* Zone of standard zonation.

LOCALITY 2

Route between Salet and Bioul, 8 km NW of Dinant, Belgium.

Section 8 in Groessens (1971).

A single sample, BEL-5, collected by Sandberg in 1971 in Banc 60 of Groessens (1971), log 6; (1974), planche 10. Sample taken in medium- to thin-bedded dark grey cherty biomicrite of the "Facies de Leffe", interpreted as being in the slope facies.

Fauna recovered from 3.1 kg of sample

Mestognathus praebeckmanni sp. nov. morphotype 2 (2); *Gnathodus semiglaber* (3); *Bispathodus utahensis* (4); miscellaneous ramiform elements (23).

Zone determination

Mestognathus praebeckmanni Zone of *Mestognathus*-based shallow-water zonation; *Scaliognathus anchoralis*-*Doliognathus latus* Zone of standard zonation.

LOCALITY 3

r 60 000 h 86 160. Amusement Park, Cromford (Blauer See), Ratingen, Westphalia, Federal Republic of Germany. Kettwig Map Sheet 1:25 000.

A single sample, GER-80-1, collected by Sandberg in 1980 in Bed 58 of the Cromford Profil of Paproth, Stoppel, and Conil (1973:135 and table 1) in yellowish-brown weathering, very finely crystalline dolomitized calcarenite.

Fauna recovered from 2.7 kg of sample

Mestognathus praebeckmanni sp. nov. morphotype 3 (1); *Scaliognathus anchoralis europensis* (31); *Gnathodus pseudosemiglaber?* (6); *Polygnathus bischoffi* (2); *Bispathodus utahensis* (18); *Hindeodella segaformis* (9); miscellaneous ramiform elements (14).

Zone determination

Mestognathus praebeckmanni Zone of *Mestognathus*-based shallow-water zonation; *Scaliognathus anchoralis*-*Doliognathus latus* Zone of standard zonation.

LOCALITY 4

r 76 070 h 89 430. Abandoned Zippenhaus Quarry, near railroad track from Neviges to Langenberg, Westphalia, Federal Republic of Germany.

Velbert Map Sheet 1:25 000.

Two samples, GER-80-5 and GER-80-6, collected by Sandberg in 1980 from section described by Paproth, Stoppel, and Conil (1973:70, fig. 3; 138, table 4).

Sample GER-80-5 was taken from Bed 11 in medium, olive-grey biomicrite.

Fauna recovered from 2.8 kg of sample

Mestognathus beckmanni (9); *Gnathodus homopunctatus*

(22), *G. semiglaber* (2), *G. pseudosemiglaber* (15), *G. bilineatus?* (22), *G. cf. G. bilineatus* (30), *G. spp. unsorted* (401); *Polygnathus triangulus* (45), *P. bischoffi* (1); miscellaneous ramiform elements (288).

Sample GER-80-6 was taken from near the top of Bed 17 in a medium grey, finely crystalline, slightly bioclastic limestone.

Fauna recovered from 2.2 kg of sample

Mestognathus beckmanni (4); *Gnathodus homopunctatus* (6), *G. pseudosemiglaber* (35), *G. cuneiformis* (22), *G. cf. G. bilineatus* (13); *Geniculatus cf. G. glottoides* (14); miscellaneous ramiform elements (35).

Zone determination

Mestognathus beckmanni Zone of *Mestognathus*-based shallow-water zonation; *Scaliognathus anchoralis*–*Gnathodus bilineatus* interregnum of German authors.

LOCALITY 5

Section beside Rockfield House, Kingscourt Outlier, 4.3 km on a bearing of N100° E from Nobber, Co. Meath, Republic of Ireland.

Five samples, nos. 21, 28, 30, 31, and 35, taken in Kilbride Limestone at 11.6, 25.6, 28.4, 29.6, and 26.4 m above the base of the section and containing 1, 6, 9, 1, and 2 *Mestognathus praebeckmanni* sp. nov., respectively. One sample, no. 17, taken from the top of the stream section 1.6 km (on a bearing of S60°N) from locality 5, contained one specimen of the same species. Collections, determinations, and information for this locality from I. S. Johnston (pers. comm., 1983 and in manuscript, 1985).

Fauna recovered from 7.1 kg (combined weight of six samples)

Mestognathus praebeckmanni sp. nov. (mostly) morphotype 1; *Scaliognathus anchoralis*; *Polygnathus bischoffi*, *P. mehli mehli*; *Pseudopolygnathus minutus*; gen. nov. A Johnston; *Gnathodus simplicatus*; *Apatognathus* spp.; Tournaisian foraminifera.

Zone determination

Scaliognathus anchoralis–*Doliognathus latus* Zone of standard zonation; *Mestognathus praebeckmanni* Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 6

Lat. 53°10'46.6"; Long. 121°34'13.3" NTS 5893, E59556. On logging road south of creek emptying into Big Valley Creek, east of Cape Creek, east-central British Columbia, Canada.

McBride Map Sheet (93H).

Three samples, 12-2, 12-2/80, and 12-2/81, collected by

L. C. Struik and M. J. Orchard at GSC localities C-86251, C-102687, and C-101910 in 1978, 1980, and 1981, respectively.

Fauna recovered from 5.1 kg (combined weight of two samples; plus unknown quantity processed in 1978)

Mestognathus praebeckmanni sp. nov. (2), *M. sp. indet.* (1); *Bispathodus* sp. indet. (4); *Polygnathus cf. P. communis* (27); ramiform fragments. Colour alteration index = 6.

Zone determination

Mestognathus praebeckmanni Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 7

NTS 5891, E59531. North side of unnamed creek, small cliff exposure of coarsely crinoidal limestone, 3.5 km at 219° from Two Sisters Mountain, east-central British Columbia, Canada.

McBride Map Sheet (93H).

Two samples, 80-6 and MC81/32A, collected by L. C. Struik and M. J. Orchard at GSC localities C-102691 and C-102562 in 1980 and 1981, respectively.

Fauna recovered from 14 kg (combined weight of two samples)

Mestognathus praebeckmanni sp. nov. morphotype 1 (17), *M. harmalai* sp. nov. (1); *Hindeodus cf. H. cristulus* Pa element (2); *Pseudopolygnathus?* sp. (1); fragmentary ramiform elements, ichthyoliths. Colour alteration index = 5.

Zone determination

Mestognathus praebeckmanni Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 8

NTS 58743, E615375. 2 km SSW of Mount Tinsdale, east-central British Columbia, Canada.

McBride Map Sheet (93H).

Two collections of unknown stratigraphic relationship to each other made as sample 46-23/80 by L. C. Struik at GSC locality C-102688 in 1980.

Fauna recovered from 3.2 kg (combined weight of two samples)

Eotaphrus burlingtonensis (8); *Hindeodella segaformis* (~3); *Polygnathus communis* (100+), *P. mehli* (8), *P. spp.* (12); *Hindeodus cristulus* Pa element (1); *Bispathodus* spp. (8); *Clydagnathus* sp. (1); *Mestognathus praebeckmanni* sp. nov. (1); numerous ramiform elements. Colour alteration index = 5.

Zone determination

Uncertain because of sample combination.

LOCALITY 9

Lat. 57°54'40"; Long. 127°40'25". Northern British Columbia, Canada.

Toodoggone Map Sheet (94E).

One sample, GAT 79/33B, collected by L. Thorstad at GSC locality C-86321 in 1979.

Fauna recovered from 1.6 kg of sample

Mestognathus beckmanni (2), *M. praebeckmanni* sp. nov. morphotype 2 or 3 (1), *M.* sp. indet. (1). Colour alteration index = 7.

Zone determination

Mestognathus beckmanni Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 10

Lat. 57°56'10"; Long. 127°42'25". Northern British Columbia, Canada.

Toodoggone Map Sheet (94E).

Two samples, GAT 79 and GAT 79/94, collected by L. Thorstad in 1979 at GSC localities C-86322 and C-86323, respectively.

Fauna recovered from unknown combined weight

Mestognathus beckmanni (8), *M. praebeckmanni*? sp. nov. (1), *M.* spp. (15); unidentified polygnathid? fragment (1); ozarkodiniform element (1). Colour alteration index = 7.

Zone determination

Mestognathus beckmanni Zone of *Mestognathus*-based shallow-water zonation.

Note for Localities 9 and 10: *M. beckmanni* is known, and is practically the only conodont recovered, from buff to orange-weathering dolomitic carbonate beds, 1 to 2 m thick, containing abundant crinoidal debris. These beds, which are interlayered with sericite schist, occur amidst a suite of volcanic and volcanoclastic rocks metamorphosed to greenschist facies. These structurally complex rocks appear to have undergone at least two phases of metamorphism. Chemically and lithologically they resemble an island-arc suite (Thorstad, 1980).

LOCALITY 11

Lat. 67°04'55"; Long. 152°28'25". South foot of slope from mafic peak, Heart Mountain, north-central Alaska, United States.

Wiseman A-5 Quadrangle.

One sample, 73 Tr 7.1 (USGS collection 28582-PC), collected by Irving Tailleux in 1973 from fossiliferous limestone/marble of unnamed unit.

4.1 kg of limestone was processed by Anita Harris and Kirk Denkler (USGS, Washington) in 1981 for conodonts. 145.5 g of +20 mesh insoluble residue remained.

Fauna recovered (determinations by Sandberg)

Pseudopolygnathus oxypageus morphotype 2 (1); *Gnathodus semiglaber* (1); *Doliognathus latus* morphotype 2 (2); *Mestognathus praebeckmanni* morphotype 1 or 2 (1); *Eotaphrus burlingtonensis* late? morphotype with small basal cavity (2); *Polygnathus communis communis* (5); *Scaliognathus dockali* (3); *Hindeodella segaformis* fragments (16); *Bactrognathus* sp. nov. Lane, Sandberg, and Ziegler, Pa element (1) and Pb element (1). Colour alteration index = 4½.

Zone determination

Scaliognathus anchoralis–*Doliognathus latus* Zone of standard zonation.

Note: We have been informed by Anita Harris, USGS, Washington (pers. comm., 1985) that additional localities for *Mestognathus* have recently been found in Alaska.

LOCALITY 12

Lat. 54°06'21"; Long. 120°12'27". Single sample taken by A. C. Higgins 27.5 m above base of Pekisko Formation, GSC locality C-93515, sample 81-RAH-ACH-1, Jarvis Lakes area, Monkman Pass region, northeastern British Columbia, Canada. Collections, determinations, and information for this locality by A. C. Higgins (pers. comm., 1983), except as noted.

Fauna present

Polygnathus communis communis; *Hindeodus?* *penescitulus*; *Neoprioniodus barbatus* and two specimens of *Clydagnathus gilwernensis*–*Mestognathus harmalai* sp. nov. transition (smaller of two lost during electron microscopy). (Determination of transition species by authors.)

Zone determination

Siphonodella isosticha–Upper *S. crenulata* Zone of standard zonation.

Additional comments

Siphonodella isosticha occurs 10 m below the sample with the *Clydagnathus*–*Mestognathus* transition species.

LOCALITY 13

Type section of the Miller Creek Formation (Moore *in* Geldsetzer et al., 1980), lower Windsor Group, exposed in the Miller Creek gypsum quarry of Fundy Gypsum Co. Ltd, Hants Co., Nova Scotia.

Windsor Map Sheet 21A/16 East Half 1:50 000.
Fisher and Belmont members of the Miller Creek Formation (Moore *in* Geldsetzer et al., 1980) sampled in 1975 by von Bitter in southwest corner of quarry (see Dhindsa, 1984).

Sample Fisher-2-1 0.38 m Limestone, blocky, grey, irregularly bedded; upper 12 cm contains 4 cm thick shaly interval above which are irregular weathering nodular beds. Sample taken between the base and 0.38 m above the base of the member.

Fauna recovered from 2 kg of sample

Mestognathus bipluti (3), *M. beckmanni* (5), *M. spp.* (5); *Clydagnathus windsorensis* Pa element (1); *Cavusgnathus unicornis* Pa element (50); *Vogelgnathus? campbelli* (50); *Spathognathodus? sp. nov.* A von Bitter (3); *Gnathodus girtyi* (3); unidentified ramiform and other elements (23).

Sample Bel-2-3 0.28 m Limestone, massive bedded, containing crinoid fragments and nodular weathering productid brachiopods; unit is finely pitted owing to oolites and/or microfossils weathering out; uppermost 15 cm green shale with nodules of gypsum; upper contact of member is with greenish gypsum. Sample taken from between 1.5 m above the base to the top of the member.

Fauna recovered from 2 kg of sample

Mestognathus bipluti (2), *M. spp.* (2); *Taphrognathus transatlanticus* Pa element (26); *Clydagnathus windsorensis* Pa element (14); *Gnathodus spp.* (3); *Cavusgnathus unicornis* Pa element (66); *Paragnathodus scotiaensis* (50); *Vogelgnathus? campbelli* (668); *Spathognathodus? sp. nov.* A von Bitter (78); *Kladognathus tenuis* (69); *Hindeodus cristulus* Pa element (13); unidentified ramiform and other elements (118).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 14

Type section of the Wentworth Formation (Moore *in* Geldsetzer et al., 1980), lower Windsor Group, exposed in the Wentworth gypsum quarry of Fundy Gypsum Co. Ltd, Hants Co., Nova Scotia, Canada. According to Moore (*in* Geldsetzer et al., 1980), this section is overturned.

Windsor Map Sheet 21A/16 East Half 1:50 000.

Section sampled in 1973 and 1975 by von Bitter in haulage road section (see Dhindsa, 1984).

One sample, Went-1-1, taken of the Fisher Member of the Miller Creek Formation of Moore (*in* Geldsetzer et al., 1980).

Went-1-1 1.85 m Limestone, earthy, yellow to yellowish-brown weathering; lowest 53 cm is medium to thick-bedded; next higher 53 cm is thin-bedded, grey limestone; next higher 53 cm is medium-bedded limestone; uppermost 26 cm is nodular limestone breccia; upper and lower contacts of overall unit indistinct, sampled as a single sampling unit. Sample is of entire thickness of member.

Fauna recovered from 2 kg of sample

Mestognathus sp. (1); *Cavusgnathus unicornis* Pa element (6); unidentified ramiform elements (4).

Two samples, St.Cr-2-5 and St.Cr-2-4, taken in the St Croix Member of the Wentworth Formation of Moore (*in* Geldsetzer et al., 1980).

St.Cr-2-5 10 cm Shale, black, earthy. Sample taken between 3.30 and 3.40 m above apparent base of member.

Fauna recovered from 1.82 kg of sample

Mestognathus beckmanni (2), *M. sp.* (1); *Clydagnathus windsorensis* Pa element (41); *Cavusgnathus unicornis* Pa element (1); *Paragnathodus scotiaensis* (1); *Spathognathodus? sp. nov.* A von Bitter (94); unidentified ramiform elements (16).

St.Cr-2-4 0.46 m Limestone, single medium-bedded unit, slightly platy; uppermost part is irregular weathering nodular algal-oncolite unit. Sample taken between 2.84 and 3.30 m above apparent base of member.

Fauna recovered from 2 kg of sample

Mestognathus bipluti (2), *M. beckmanni* (1); *Clydagnathus windsorensis* Pa element (6); *Paragnathodus scotiaensis* (1); unidentified ramiform elements (5).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 15

Type section of Herbert River Member (Moore, 1967) of the Murphy Road Formation (Giles, 1981:8), upper Windsor Group, exposed south of railroad bridge on tidal slope and in bluff on Avon River, Windsor, Hants Co., Nova Scotia. Windsor Map Sheet 21A/16 East Half 1:50 000.

Section 5 of Bell (1929:50).

Three samples, Hb-1-5, Hb-1-6, and Hb-1-7, taken between the apparent base and 2.79 m above the apparent base of the Herbert River Member. The three units sampled are part of unit (g) of section 5 of Bell (1929:50). Moore (1967:249) interpreted this section to be overturned. If this interpretation is correct then sampling units Hb-1-5, Hb-1-6, and Hb-1-7 are successively younger.

Hb-1-5 1.22 m Limestone, grey, very shaly and nodular weathering; weathers brownish-tan and is recessive; thin to medium irregularly bedded. From 1.58 to 2.80 m above *apparent* base.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (2).

Hb-1-6 0.81 m Limestone, irregular and nodular bedding, earthy reddish-brown weathering. From 0.76 to 1.58 m above *apparent* base.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (1), *M. sp.* (juvenile) (1), *M. sp.* (1).

Hb-1-7 0.76 m Limestone, nodular, red weathering. From 0 to 0.76 m above *apparent* base.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (8), *M. beckmanni* (3), *M. spp.* (juveniles) (2), *M. spp.* (4).

One sample, Hb-1-8, taken between the *apparent* base and 23 cm below the *apparent* base of the Herbert River Member. This sampling unit is unit (f) of Bell (1929:50), a unit that would be younger than sampling unit Hb-1-7, if the interpretation of an overturned section (Moore, 1967:249) is correct.

Hb-1-8 0.23 cm sampled Siltstone, green.

Mestognathids recovered from 2 kg of sample
Mestognathus spp. (2).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 16

Type section of Avon Member (Moore, 1967) of the Murphy Road Formation (Giles, 1981:8), upper Windsor Group, exposed north of railroad bridge and south of former road bridge on tidal slope and in bluff on east bank of Avon River, Windsor, Hants Co., Nova Scotia.

Windsor Map Sheet 21A/16 East Half 1:50 000.

Section 9 of Bell (1929:52).

Two samples, Avn-1-4 and Avn-1-5, taken in the Avon Member. Avn-1-4 and Avn-1-5 probably taken in units (d) and (e), respectively, of section 9 of Bell (1929:52).

Avn-1-4 0.84 m Limestone, grey, medium to thick-bedded; middle portion weathers more shaly. Sample taken between 2.67 and 3.51 m above base of member.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (6).

Avn-1-5 0.86 m Limestone, grey, weathering brown, medium to thick-bedded, bioclastic. Sample taken between 3.51 and 4.37 m above base of member.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (6).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 17

Type section of Wallace Point Member (Moore, 1967) of the Murphy Road Formation (Giles, 1981:8), upper Windsor Group, exposed at Wallace Point, mouth of the Kennetcook River, Hants Co., Nova Scotia.

Windsor Map Sheet 21A/16 East Half 1:50 000.

Section 10 of Bell (1929:53).

Three samples, WaPt-1-1, WaPt-1-2, and WaPt-1-3, taken between the base and 1.80 m above the base of the Wallace Point Member. The three units sampled are unit (a) of section 10 of Bell (1929:53) and are equivalent to the lowest three units of the Wallace Point Member shown by Moore (1967, fig. 2).

WaPt-1-1 0.8 m Limestone, bluish-grey, thin-bedded, pitted owing to weathered microfossils. Interbedded with clay-rich, blue-coloured shale partings. Basal 0.8 m of member.

Mestognathid recovered from 2 kg of sample
Mestognathus beckmanni (1).

WaPt-1-2 0.43 m Limestone, medium grey, medium-bedded, in part laminated. Lower part sandy, and upper 5 to 10 cm more carbonate rich and contains brachiopods. Sample taken from 8 to 51 cm above base of member.

Mestognathids recovered from 2 kg of sample
Mestognathus bipluti (4), *M. sp.* (juvenile) (1), *M. spp.* (5).

WaPt-1-3 1.29 m Limestone, medium grey, thin to medium-bedded; shaly, slightly nodular weathering; brachiopods common, especially in lower portion. Sample taken from 51 to 180 cm above base of member.

Fauna recovered from 2 kg of sample

Mestognathus bipluti (21), *M. beckmanni* (5), *M. spp.* (juveniles) (6), *M. spp.* (8); *Gnathodus bilineatus* Pa

element (46), *G. girtyi* Pa element (2); *Paragnathodus scotiaensis* (5); *Vogelgnathus? campbelli* (3); *Apatognathus* sp. (1); *Ozarkodina laevipostica* (1); *Cavusgnathus?* sp. Pa element (1); and numerous unidentified conodont fragments.

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 18

Borehole SB-1 of the United States Borax and Chemical Corporation in the Windsor Group, 3.9 km northeast of Stewiacke, Colchester Co., Nova Scotia, at intersection of the Stewiacke River and Canadian National Railway track; on south side of river and west of track just east of Highway 2. (See Giles and Boehner, 1979; Utting, 1980, fig. 1; Giles, 1981; Weston, 1985.) Our usage of the names of members stratigraphically below the Herbert River Member is in accord with Utting (1980:1032). These names, although used by Giles and Boehner (1979), have not been formally described and are therefore placed in quotation marks.

Shubenacadie Map Sheet 11E/3 1:50 000.

One sample, Mosh-15-1, taken from the total thickness of "Mosher Road Member" of the MacDonald Road Formation (Giles, 1981:7) in borehole SB-1 between 479.23 and 476.86 m.

Mosh-15-1 2.36 m Dolostone, thick to thin-bedded alternating layers, anhydrite nodules in upper portion; bryozoans, whole brachiopods, echinoderm fragments present—more abundant in lower portion. Sample taken from base to 2.36 m above base of member.

Fauna recovered from 4.88 kg of core

Mestognathus sp. (juvenile) (1); *Taphrognathus transatlanticus* Pa element (3); *Cavusgnathus unicornis* Pa element (1); *Paragnathodus scotiaensis* (8); numerous unidentified ramiform elements.

One sample, Clov-13-4, taken in borehole SB-1 in the "Cloverdale Member" (Giles and Boehner, 1979) of the MacDonald Road Formation (Giles, 1981:7) between 455.49 and 455.14 m.

Clov-13-4 0.35 m Dolostone, generally thick-bedded, calcite rich and burrowed at top of sampling unit; disturbed, thin-bedded in lower part; ghosts of shell and echinoderm fragments present. Sample taken from 1.52 to 1.87 m above base of member.

Fauna recovered from 1.09 kg of core

Mestognathus beckmanni (1); *Cavusgnathus* sp. (1).

Three samples, HerbR-8-4, HerbR-8-5, and HerbR-7-7, taken in the Herbert River Member (Moore, 1967) of the

Green Oaks Formation (Giles, 1981:8) in borehole SB-1 between 322.29 and 320.30 m, 320.30 and 317.75 m, and 317.25 and 316.79 m, respectively. Samples taken between 2.96 and 4.95 m, 4.95 and 7.50 m, and 8.00 and 8.46 m above base of member, respectively.

HerbR-8-4 1.99 m Dolostone, thick-bedded, containing anhydrite nodules; burrows common; ghosts of echinoderms, gastropods, and other shells present.

Mestognathid recovered from 4.1 kg of core

Mestognathus beckmanni (1).

HerbR-8-5 2.55 m Dolostone, thick irregularly bedded, wispy inclusions of possible organic origin; burrowed.

Mestognathids recovered from 4.83 kg of core

Mestognathus bipluti (2), *M. beckmanni* (2).

HerbR-7-7 0.46 m Dolostone, thick-bedded, burrows common.

Fauna recovered from 1.18 kg of core

Mestognathus bipluti (7), *M. beckmanni* (42), *M. spp.* (juveniles) (4), *M. spp.* (14); *Gnathodus bilineatus* (1).

One sample, Avn-5-1, taken in the Avon Member (Moore, 1967) of the Green Oaks Formation (Giles, 1981:8) in borehole SB-1 between 263.43 and 261.44 m. Sample taken between the base and 1.99 m above base of member.

Avn-5-1 1.99 m Dolostone, medium to thick-bedded, containing anhydrite nodules; planar algal? laminations present; brachiopod concentration near top.

Mestognathids recovered from 3.36 kg of core

Mestognathus bipluti (14), *M. beckmanni* (6), *M. spp.* (juveniles) (5), *M. sp.* (1).

Two samples, MeaR-4-1 and MeaR-4-3, taken in the Meander River Member (Moore, 1967) of the Green Oaks Formation (Giles, 1981:8) in borehole SB-1 between 244.14 and 242.69 m, and 242.69 and 241.16 m, respectively. (Giles and Boehner, 1979; Utting, 1980, fig. 2.)

MeaR-4-1 1.45 m Dolostone, medium-bedded, thin interbedded laminated layers throughout, burrows common; ghosts of ooids and ostracods. Sample taken between base and 1.45 m above the base of the member.

Fauna recovered from 3.15 kg of core

Mestognathus sp. (1); *Gnathodus bilineatus* (1).

MeaR-4-3 1.53 m Dolostone, medium to thick-bedded, irregular wispy inclusions of possible organic material in lower portion; echinoderm and shell fragments common.

Sample taken between 1.45 and 2.98 m above base of member.

Fauna recovered from 3.28 kg of core

Mestognathus spp. (2); *Cavusgnathus unicornis* Pa element (3); *Paragnathodus scotiaensis* (1); *Apatognathus* sp. (1).

Two samples, WaPt-3-2 and WaPt-3-3, taken in the Wallace Point Member (Moore, 1967) of the Green Oaks Formation (Giles, 1981:8) in borehole SB-1 between 222.03 and 221.11 m, and 221.11 and 218.37 m, respectively.

WaPt-3-2 0.92 m Dolostone, medium to thick-bedded; ghost fossils of pelmatozoan and shell material common. Sample taken between 0.61 and 1.53 m above base of member.

Fauna recovered from 2.11 kg of core

Mestognathus bipluti (3), *M. beckmanni* (3), *M.* spp. (2); *Cavusgnathus unicornis* Pa element (5); *Hindeodus cristulus* Pa element (7); *Gnathodus bilineatus* (14); *Paragnathodus scotiaensis* (6); *Apatognathus* sp. (1).

WaPt-3-3 2.74 m Dolostone, medium to thick, irregularly bedded; wispy inclusions of possible organic origin; some ghosts of shell material. Sample taken between 1.53 and 4.27 m above base of member.

Fauna recovered from 5.04 kg of core

Mestognathus bipluti (7), *M. beckmanni* (3), *M.* sp. (juvenile) (1); *Hindeodus cristulus* Pa element (9); *Gnathodus bilineatus* (8); *Paragnathodus scotiaensis* (13); *Apatognathus* spp. (6).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation (samples HerbR-7-7 to WaPt-3-3). Below the lowest occurrence of *M. bipluti* in HerbR-7-7, no zonal determination, based on *Mestognathus*, is possible.

LOCALITY 19

Northumberland Strait shore, between outlet of McAras Brook and Knoydart Point, Antigonish Co., Nova Scotia, Canada.

Merigomish Map Sheet 11E/9 1:50 000. Stop 4 of Giles (*in* Geldsetzer et al., 1980:17, fig. 8). Member designated by a combination of a letter and a number is regarded as an informal stratigraphic unit and is therefore placed in quotation marks.

The lowest carbonate bed of the Ardness Formation, upper Windsor Group, the "D₁ Limestone" of Giles (*in* Geldsetzer et al., 1980, fig. 8), was sampled as grab-sample Ard-1-1.

Mestognathid recovered from 2.59 kg of sample

Mestognathus beckmanni (1).

Zone determination

Indeterminate.

LOCALITY 20

Port Hood Island, Inverness Co., Cape Breton Island, Nova Scotia, Canada.

Port Hood Map Sheet 11K/4 1:50 000.

See von Bitter (1976). Members designated by combination of a letter and a number are regarded as informal stratigraphic units and are therefore placed in quotation marks. The "C₃ Limestone" (upper Windsor Group) of Stacy (1953) and Schenk (1969) was sampled.

PHI-C₃-4 1.77 m Limestone, oolitic, light grey, weathers buff; unit makes up main point jutting into sea. Sample taken between 1.83 and 3.60 m above the base of the "C₃ Limestone".

Fauna recovered from 2 kg of sample

Mestognathus bipluti (1), *M.* spp. (4); *Gnathodus bilineatus* (1).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 21

Port Hood Island, Inverness Co., Cape Breton Island, Nova Scotia, Canada.

Port Hood Map Sheet 11K/4 1:50 000.

See von Bitter (1976).

Two samples, PHI-D₁-2 and PHI-D₁-3, taken in the "D₁" or "Giant Ripple Limestone" (upper Windsor Group) of Stacy (1953) and Schenk (1969).

PHI-D₁-2 1.07 m Limestone, medium grey, medium-bedded, with two or three thin partings. Identified as biolithite by Schenk (1969, fig. 4). Unit has characteristic mottled appearance owing to presence of fingerlike algal stromatolites (Schenk, 1969, fig. 12). Stromatolites are medium grey, hard, and weather in relief. Fillings between are a tan colour, softer, and weather out. Base of sampling unit contains 2.5 to 5.0 cm wide pitted structures, possibly owing to algae. Sample taken between 0.56 and 1.63 m above the base of "D₁ Limestone".

Fauna recovered from 2 kg of sample

Mestognathus bipluti (6), *M. beckmanni* (2), *M.* spp. (juveniles) (2), *M.* spp. (10); *Clydagnathus windsorensis* Pa element; *Gnathodus bilineatus*; *Paragnathodus scotiaen-*

sis; *Apatognathus* spp.; *Hindeodus cristulus* Pa element, *H.?* *scitulus*; *Spathognathodus?* sp. nov. A von Bitter; unidentified ramiform and other elements.

PHI-D₁-3 3.04 m Limestone, brownish-grey, in part oolitic, weathering buff; thick-bedded, massive appearance and breaking irregularly. Identified as brecciated oosparite by Schenk (1969, fig. 4). Bottom 2.13 m vuggy; upper 0.91 m is oolitic and contains abundant brachiopods that have flatter valves facing downwards.

Sample taken between 1.63 and 4.67 m above base of "D₁ Limestone". Top of sampling unit bears the "giant ripples" of Schenk (1969, fig. 9).

Fauna recovered from 2 kg of sample

Mestognathus bipluti (2), *M.* sp. (juvenile) (1), *M.* spp. (4); *Gnathodus girtyi*; *Apatognathus* spp.; *Hindeodus cristulus* Pa element; *Vogelgnathus?* *campbelli*.

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 22

Île Boudreau, Magdalen Islands, Quebec, Canada.
Île de l'Est Map Sheet 11N11 and 11N12 1:50 000.

One sample, IDM-3-21, taken by Plint-Geberl (1982) in the lithologically homogenous Bassin-aux-Huîtres Member, upper Windsor Group, exposed as steep cliffs on the south side of Île Boudreau. Sample taken in area A of Plint and von Bitter (1986) and von Bitter and Plint (in press).

IDM-3-21 6.0 m Limestone, medium grey, fine-grained, weathering light grey to buff; fracture uneven with obscured bedding, shaly in upper part; productid brachiopods common, cephalopods and gastropods present. Sample taken between 30 and 36 m above the base of the member.

Fauna recovered from 2 kg of sample

Mestognathus bipluti (5), *M.* sp. (juvenile) (1), *M.* spp. (3); *Clydagnathus windsorensis* Pb element (6), M element (3), Sb element (1); unidentified ramiform and other elements (60).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 23

Capelin Cove, south of Codroy, southwestern Newfoundland, Canada.

Codroy Map Sheet 11O/14W 1:50 000.

Section B of Bell (1948); upper Codroy Group; Locality 13 of von Bitter and Plint-Geberl (1982); see also Baird and Cote (1964).

Sample Cod-1-9 taken in the uppermost 1.68 m of unit 42b of Bell (1948:9). This is first marine carbonate bed in Capelin Cove north of Searston Fault of Bell (1948:7,8). Strata dipping south; underlain by marine shale bed sampled as Cod-1-10.

Cod-1-9 1.68 m Limestone, medium-bedded, black weathering, fossiliferous; contains brachiopods (*spiriferids* and *Martinia* sp.) and gastropods (*Euphemites* sp.).

Fauna recovered from 2 kg of sample

Mestognathus bipluti (2), *M.* spp. (2); *Vogelgnathus?* *campbelli* (4); *Spathognathodus?* sp. nov. A von Bitter (5); *Gnathodus bilineatus* (5); *Hindeodus?* *scitulus* (2); *Ozarkodina laevipostica* (1); *Apatognathus* sp. (1); unidentified ramiform and other elements (16).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

LOCALITY 24

Woody Cove, south of Codroy, southwestern Newfoundland, Canada.

Codroy Map Sheet 11O/14W 1:50 000.

Part of section D of Bell (1948); upper portion of the lower Codroy Group and the upper Codroy Group of Baird and Cote (1964); Locality 12 of von Bitter and Plint-Geberl (1982).

One sample, Cod-1-15, taken ~75 m south of most southerly gypsum exposure in Woody Cove. Sample taken of resistant carbonate bed that is more shaly towards base and contains crushed productid brachiopods.

Cod-1-15 7 to 9 m Limestone, medium-bedded, black, grading into black argillaceous shale towards top and bottom.

Fauna recovered from 2 kg of sample

Mestognathus beckmanni (2), *M.* spp. (4); *Clydagnathus windsorensis* Pa element (9); *Bispathodus?* sp. (1); *Gnathodus* spp. (2); *Hindeodus?* *scitulus* (1); *Apatognathus* sp. (1); unidentified ramiform and other elements (11).

Zone determination

Mestognathus bipluti Zone of *Mestognathus*-based shallow-water zonation.

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Note: Late in the production process we became aware of the following publication discussing new collections of *Mestognathus* in England, South Wales, and the Republic of Ireland:

- AUSTIN, R. L. and R. B. DAVIES
1984 Problems of recognition and implications of Dinantian conodont biofacies in the British Isles. *Geological Society of America, Special Paper* 196:195–228.

We are unable to confirm the identification of their three illustrated specimens of *Mestognathus beckmanni*. The figured specimen identified as *M. neddensis* is placed in *M. bipluti* by us.

Plates

Plate 1, figs. 1–34

Type specimens of previously proposed species of *Mestognathus* and two specimens questionably referred to *Mestognathus* by Globensky. Figs. 1–34 copied photographically and reproduced here at approximately the same size as original illustrations.

Figs. 1–8. *Mestognathus beckmanni* Bischoff, 1957, type specimens, all $\times 20$.

1–4. Holotype (pl. 2, figs. 4a–d of Bischoff, 1957), PUM Bi 1957/35.

5. Paratype (pl. 2, fig. 5 of Bischoff, 1957), PUM Bi 1957/36.

6. Paratype (pl. 2, fig. 6 of Bischoff, 1957), PUM Bi 1957/37.

7. Paratype (pl. 2, fig. 8 of Bischoff, 1957), PUM Bi 1957/38.

8. Paratype (pl. 2, fig. 9 of Bischoff, 1957), PUM Bi 1957/39.

Figs. 9–10. *Mestognathus bipluti* Higgins, 1961, type specimens, both $\times 20$.

9. Holotype (pl. X, fig. 1 of Higgins, 1961), US E1.E1.1.

10. Paratype (pl. X, fig. 2 of Higgins, 1961), US E1.E1.2.

Fig. 11. *Mestognathus?* sp. A of Globensky (1967, pl. 57, fig. 18) (here considered a worn Pa element of *Cavusgnathus unicornis* Youngquist and Miller), UNB 64-F-226 (KD-7), $\times 30$.

Fig. 12. *Mestognathus?* sp. B of Globensky (1967, pl. 57, fig. 1) (here considered the Pa element of *Clydagnathus windsorensis* (Globensky)), UNB 64-F-218 (KD-7), $\times 50$.

Figs. 13–21. *Mestognathus neddensis* Rhodes, Austin, and Druce (1969), type specimens, all $\times 31.5$.

13–15. Holotype (pl. 15, figs. 6a–c of Rhodes, Austin, and Druce, 1969) (here considered *Mestognathus bipluti*), BMNH X 250.

16–18. Paratype (pl. 15, figs. 4a–c of Rhodes, Austin, and Druce, 1969) (here considered *Mestognathus* sp.), BMNH X 251.

19–21. Paratype (pl. 15, figs. 5a–c of Rhodes, Austin, and Druce, 1969) (here considered *Mestognathus* sp.), BMNH X 252.

Figs. 22–25. *Mestognathus dhuensis* Globensky, 1967, type specimens, all $\times 50$.

22. Holotype (pl. 57, fig. 21 of Globensky, 1967) (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19).

23. Paratype (pl. 57, fig. 22 of Globensky, 1967) (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6).

24. Paratype (pl. 57, fig. 23 of Globensky, 1967) (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1).

25. Paratype (pl. 57, fig. 24 of Globensky, 1967) (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6).

Figs. 26–34. *Mestognathus groessensi* Belka, 1983, type specimens.

26–28. Holotype (pl. 1, figs. 1a, 1c, and 1b, respectively, of Belka, 1983), unnumbered, $\times 55$, $\times 50$, and $\times 55$, respectively.

29,30. Paratype (pl. 2, figs. 1a,b of Belka, 1983), unnumbered, $\times 55$ and $\times 60$, respectively.

31. Paratype (pl. 1, fig. 2 of Belka, 1983), unnumbered, $\times 55$. Illustrates asymmetric basal cavity similar to that of *M. harmalai* sp. nov. (Pl. 5, figs. 3,4), but note lack of posterior process.

32,33. Paratype (pl. 2, figs. 2b and 2a, respectively, of Belka, 1983) (here reassigned to *Mestognathus praebeckmanni* sp. nov.), unnumbered, both $\times 35$.

34. Paratype (pl. 2, fig. 6 of Belka, 1983) (here reassigned to *Mestognathus praebeckmanni* sp. nov.), unnumbered, $\times 60$.

In comparing the two specimens reassigned by us to *M. praebeckmanni* sp. nov., note the more arched and thinner platform in relation to the holotype of *M. groessensi* Belka (Pl. 1, fig. 26). Compare with the left lateral views of *M. praebeckmanni* sp. nov. (Pl. 8, figs. 3–5).

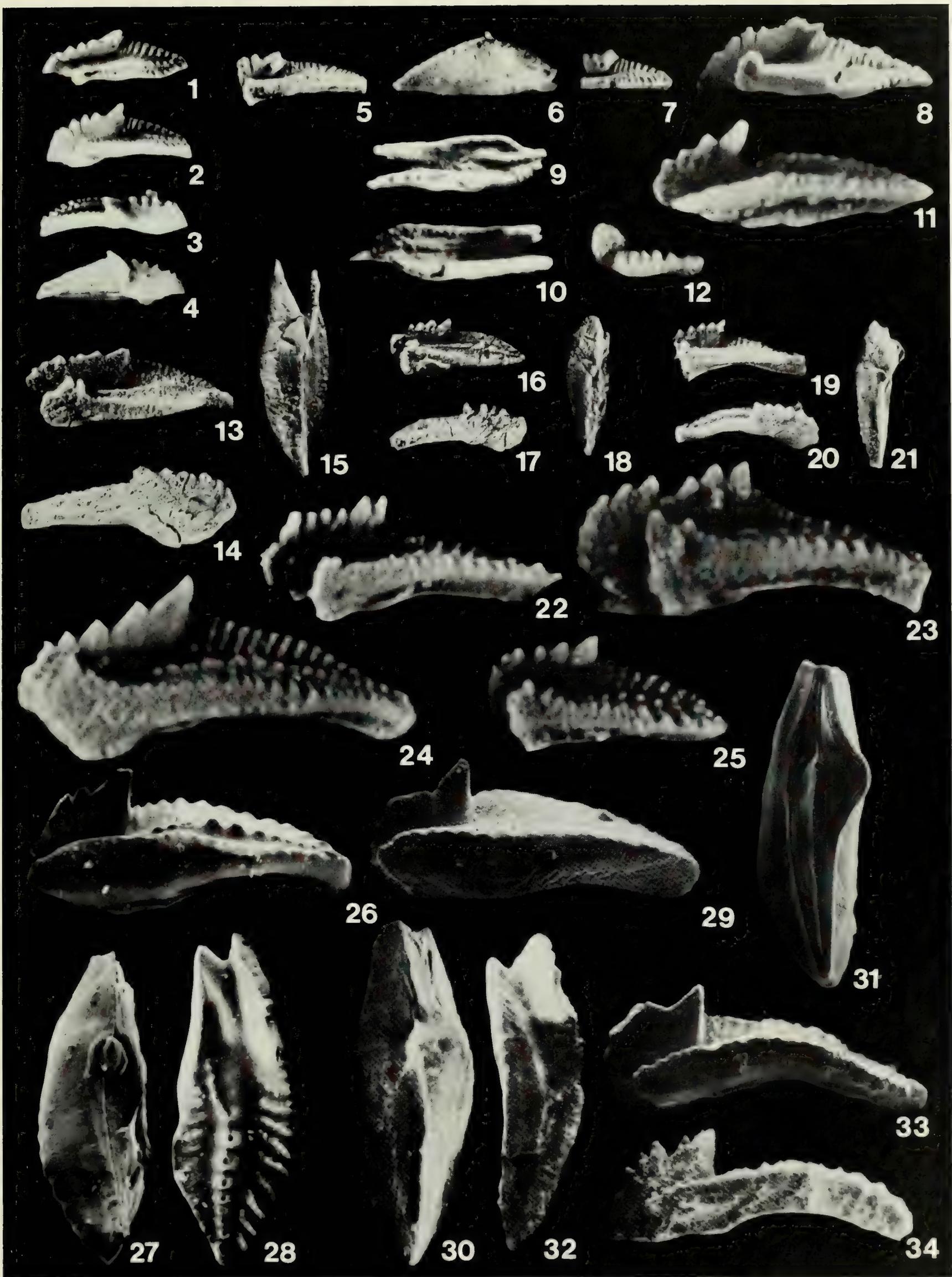


Plate 2, figs. 1-14

Upper views of type specimens of species of *Mestognathus* named prior to 1983.

Figs. 1-5. *Mestognathus beckmanni* Bischoff, 1957.

1. Holotype, PUM Bi 1957/35, × 70.
2. Paratype, PUM Bi 1957/36, × 70.
3. Paratype, PUM Bi 1957/37, × 63.
4. Paratype, PUM Bi 1957/38, × 100.
5. Paratype, PUM Bi 1957/39, × 43.

Figs. 6,7. *Mestognathus bipluti* Higgins, 1961.

6. Holotype, US E1.E.1, × 59.
7. Paratype, US E1.E1.2, × 68.

Figs. 8-11. *Mestognathus dhuensis* Globensky, 1967.

8. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19), × 135.

9. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), × 117.

10. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), × 108.

11. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), × 144.

Figs. 12-14. *Mestognathus neddensis* Rhodes, Austin, and Druce, 1969.

12. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 63.

13. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 108.

14. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 99.



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Plate 3, figs. 1–14

Lower views of type specimens of species of *Mestognathus* named prior to 1983.

Figs. 1–5. *Mestognathus beckmanni* Bischoff, 1957.

1. Holotype, PUM Bi 1957/35, × 72.
2. Paratype, PUM Bi 1957/36, × 75.
3. Paratype, PUM Bi 1957/37, × 61.
4. Paratype, PUM Bi 1957/38, × 116.
5. Paratype, PUM Bi 1957/39, × 39.

Figs. 6,7. *Mestognathus bipluti* Higgins, 1961.

6. Holotype, US E1.E.1, × 59.
7. Paratype, US E1.E1.2, × 70.

Figs. 8–11. *Mestognathus dhuensis* Globensky, 1967.

8. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19), × 135.

9. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), × 99.

10. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), × 99.

11. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), × 144.

Figs. 12–14. *Mestognathus neddensis* Rhodes, Austin, and Druce, 1969.

12. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 72.

13. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 126.

14. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 126.



Plate 4, figs. 1-14

Left lateral views of type specimens of species of *Mestognathus* named prior to 1983.

Figs. 1-5. *Mestognathus beckmanni* Bischoff, 1957.

1. Holotype, PUM Bi 1957/35, × 68.
2. Paratype, PUM Bi 1957/36, × 68.
3. Paratype, PUM Bi 1957/37, × 56.
4. Paratype, PUM Bi 1957/38, × 113.
5. Paratype, PUM Bi 1957/39, × 43.

Figs. 6,7. *Mestognathus bipluti* Higgins, 1961.

6. Holotype, US E1.E.1, × 51.
7. Paratype, US E1.E1.2, × 47.

Figs. 8-11. *Mestognathus dhuensis* Globensky, 1967.

8. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19), × 108.

9. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), × 109.

10. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), × 78.

11. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), × 117.

Figs. 12-14. *Mestognathus neddensis* Rhodes, Austin, and Druce, 1969.

12. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 56.

13. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 108.

14. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 90.

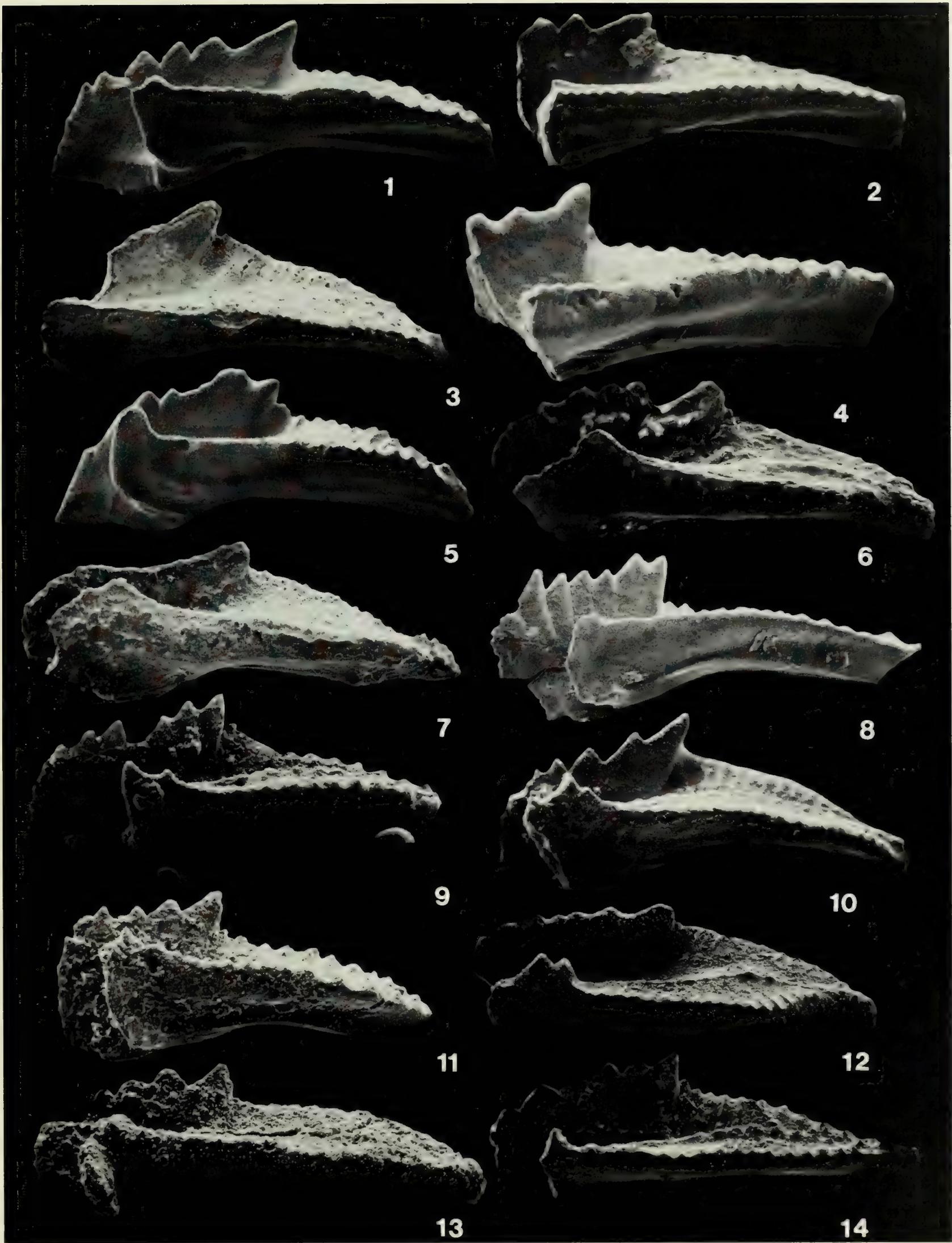


Plate 5, figs. 1-7

Mestognathus harmalai sp. nov., Lower *Gnathodus typicus* Zone (Tournaisian), locality 1, Joana Limestone, Tooele Co., Utah, United States.

Figs. 1,2,5,6. Holotype, mature specimen, USNM 257751, sample PC-2B(R).

1. Upper view, $\times 43$.
2. Lower view showing relatively small everted basal cavity, $\times 43$.
5. Upper lateral oblique view, $\times 53$.
6. Lower view, detail of basal pit, $\times 200$.

Figs. 3,4. Paratype, juvenile specimen showing relatively large uneverted basal cavity, USNM 257752, illustrated by Harmala (1982, pl. 1, figs. 6,7) as *Clydagnathus* cf. *C. cavusformis* Rhodes, Austin, and Druce, 1969, sample Harmala PCM-35.

3. Lower view, $\times 60$.

4. Lower view, detail of basal cavity, prior to eversion, $\times 150$.

Fig. 7. Paratype, USNM 257753, sample PC-2B(R), lower view, detail of basal pit, $\times 180$. Same specimen as that shown on Pl. 6, figs. 1,4,5.



Plate 6, figs. 1–10

Mestognathus harmalai sp. nov., Lower *Gnathodus typicus* Zone (Tournaisian), locality 1, Joana Limestone, Tooele Co., Utah, United States.

Figs. 1,4,5. Paratype, USNM 257753, specimen retaining some upper surface characteristics of *Clydagnathus gilwernensis* ancestor, sample PC-2B(R).

1. Left lateral view, $\times 39$.
4. Left lateral view, detail of low parapet area, $\times 80$.
5. Lower view, $\times 39$.

Figs. 2,6–10. Paratype, USNM 257754, sample PC-2A.

2. Upper lateral oblique view, $\times 40$.

6. Upper view, $\times 32$.

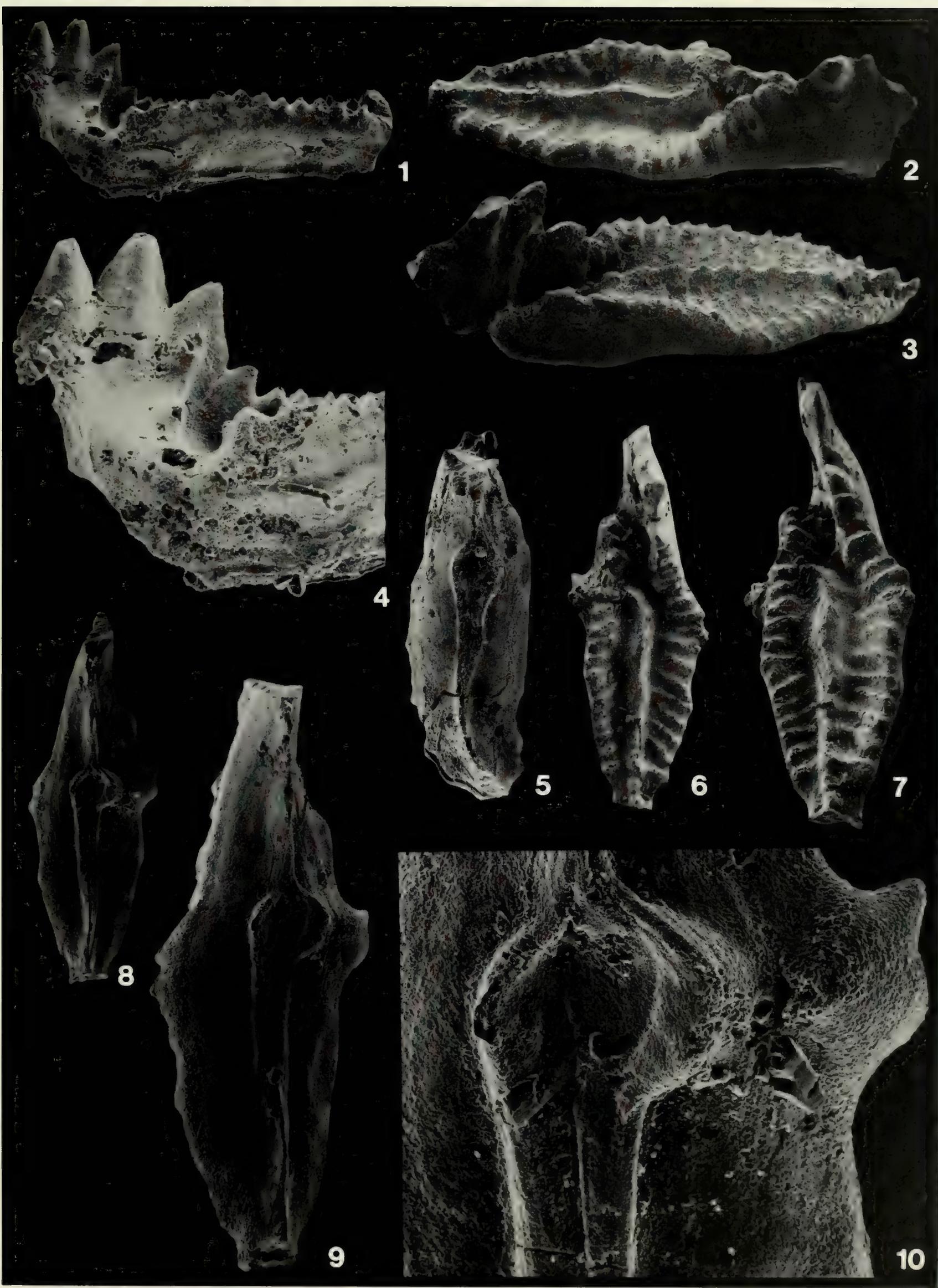
7. Upper oblique view, $\times 40$.

8. Lower view, $\times 33$.

9. Lower oblique view, $\times 55$.

10. Lower view, detail of basal pit and anterior end of pseudo-keel, $\times 160$.

Fig. 3. Paratype, USNM 257755, illustrated by Harmala (1982, pl. 1, figs. 1–5) as *Clydagnathus* cf. *C. cavusformis* Rhodes, Austin, and Druce, 1969, oblique left lateral view, sample Harmala PCM-35, $\times 40$.



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Plate 7, figs. 1–10

Mestognathus praebeckmanni sp. nov. morphotype 1 or 2, and *Clydagnathus gilwernensis*–*Mestognathus harmalai* sp. nov. transition, Alaska, United States, and British Columbia, Canada, respectively.

Figs. 1–5. *Mestognathus praebeckmanni* sp. nov. morphotype 1 or 2, USNM 257756, *Scaliognathus anchoralis*–*Doliognathus latus* Zone, locality 11, north-central Alaska, USGS collection 28582-PC, sample 73Tr7.1.

1. Upper view, $\times 111$.
2. Lower view, $\times 101$.

3–5. Left lateral views, $\times 59$, $\times 163$, and $\times 98$, respectively.

Figs. 6–10. *Clydagnathus gilwernensis*–*Mestognathus harmalai* sp. nov. transition, GSC 68885, *Siphonodella isosticha*–Upper *S. crenulata* Zone, locality 12, northeast British Columbia, Canada, sample 81-RAH-ACH-1.

6. Upper view, $\times 114$.

7. Lower view, $\times 104$.

8–10. Left lateral views, $\times 68$, $\times 91$, and $\times 182$, respectively.

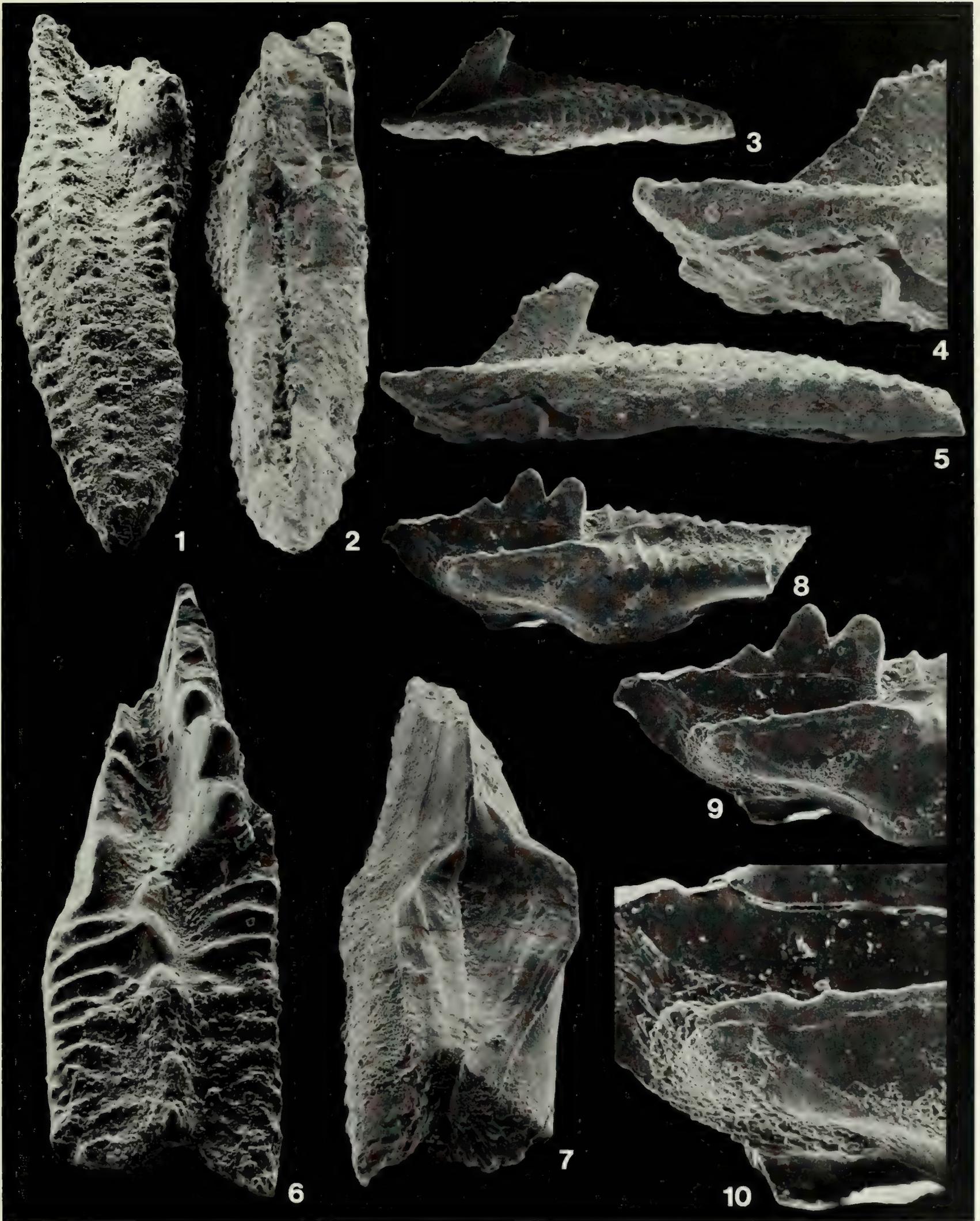


Plate 8, figs. 1–11

Mestognathus praebeckmanni sp. nov., *Scaliognathus anchoralis*
–*Doliognathus latus* Zone (Tournaisian; Tn_{3c}), Europe.

Figs. 1–4,8,10. Holotype, morphotype 2, USNM 257757, sample
BEL-5, locality 2, Banc 60 of Groessens (1971, log 6), Belgium.

1. Upper view, × 40.
2. Lower view, × 47.
3. Right lateral view, × 40.
4. Left lateral view, × 43.
8. Lower view, basal pit detail, × 150.
10. Left lateral view, parapet area detail showing notch created
by exit of adcarinal trough, × 120.

Figs. 5–7,9,11. Paratype, morphotype 3, USNM 257758, sample
GER-80-1, locality 3, Cromford (Blauer See), Bed 58 of Paproth,
Stoppel, and Conil (1973), Federal Republic of Germany.

5. Left lateral view, × 47.
6. Upper view, × 40.
7. Lower view, × 39.
9. Lower view, basal cavity detail, × 130.
11. Left lateral view, detail showing low parapet area and
cross-section of adcarinal trough, × 110.



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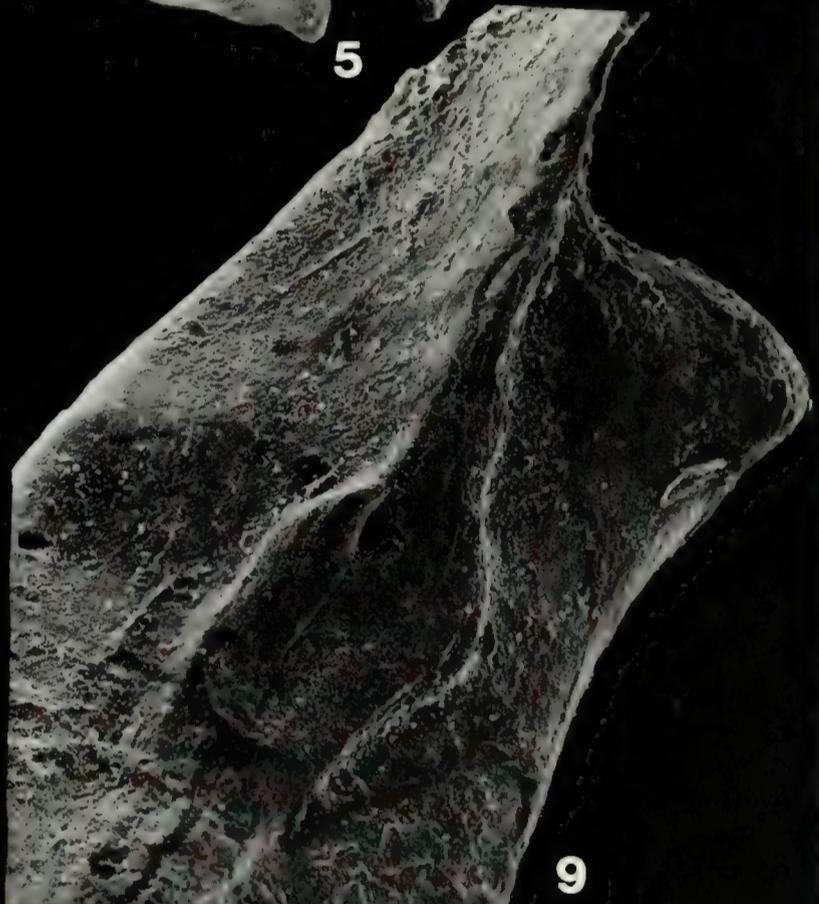
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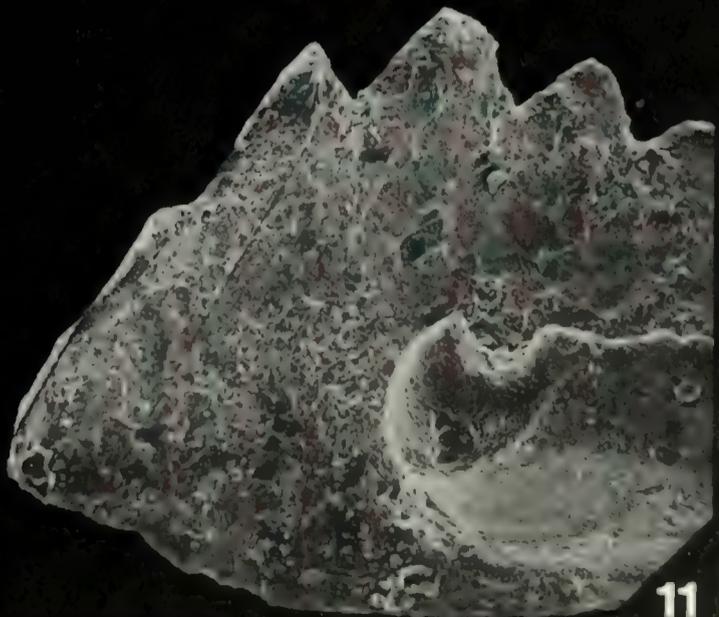
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Plate 9, figs. 1–11

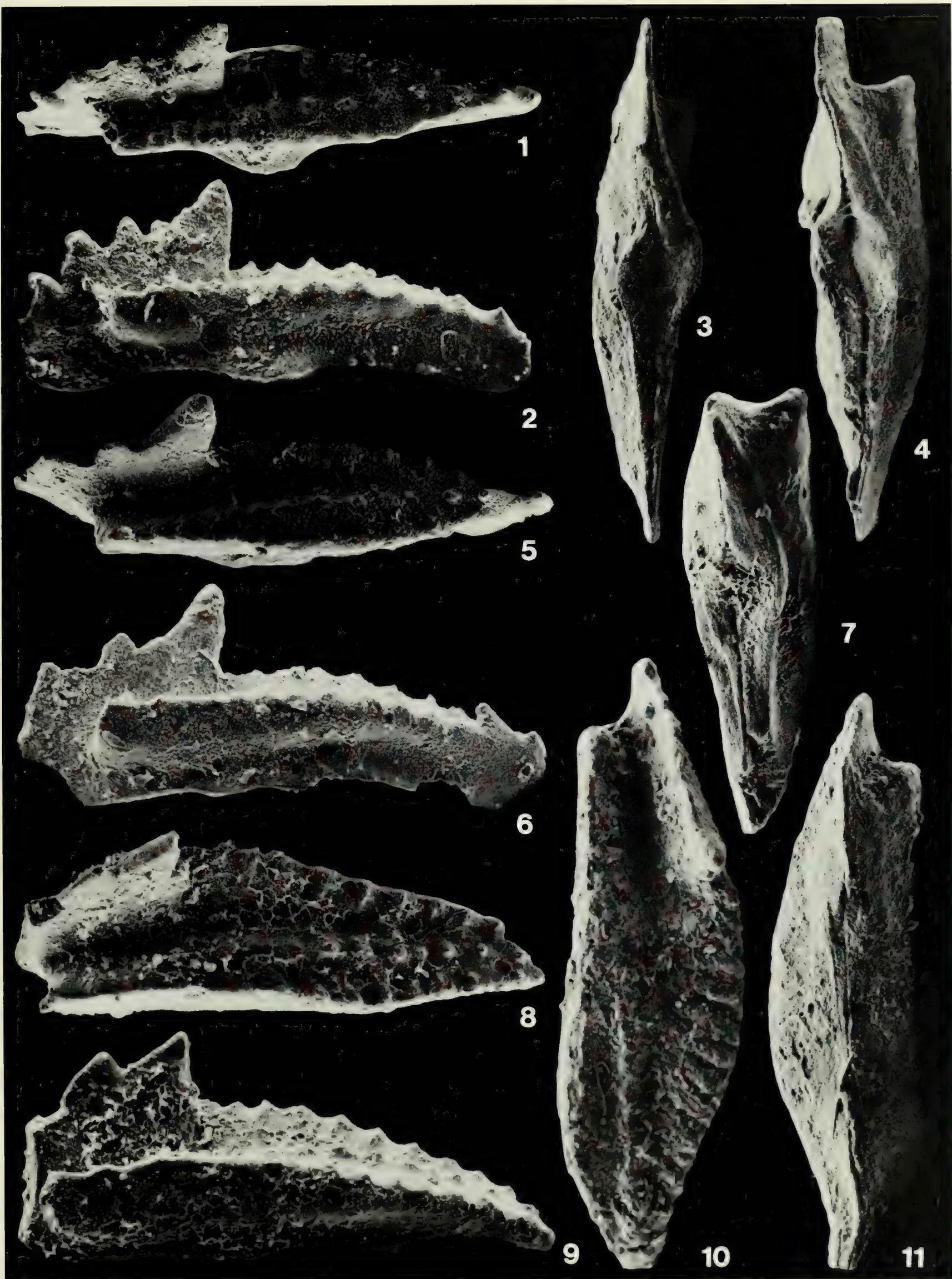
Mestognathus praebeckmanni sp. nov., morphotype 1. Illustration of specimens figured by I. S. Johnston (ms., 1985, figs. 3.20–3.30; fig. 4.1) as *Mestognathus* sp. A, *Scaliognathus anchoralis*–*Doliognathus latus* Zone (Tournaisian), locality 5, Kingscourt Outlier, Rockfield House near Nobber, Co. Meath, Republic of Ireland.

1–3. TCD 23161, sample 30, upper, left lateral, and lower views, respectively, all $\times 132$.

4–6. TCD 23162, sample 28, lower, upper, and left lateral views, respectively, all $\times 158$.

7–9. TCD 23163, sample 28, lower, upper, and left lateral views, $\times 109$, $\times 133$, and $\times 133$, respectively.

10,11. TCD 23164, sample 30, upper and lower views, respectively, both $\times 80$.



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Plate 10, figs. 1–11

Mestognathus harmalai sp. nov., *Mestognathus praebeckmanni* sp. nov., and *Mestognathus* cf. *M. praebeckmanni* sp. nov., British Columbia, Canada, and Republic of Ireland.

Figs. 1,2. *Mestognathus praebeckmanni* sp. nov. morphotype 1, left lateral views, GSC 68878, locality 7, east-central British Columbia, Canada, sample MC81/32A, $\times 70$ and $\times 141$, respectively.

Figs. 3, 4. *Mestognathus praebeckmanni* sp. nov. morphotype 2 or 3, left lateral views, GSC 68879, locality 9, northern British Columbia, Canada, sample GAT 79/33B, $\times 46$ and $\times 88$, respectively.

Figs. 5–7. *Mestognathus praebeckmanni* sp. nov., probably morphotype 2, TCD 23185, *Scaliognathus anchoralis*–*Doliognathus latus* Zone (Tournaisian), locality 5, Kingscourt Outlier,

Rockfield House near Nobber, Co. Meath, Republic of Ireland, sample 28 of I. S. Johnston (ms., 1985).

5,6. Left lateral views, $\times 67$ and $\times 161$, respectively.

7. Upper view, $\times 68$.

Figs. 8,9. *Mestognathus harmalai* sp. nov., GSC 68880, locality 7, British Columbia, Canada, sample MC81/32A, left lateral views, $\times 64$ and $\times 148$, respectively.

Figs. 10,11. *Mestognathus praebeckmanni* sp. nov., holotype, morphotype 2, USNM 257757, *Scaliognathus anchoralis*–*Doliognathus latus* Zone (Tournaisian; Tn_{3c}), locality 2, Banc 60 of Groessens (1971, log 6), Belgium, sample BEL-5.

10. Left lateral view of platform showing position of honeycombed ultrasculpture, $\times 176$.

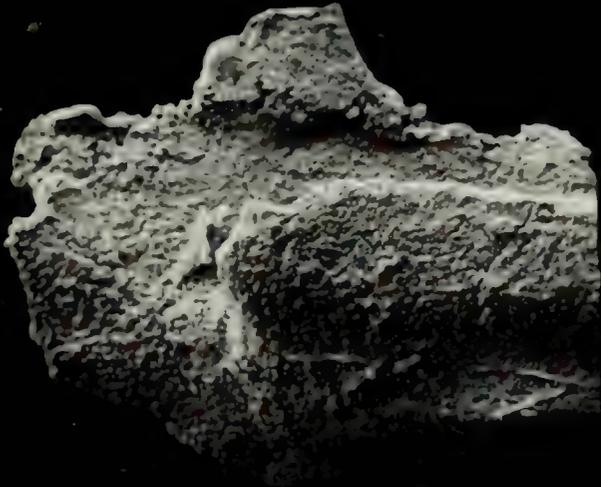
11. Detail of honeycombed ultrasculpture, $\times 1280$.



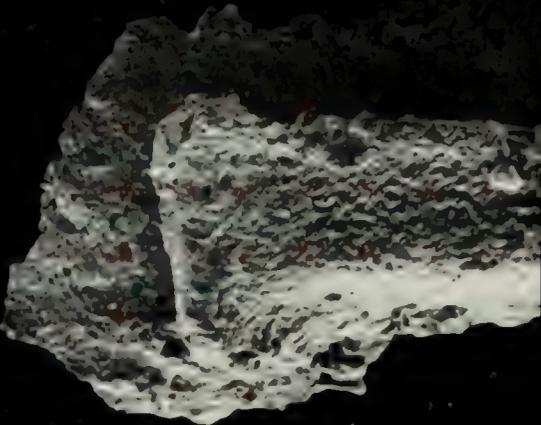
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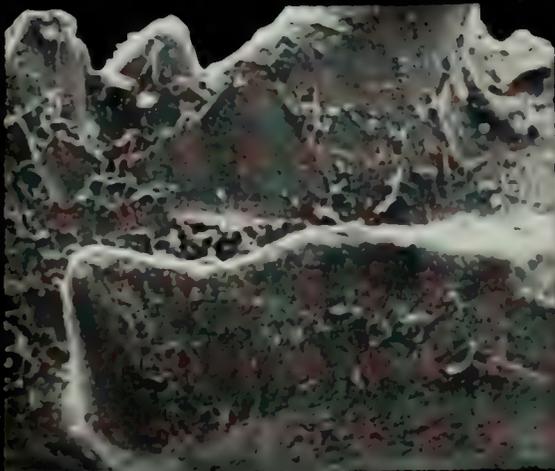
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Plate 11, figs. 1–12

Mestognathus praebeckmanni sp. nov., *Mestognathus harmalai* sp. nov., Northern Ireland and British Columbia, Canada.

Figs. 1–3,5,6. *Mestognathus praebeckmanni* sp. nov. morphotype 1 or 2, Mil(C)628/5, illustrated by Austin and Mitchell (1975, pl. 1, fig. 21) as *M. beckmanni*, indeterminate zone (Tournaisian), Mullaghsillogagh Quarry, Co. Fermanagh, Northern Ireland.

1. Upper view, $\times 124$.
- 2,3. Upper views, overall and detail, $\times 117$ and $\times 189$, respectively.
- 5,6. Left lateral views, $\times 72$ and $\times 163$, respectively.

Figs. 4,7,8. *Mestognathus praebeckmanni* sp. nov. morphotype 1, GSC 68881, locality 7, east-central British Columbia, Canada, sample MC81/32A.

4. Left lateral view, detail, $\times 169$.
7. Upper view, $\times 114$.
8. Lower view, $\times 129$.

Figs. 9,10. *Mestognathus praebeckmanni* sp. nov. morphotype indeterminate, GSC 68884, locality 7, east-central British Columbia, Canada, sample MC81/32A.

9. Lower view, $\times 128$.
10. Left lateral view, $\times 104$.

Figs. 11,12. *Mestognathus harmalai* sp. nov., GSC 68880, locality 7, British Columbia, Canada, sample MC81/32A, upper and lower views, $\times 104$ and $\times 101$, respectively.

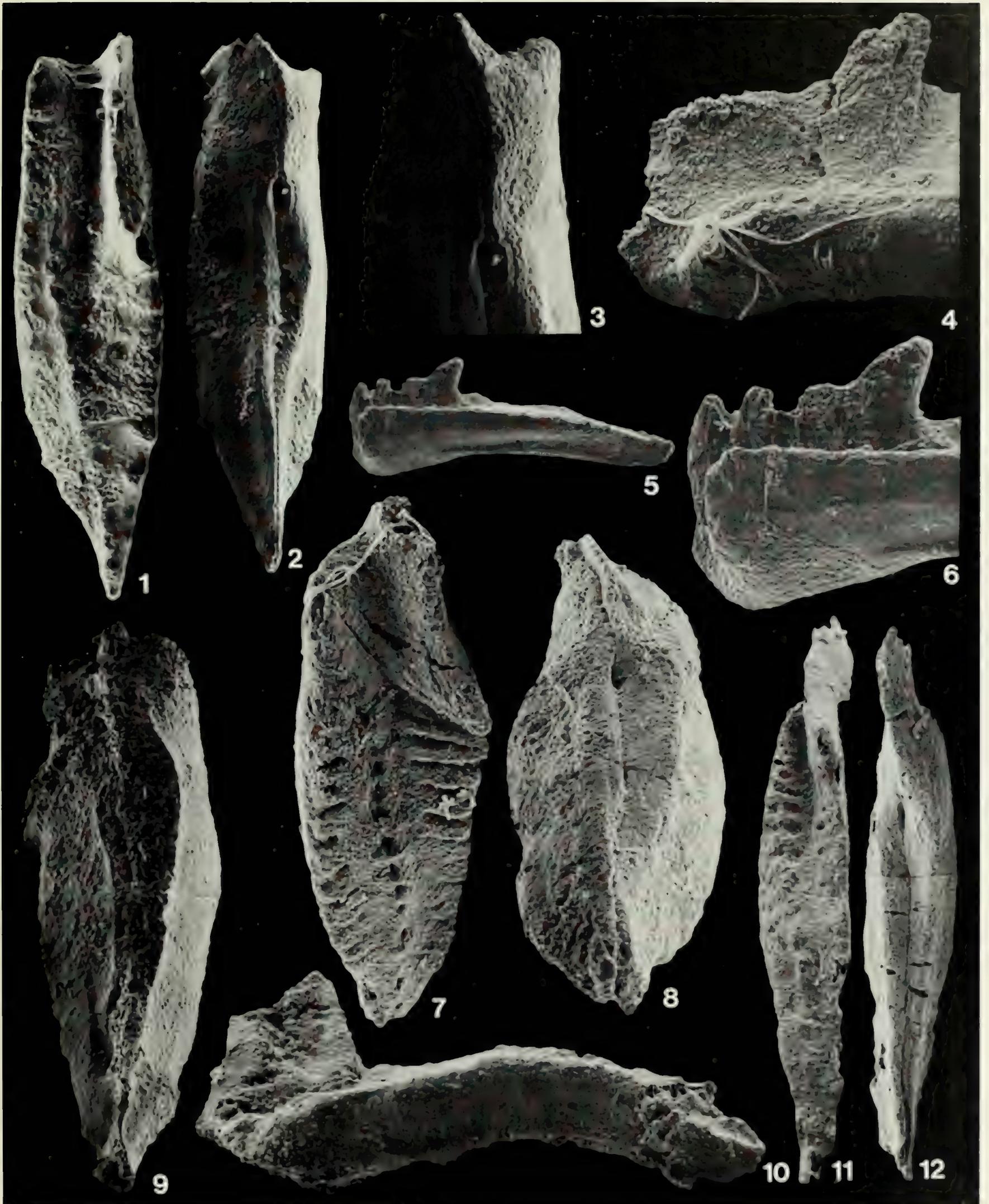


Plate 12, figs. 1–6

Mestognathus beckmanni Bischoff, type specimens of Bischoff (1957), Lower *Goniatites* Stufe (Viséan), cu III α , *locus typicus*, near Lethmathe, Map Sheet Hohenlimburg, Federal Republic of Germany.

1,4. Holotype, PUM Bi 1957/35, upper and lower views, both \times 101.

2,5. Paratype, PUM Bi 1957/36, upper and lower views, \times 101 and \times 107, respectively.

3,6. Paratype, PUM Bi 1957/37, upper and lower views, \times 88 and \times 91, respectively.



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Plate 13, figs. 1–9

Mestognathus beckmanni Bischoff, type specimens of Bischoff (1957), Lower *Goniatites* Stufe (Viséan), cu III α , *locus typicus*, near Lethmathe, Map Sheet Hohenlimburg, Federal Republic of Germany.

- 1,6. Paratype, PUM Bi 1957/38, upper and lower views, \times 144 and \times 140, respectively.
2,7. Paratype, PUM Bi 1957/39, upper and lower views, \times 66 and \times 62, respectively.

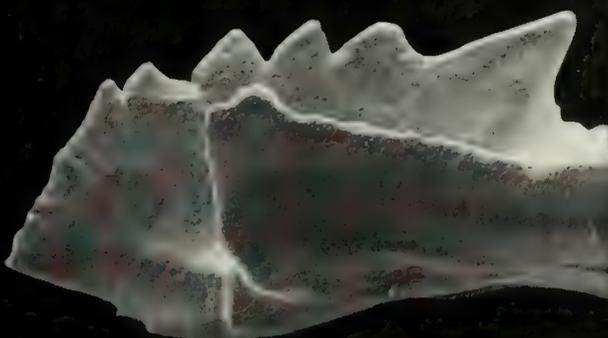
3. Holotype, PUM Bi 1957/35, left lateral view, \times 85.
4. Paratype, PUM Bi 1957/36, left lateral view, \times 94.
5. Paratype, PUM Bi 1957/37, left lateral view, \times 78.
8. Paratype, PUM Bi 1957/38, left lateral view, \times 163.
9. Paratype, PUM Bi 1957/39, left lateral view, \times 52.



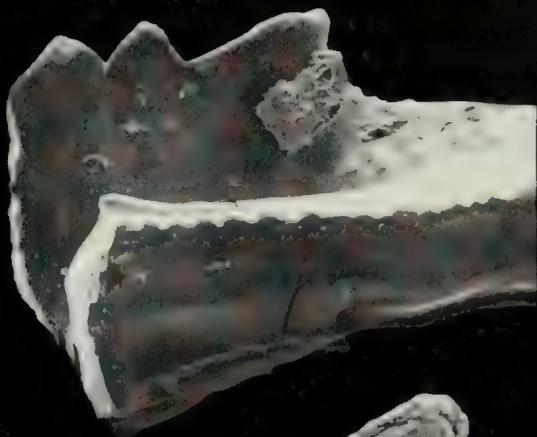
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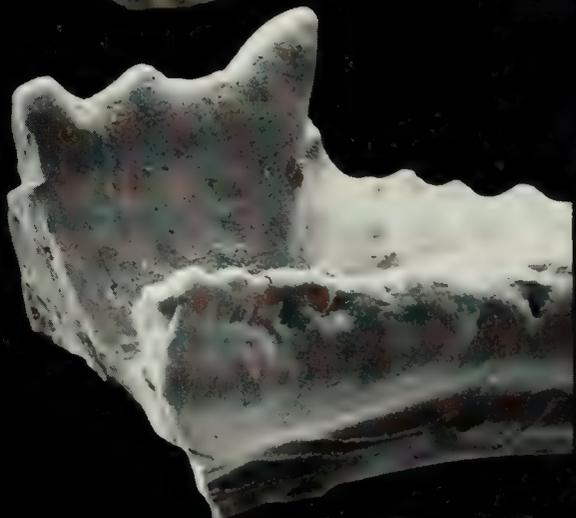
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Plate 14, figs. 1–12

Mestognathus beckmanni Bischoff, 1957, holotype, PUM Bi 1957/35, showing upper and lower surface detail. Lower *Goniatites* Stufe (Viséan), cu III α , *locus typicus*, near Lethmathe, Map Sheet Hohenlimburg, Federal Republic of Germany.

Figs. 1–9. Lower view detail.

1,2. Basal cavity detail, $\times 183$ and $\times 456$, respectively.

3,4. Closed secondary keel, $\times 420$ and $\times 900$, respectively.

5,6. Growth pit on left main keel, $\times 450$ and $\times 1800$, respectively.

7–9. Posterior half, eversion strip formed by overlapping lamellae, $\times 465$, $\times 1830$, and $\times 4560$, respectively.

Figs. 10–12. Upper views, surface sculpture, all $\times 480$.

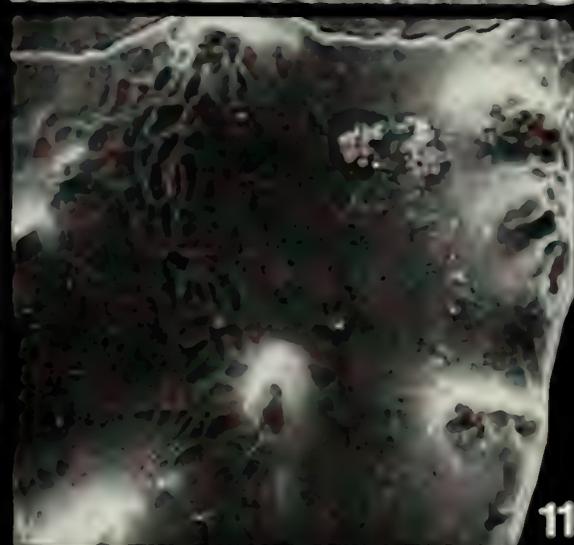
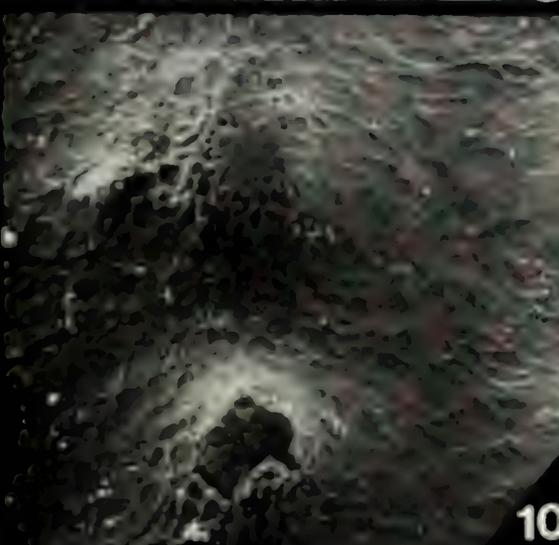
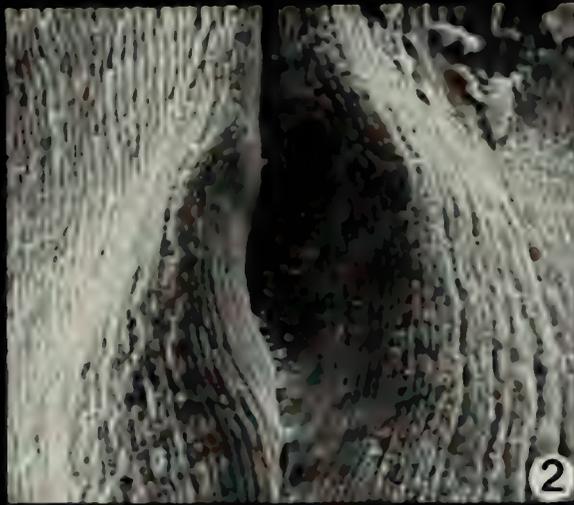


Plate 15, figs. 1–12

Mestognathus beckmanni Bischoff, paratypes of Bischoff (1957), showing upper and lower surface detail. Lower *Goniatites* Stufe (Viséan), cu III α , *locus typicus*, near Lethmathe, Map Sheet Hohenlimburg, Federal Republic of Germany.

1. Paratype, PUM Bi 1957/36, lower view, basal cavity, \times 480.
2. Paratype, PUM Bi 1957/37, lower view, basal cavity, \times 420.
3. Paratype, PUM Bi 1957/37, lower view, lamellar detail, \times 1680.
4. Paratype, PUM Bi 1957/37, lower view, lamellar detail, \times 8400.
5. Paratype, PUM Bi 1957/38, lower view, basal cavity, \times 420.

6. Paratype, PUM Bi 1957/38, upper view, surface sculpture, \times 570.

Figs. 7–12. Paratype, PUM Bi 1957/39, lower views.

7. Anterior half, \times 95.
8. Basal cavity, \times 189.
9. Eversion strip with growth pits, \times 465.
10. Closed secondary keel with growth pit, \times 465.
11. Posterior half, eversion strip, \times 192.
12. Last lamella (on right) forming eversion strip, \times 1812.

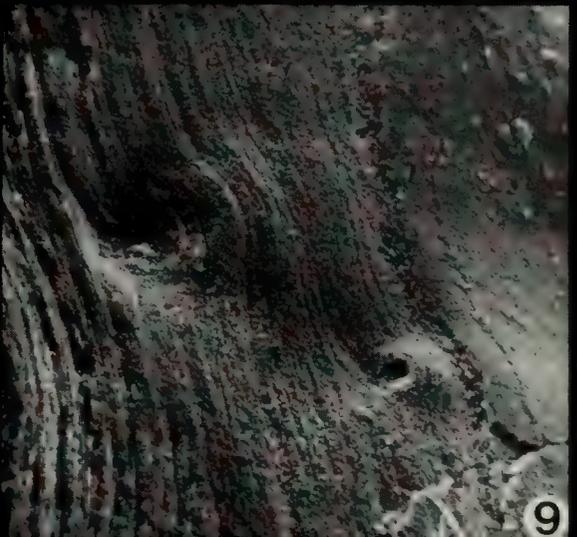


Plate 16, figs. 1–12

Mestognathus beckmanni Bischoff, Federal Republic of Germany and British Columbia, Canada; all (except fig. 11) *Gnathodus texanus* Zone, Viséan (Bed 11 = V_{1a}; Bed 17 = V_{1b}), locality 4, Zippenhaus Quarry, between Neviges and Langenberg, Federal Republic of Germany.

Figs. 1, 2, 8, 12. USNM 257759, sample GER-80-5, from Bed 11 of Paproth, Stoppel, and Conil (1973).

1. Upper view, × 40.
2. Lower view, × 39.
8. Right lateral oblique view, × 40.
12. Lower view, basal pit detail showing narrow pseudokeel and bifurcation of secondary keel on right from main keel on left, × 120.

Figs. 3, 4, 9, 10. USNM 257760, sample GER-80-5, from Bed 11 of

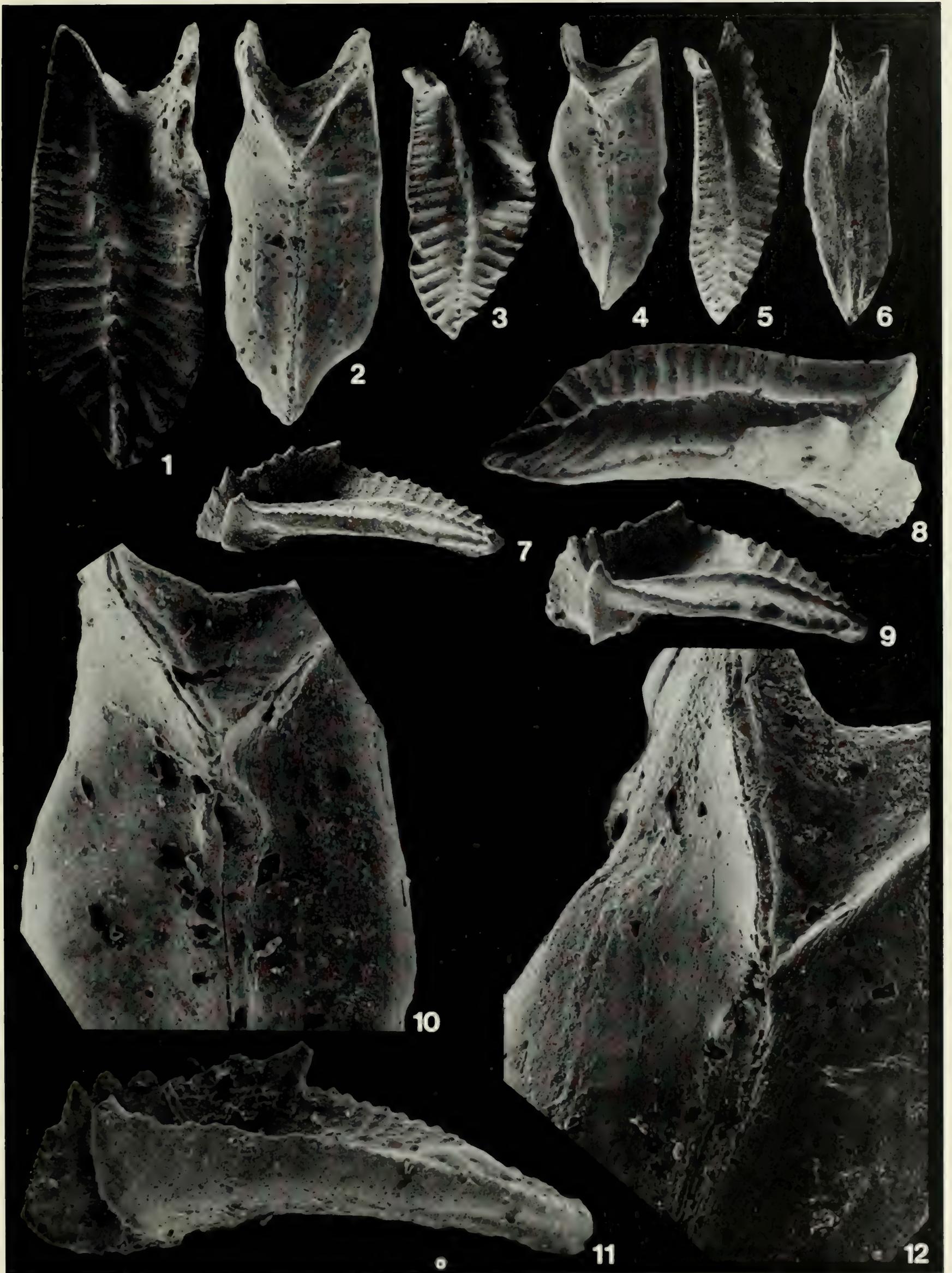
Paproth, Stoppel, and Conil (1973, fig. 3).

3. Upper view, × 40.
4. Lower view, × 39.
9. Left lateral view, × 40.
10. Lower view, basal pit detail showing same features as Pl. 4, fig. 12, × 130.

Figs. 5–7. USNM 257761, sample GER-80-6, from Bed 17 of Paproth, Stoppel, and Conil (1973, fig. 3).

5. Upper view, × 40.
6. Lower view, × 43.
7. Left lateral view, × 40.

Fig. 11. GSC 68882 (specimen lost), left lateral view, locality 9, northern British Columbia, Canada, sample GAT 79/33B, × 75.



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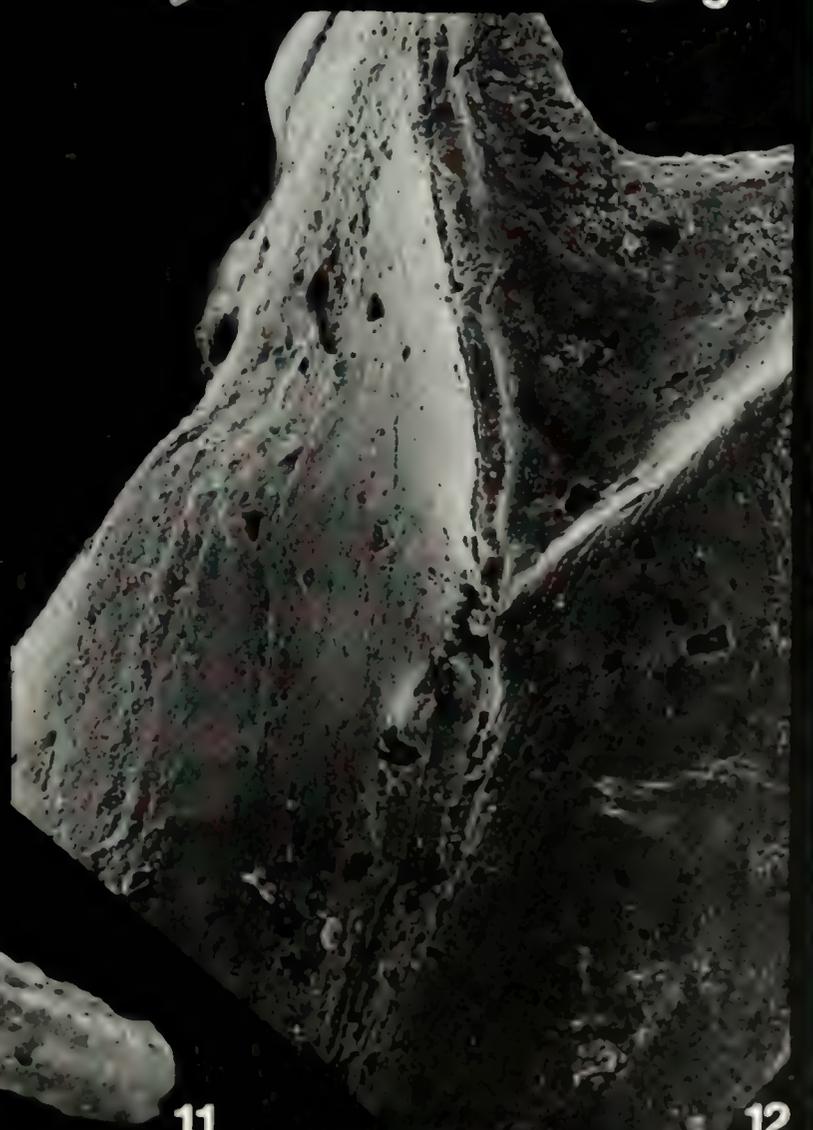
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Plate 17, figs. 1–13

Mestognathus cf. *M. beckmanni* Bischoff (ROM 43401, fig. 1) and *Mestognathus beckmanni* Bischoff (figs. 2–13), left lateral views of ontogenetic growth series, decreasing in size but increasing in magnification towards the bottom, Viséan; all specimens (except ROM 43404 (fig. 4), 43405 (fig. 5), 43412 (fig. 12), and 43413 (fig. 13) from the lower Windsor Group) are from the upper Windsor Group. All specimens from Hants Co., Nova Scotia, Canada.

1. ROM 43401, locality 15, Herbert River Member, sample Hb-1-7, × 60.
2. ROM 43402, locality 15, Herbert River Member, sample Hb-1-7, × 65.
3. ROM 43403, locality 17, Wallace Point Member, sample WaPt-1-3, × 96.
4. ROM 43404, locality 14, St Croix Member, sample St.Cr-2-4, × 97.
5. ROM 43405, locality 14, St Croix Member, sample St.Cr-2-5, × 108.
6. ROM 43406, locality 17, Wallace Point Member, sample WaPt-1-3, × 117.
7. ROM 43407, locality 17, Wallace Point Member, sample WaPt-1-1, × 117.
8. ROM 43408, locality 15, Herbert River Member, sample Hb-1-7, × 119.
9. ROM 43409, locality 15, Herbert River Member, sample Hb-1-7, × 122.
10. ROM 43410, locality 17, Wallace Point Member, sample WaPt-1-3, × 122.
11. ROM 43411, locality 17, Wallace Point Member, sample WaPt-1-3, × 128.
12. ROM 43412, locality 13, Fisher Member, sample Fisher-2-1, × 144.
13. ROM 43413, locality 13, Fisher Member, sample Fisher-2-1, × 149.

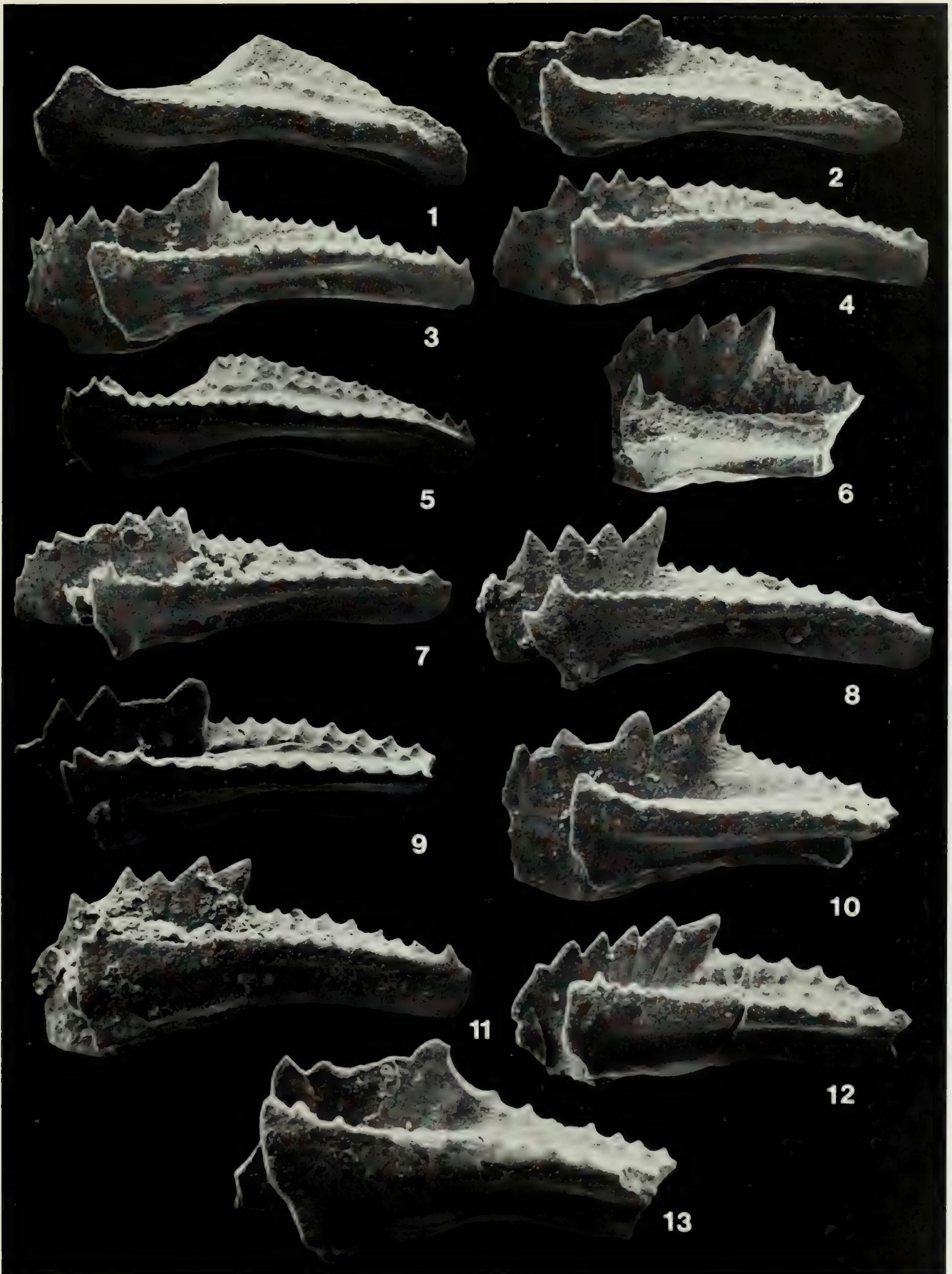


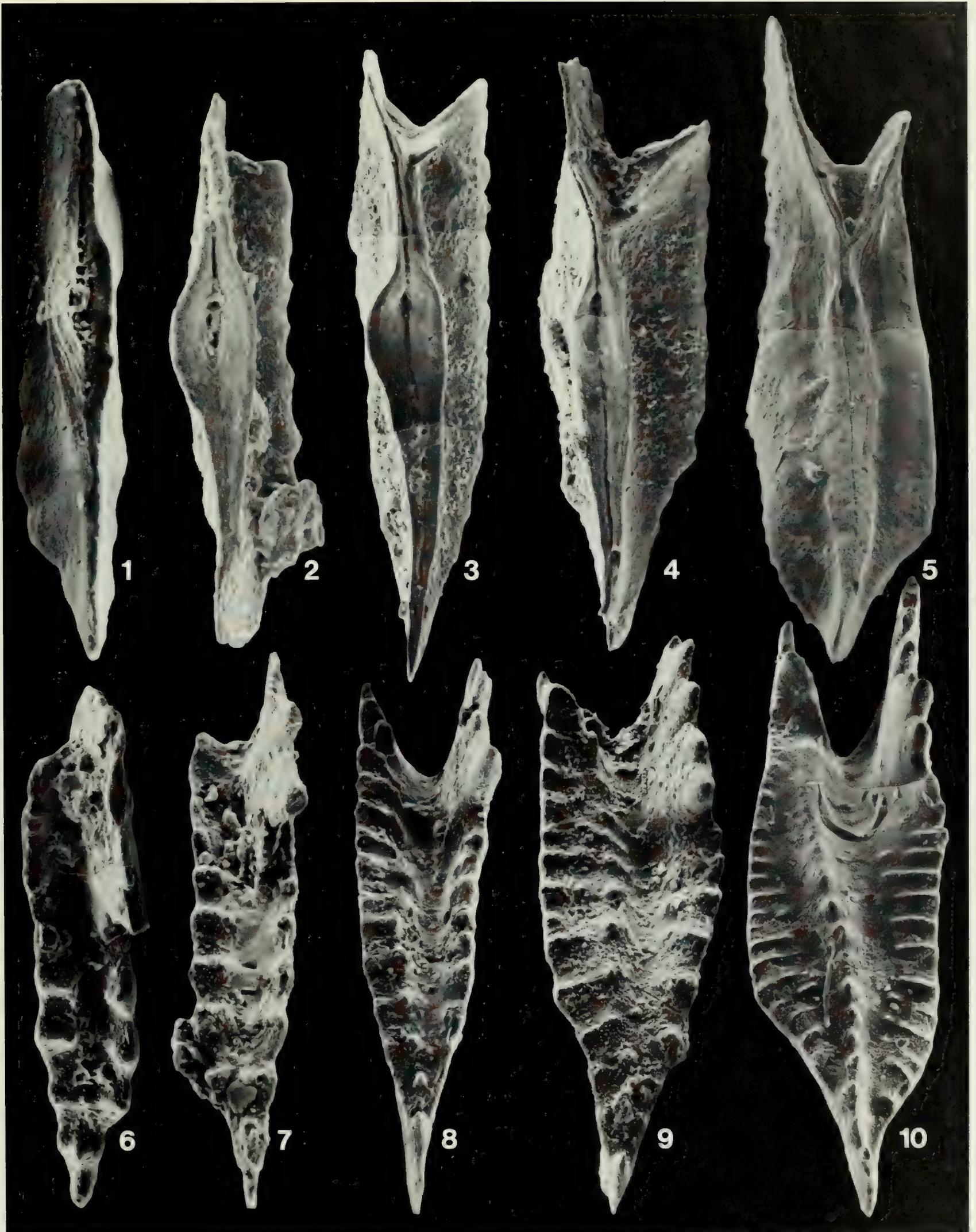
Plate 18, figs. 1–10

Mestognathus spp.—*Mestognathus bipluti* Higgins ontogenetic growth series, Viséan, upper Windsor Group; all (except ROM 43422 (figs. 5,10) from Inverness Co., Nova Scotia) are from Hants Co., Nova Scotia.

Figs. 1–5. Lower views showing decrease in size of basal cavity, increase in eversion of basal cavity, and development of secondary keel with increase in size.

Figs. 6–10. Upper views showing development of elevated secondary trough by “spreading” of left lateral nodes to form transverse ridges and carinal nodes with increase in size.

- 1,6. *Mestognathus* sp., ROM 43417, locality 15, Herbert River Member, sample Hb-1-7, $\times 404$ and $\times 375$, respectively.
- 2,7. *Mestognathus* sp., ROM 43416, locality 15, Herbert River Member, sample Hb-1-7, $\times 374$ and $\times 358$, respectively.
- 3,8. *Mestognathus* sp., ROM 43414, locality 17, Wallace Point Member, sample WaPt-1-3, $\times 288$ and $\times 272$, respectively.
- 4,9. *Mestognathus bipluti*, ROM 43433, locality 17, Wallace Point Member, sample WaPt-1-3, $\times 208$ and $\times 221$, respectively.
- 5,10. *Mestognathus bipluti*, ROM 43422, locality 21, “D₁ Limestone”, sample PHI-D₁-2, $\times 101$ and $\times 108$, respectively.



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Plate 19, figs. 1–14

Mestognathus beckmanni Bischoff, *Mestognathus bipluti* Higgins, and *Mestognathus* spp. (juveniles), detailed left lateral views of ontogenetic growth series decreasing in size but increasing in magnification towards the bottom, Viséan; all specimens (except ROM 43412 (fig. 5) from the Fisher Member of the lower Windsor Group) are from the upper Windsor Group. All specimens from Hants Co., Nova Scotia, Canada.

Figs. 1–5. *Mestognathus beckmanni* Bischoff.

1. ROM 43402, locality 15, Herbert River Member, sample Hb-1-7, × 94.
2. ROM 43403, locality 17, Wallace Point Member, sample WaPt-1-3, × 140.
3. ROM 43410, locality 17, Wallace Point Member, sample WaPt-1-3, × 172.
4. ROM 43411, locality 17, Wallace Point Member, sample WaPt-1-3, × 185.
5. ROM 43412, locality 13, Fisher Member, sample Fisher-2-1, × 208.

Figs. 6–10. *Mestognathus bipluti* Higgins.

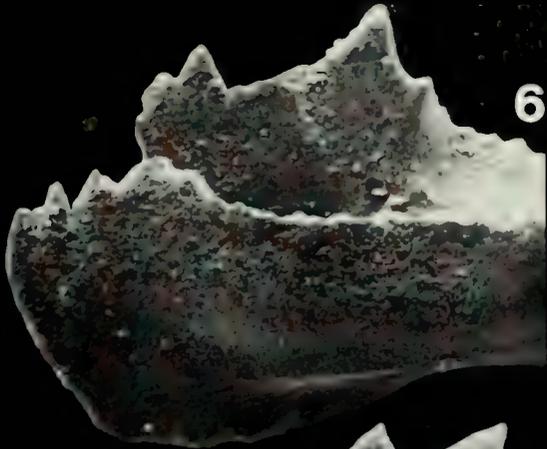
6. ROM 43423, locality 15, Herbert River Member, sample Hb-1-5, × 98.
7. ROM 43427, locality 17, Wallace Point Member, sample WaPt-1-3, × 137.
8. ROM 43430, locality 15, Herbert River Member, sample Hb-1-7, × 169.
9. ROM 43432, locality 17, Wallace Point Member, sample WaPt-1-3, × 195.
10. ROM 43433, locality 17, Wallace Point Member, sample WaPt-1-3, × 208.

Figs. 11–14. *Mestognathus* spp. (juveniles).

11. ROM 43415, locality 17, Wallace Point Member, sample WaPt-1-3, × 234.
12. ROM 43414, locality 17, Wallace Point Member, sample WaPt-1-3, × 234.
13. ROM 43416, locality 15, Herbert River Member, sample Hb-1-7, × 371.
14. ROM 43417, locality 15, Herbert River Member, sample Hb-1-7, × 371.



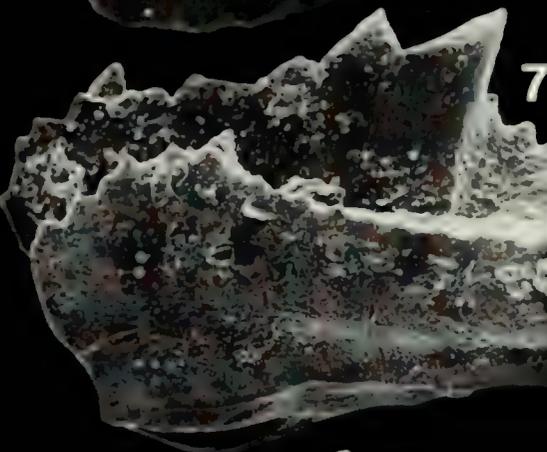
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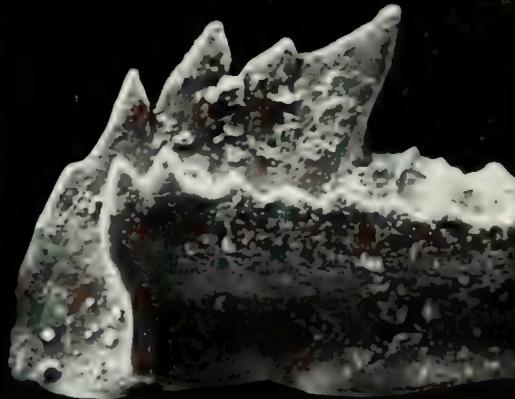
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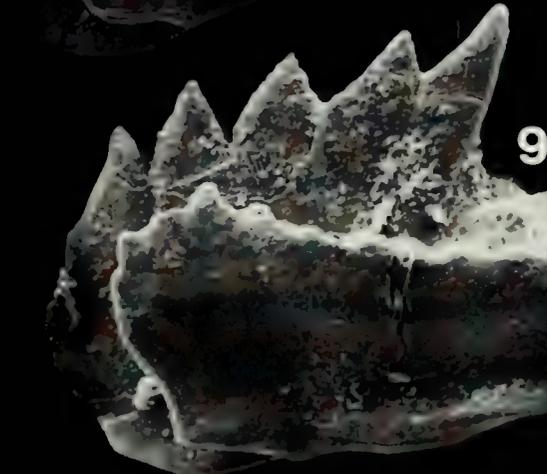
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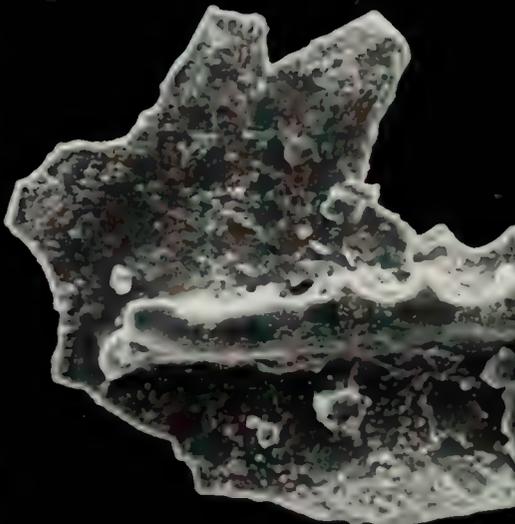
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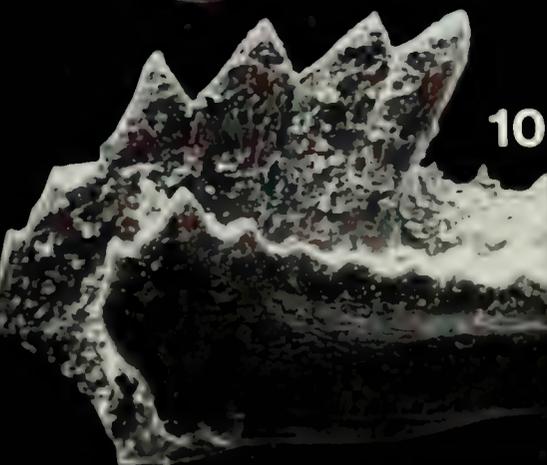
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Plate 20, figs. 1–13

Mestognathus cf. *M. beckmanni* Bischoff, *Mestognathus beckmanni* Bischoff, *Mestognathus bipluti* Higgins, and *Mestognathus?* sp. A of Globensky (1967, pl. 57, fig. 18), detailed views.

- 1,2. *Mestognathus bipluti* Higgins, ROM 43422, lower views, growth pits, Viséan, locality 21, upper Windsor Group, "D₁ Limestone", Cape Breton Island, Nova Scotia, Canada, sample PHI-D₁-2, both × 910.
3. *Mestognathus* cf. *M. beckmanni* Bischoff, ROM 43401, parapet detail, Viséan, locality 15, upper Windsor Group, Herbert River Member, Nova Scotia, Canada, sample Hb-1-7, × 150.
- 4,8. *Mestognathus bipluti* Higgins, ROM 40480, left lateral view and lower view, Viséan, locality 22, upper Windsor Group, Bassin-aux-Huitres Member, Quebec, Canada, sample IDM-3-21, × 107 and × 138, respectively.
5. *Mestognathus?* sp. A of Globensky (1967, pl. 57, fig. 18) (here considered a worn Pa element of *Cavusgnathus unicornis* Youngquist and Miller), UNB 64-F-226 (KD-7), upper view, Viséan, ?upper Windsor Group, ?Belle Marche, Cape Breton Island, Nova Scotia, Canada, × 169.

6. *Mestognathus beckmanni* Bischoff, cross-section of platform, paratype, PUM Bi 1957/39 of Bischoff (1957). Lower *Goniatites* Stufe (Viséan), cu III α , *locus typicus*, near Lethmathe, Map Sheet Hohenlimburg, Federal Republic of Germany, × 98.
- 7,9. *Mestognathus bipluti* Higgins, ROM 40478, left lateral and upper views, respectively, Viséan, locality 22, upper Windsor Group, Bassin-aux-Huitres Member, Quebec, Canada, sample IDM-3-21, × 107 and × 145, respectively.
- 10,12. *Mestognathus beckmanni* Bischoff, ROM 43402 and 43468, detailed upper views, Viséan, locality 15, upper Windsor Group, Herbert River Member, Nova Scotia, Canada, sample Hb-1-7, × 98 and × 169, respectively.
- 11,13. *Mestognathus bipluti* Higgins, ROM 43423 and 43420, detailed upper views, Viséan, locality 15, upper Windsor Group, Herbert River Member, Nova Scotia, Canada, samples Hb-1-5 and Hb-1-7, × 94 and × 169, respectively.

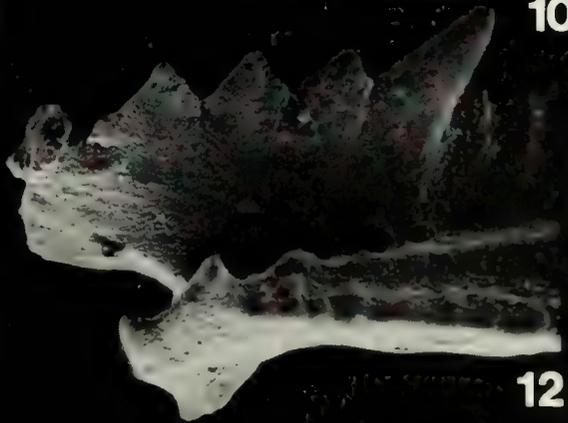
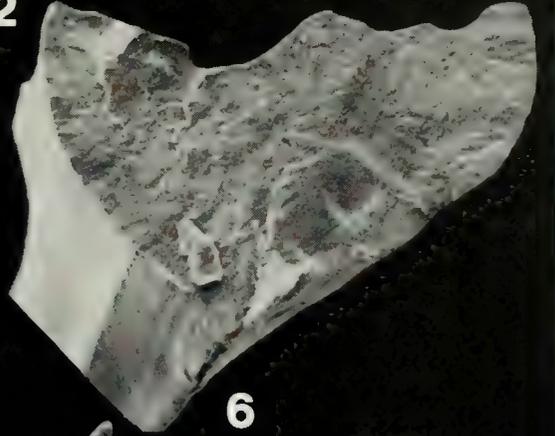


Plate 21, figs. 1–10

Mestognathus bipluti Higgins, type specimens of Higgins (1961), *Cravenoceras leion* (E_{1a}) Zone, Pendleian Stage, *locus typicus*, Cauldon, Cheadle Coalfield, North Staffordshire, England (see Higgins, 1961:211,212; 1975:3,86).

Figs. 1,3,4,6,8. Holotype, us E1.E.1.

1. Upper view, × 82.
3. Left lateral view of anterior end, × 78.
4. Anterior view, × 68.
6. Anterior view, detail of unbroken parapet, × 358.

8. Lower view, × 84.

Figs. 2,5,7,9,10. Heavily corroded paratype, us E1.E1.2.

2. Upper view, × 73.
5. Anterior view, × 72.
7. Left lateral view of anterior end, × 68.
9. Lower view, × 102.
10. Anterior view, detail of unbroken free blade, parapet, and anterior notch, × 140.



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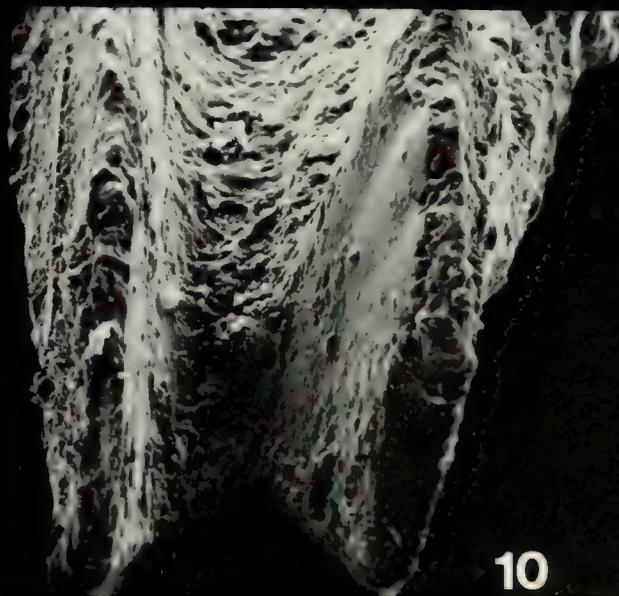
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Plate 22, figs. 1–8

Mestognathus bipluti Higgins, type specimens of Higgins (1961), *Cravenoceras leion* (E_{1a}) Zone, Pendleian Stage, *locus typicus*, Cauldon, Cheadle Coalfield, North Staffordshire, England (see Higgins, 1961:211,212; 1975:3,86).

Figs. 1,4,6,7. Holotype, us E1.E.1, detailed lower views.

1. Basal cavity and grooved secondary keel, × 410.

4,6,7. Posterior end, eversion strip with basal groove, × 494, × 197, and × 1983, respectively.

Figs. 2,3,5,8. Paratype, us E1.E1.2, detailed views.

2. Lower view, basal cavity and faintly grooved secondary keel, × 202.

3,5,8. Upper views, corrosion pits, × 98, × 202, and × 371, respectively.

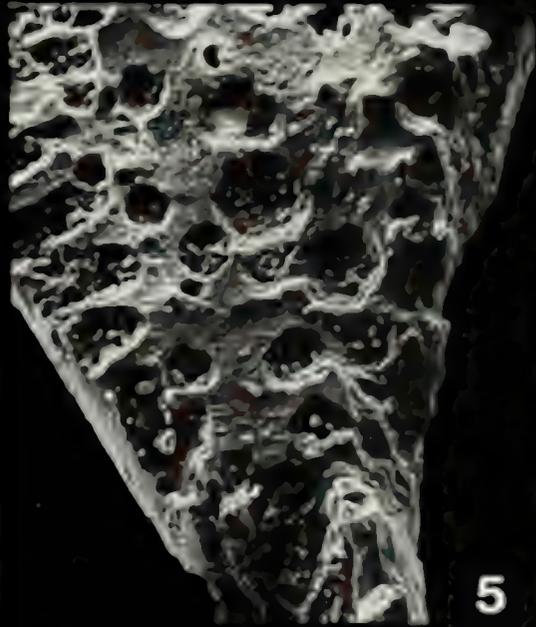


Plate 23, figs. 1–10

Mestognathus cf. *M. beckmanni* Bischoff, *Mestognathus beckmanni* Bischoff, *Mestognathus* cf. *M. bipluti* Higgins, and *Mestognathus bipluti* Higgins, topotypes.

Figs. 1,2. *Mestognathus* cf. *M. beckmanni* Bischoff, left lateral views of specimens transitional with *M. praebeckmanni* sp. nov., Viséan.

1. ROM 43419, locality 18, upper Windsor Group, "D₁ Limestone", Nova Scotia, Canada, sample Ard-1-1, × 140.
2. ROM 38492, locality 23, upper Codroy Group, Newfoundland, Canada, sample Cod-1-15, × 110.

Fig. 3. *Mestognathus beckmanni* Bischoff, GSC 68883, left lateral view, locality 9, northern British Columbia, Canada, sample GAT 79/33B, × 63.

Fig. 4. *Mestognathus* cf. *M. bipluti* Higgins, ROM 43421, oblique left lateral view of upper surface, Viséan, locality 17, upper Windsor Group, Wallace Point Member, Nova Scotia, Canada, sample WaPt-1-2, × 78.

Figs. 5–10. *Mestognathus bipluti* Higgins, left lateral views, topotypes, *Cravenoceras leion* (E_{1a}) Zone, Pendleian Stage, *locus typicus*, Cauldon, Cheadle Coalfield, North Staffordshire, England.

5,6. ROM 43434, × 155 and × 57, respectively.

7,8. ROM 43435, × 102 and × 65, respectively.

9,10. ROM 43436, × 65 and × 120, respectively.



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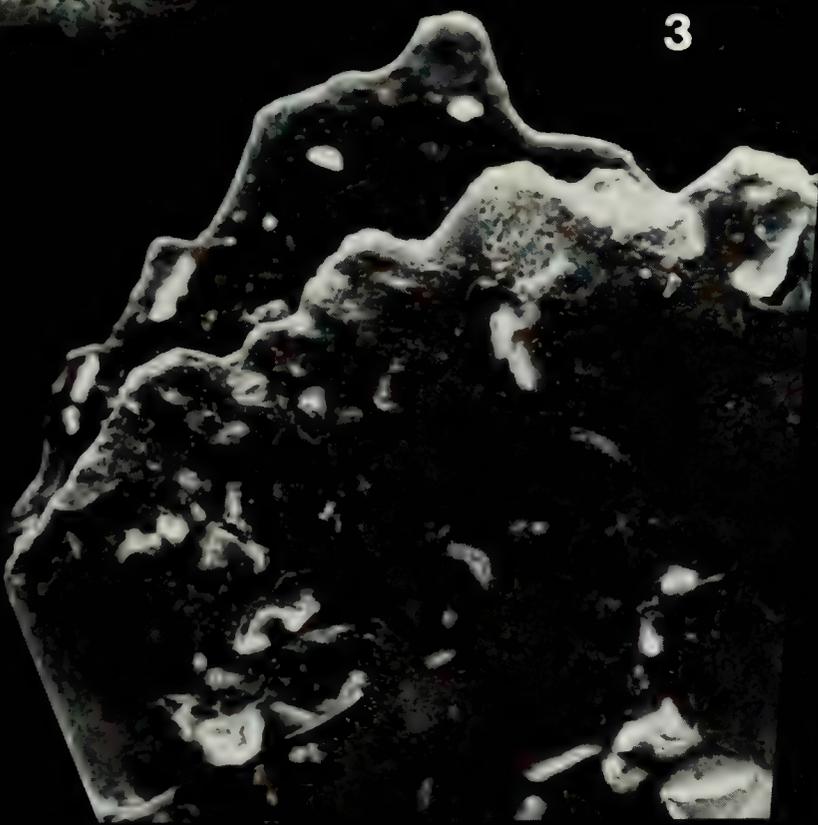
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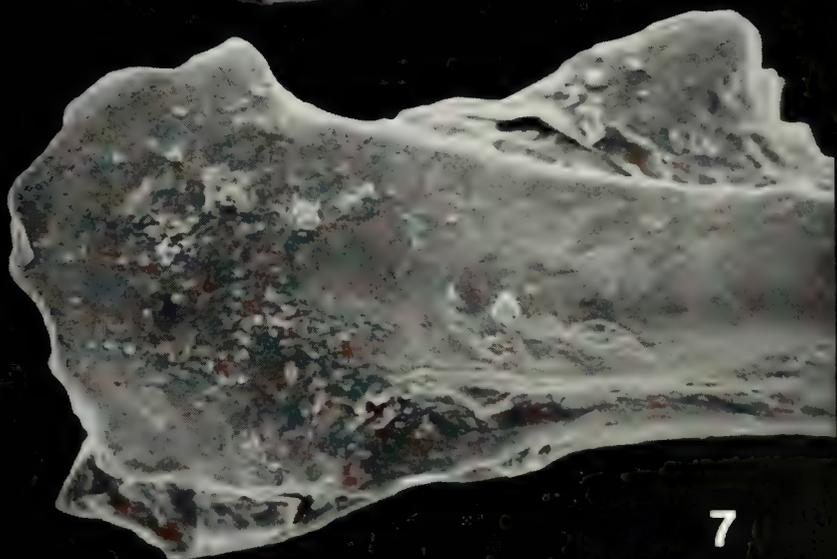
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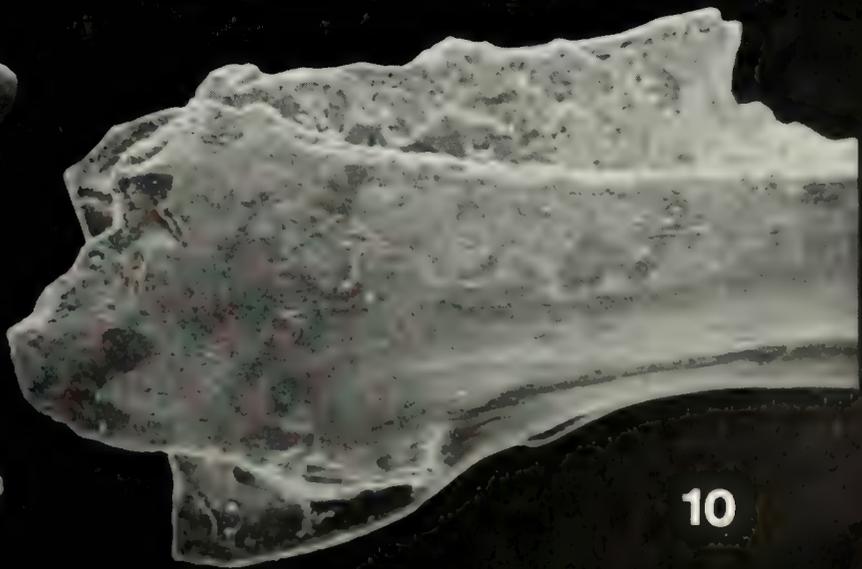
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Plate 24, figs. 1–13

Mestognathus bipluti Higgins, left lateral views of ontogenetic growth series, decreasing in size but increasing in magnification towards the bottom, Viséan, upper Windsor Group; all (except ROM 40480 (fig. 4) from locality 21 in Quebec and ROM 43422 (fig. 1) from locality 20 in Inverness Co., Nova Scotia) are from Hants Co., Nova Scotia.

1. ROM 43422, locality 20, "D₁ Limestone", sample PHI-D₁-2, × 70.
2. ROM 43423, locality 15, Herbert River Member, sample Hb-1-5, × 75.
3. ROM 43424, locality 15, Herbert River Member, sample Hb-1-7, × 77.
4. ROM 40480, locality 22, Bassin-aux-Huîtres Member, sample IDM-3-21, × 82.
5. ROM 43425, locality 15, Herbert River Member, sample Hb-1-7, × 87.
6. ROM 43426, locality 17, Wallace Point Member, sample WaPt-1-3, × 105.
7. ROM 43427, locality 17, Wallace Point Member, sample WaPt-1-3, × 105.
8. ROM 43428, locality 16, Avon Member, sample Avn-1-5, × 110.
9. ROM 43429, locality 17, Wallace Point Member, sample WaPt-1-3, × 115.
10. ROM 43430, locality 15, Herbert River Member, sample Hb-1-7, × 130.
11. ROM 43431, locality 15, Herbert River Member, sample Hb-1-7, × 135.
12. ROM 43432, locality 17, Wallace Point Member, sample WaPt-1-3, × 150.
13. ROM 43433, locality 17, Wallace Point Member, sample WaPt-1-3, × 170.



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Plate 25, figs. 1–10

Mestognathus dhuensis Globensky, 1967, type specimens, detailed upper and lower views, Viséan, *locus typicus*, Skir Dhu, Cape Breton Island, Nova Scotia, Canada.

Figs. 1–6. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19).

1. Upper view, $\times 203$.
2. Lower view, $\times 195$.
3. Lower view, detail of basal cavity showing beginning of pseudokeel, beginning of “blind” or ungrooved secondary keel, and growth pit, $\times 488$.
- 4,5. Lower views, growth pit detail, $\times 975$ and $\times 4225$, respectively.

6. Lower view, pseudokeel, $\times 975$.

Figs. 7–9. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6).

7. Upper view, $\times 167$.
8. Lower view, $\times 145$.
9. Lower view, posterior end, tilted slightly to show pseudo-keel and fixed and free blades, $\times 156$.

Fig. 10. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), posterior end, pseudokeel, basal groove, and recrystallized or overgrown crimp, $\times 520$.

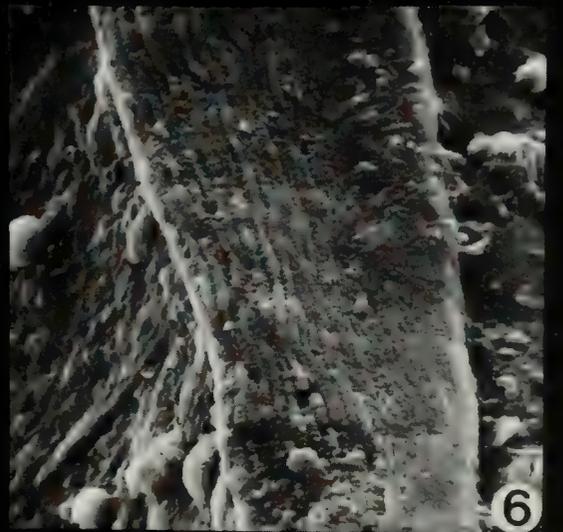


Plate 26, figs. 1-8

Mestognathus dhuensis Globensky, 1967, type specimens, detailed upper, lower, and left lateral views, Viséan, *locus typicus*, Skir Dhu, Cape Breton Island, Nova Scotia, Canada.

Figs. 1,2. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), upper and lower views, $\times 154$ and $\times 145$, respectively.

Figs. 3,4,7,8. Left lateral views, showing anterior part with parapet area.

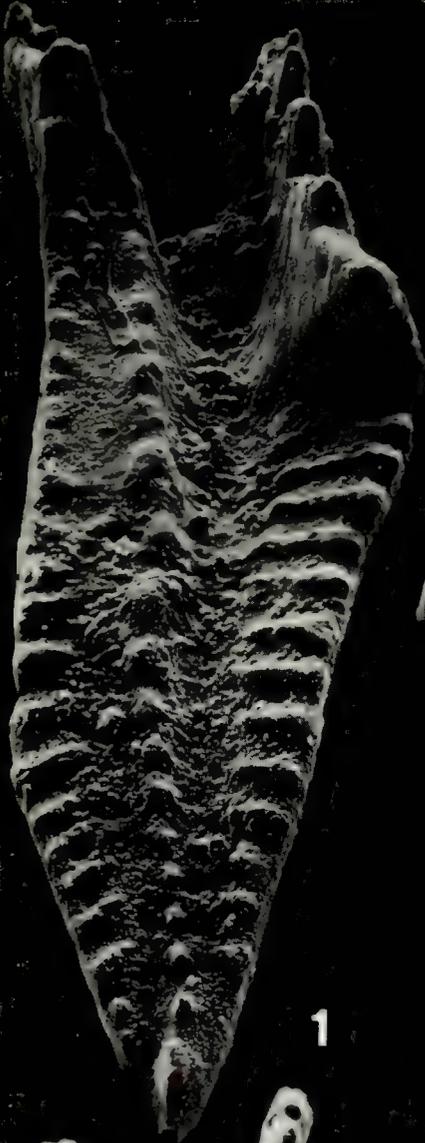
3. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19), showing incomplete parapet area, $\times 156$.

4. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), showing complete parapet, $\times 143$.

7. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), showing incomplete parapet area, $\times 114$.

8. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), showing incomplete parapet area, $\times 185$.

Figs. 5,6. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), upper and lower views, $\times 186$ and $\times 208$, respectively.



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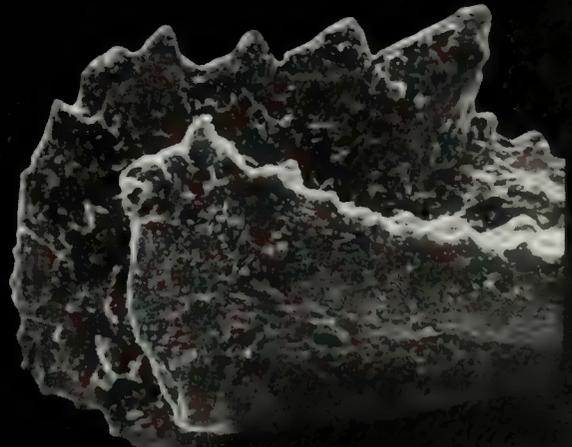
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Plate 27, figs. 1–11

Mestognathus dhuensis Globensky, 1967, type specimens, detailed lower and anterior views, Viséan, *locus typicus*, Skir Dhu, Cape Breton Island, Nova Scotia, Canada.

1. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), lower view, basal cavity and eversion strip, $\times 364$.
2. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-214 (KD-6), lower view, basal cavity, eversion strip and "blind" secondary keel, $\times 520$.
3. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), lower view, basal cavity, $\times 390$.

Figs. 4,7. Paratype (here considered *Mestognathus beckmanni*), UNB 64-F-215 (KD-6), anterior views.

4. Free and fixed blades, anterior notch, and unbroken parapet, $\times 182$.
7. Unbroken parapet, $\times 455$.

Figs. 5,6. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), lower views, posterior end, pseudokeel and recrystallized or overgrown crimp, $\times 366$ and $\times 715$, respectively.

Figs. 8,9. Paratype (here considered *Mestognathus bipluti*), UNB 64-F-217 (MV-1), anterior views.

8. Free and fixed blades, anterior notch, and slightly damaged parapet, $\times 111$.
9. Slightly broken parapet, $\times 224$.

Figs. 10,11. Holotype (here considered *Mestognathus* sp.), UNB 64-F-216 (MH-2-19), anterior views.

10. Free and fixed blades, anterior notch, and broken parapet, $\times 221$.
11. Broken parapet, $\times 553$.

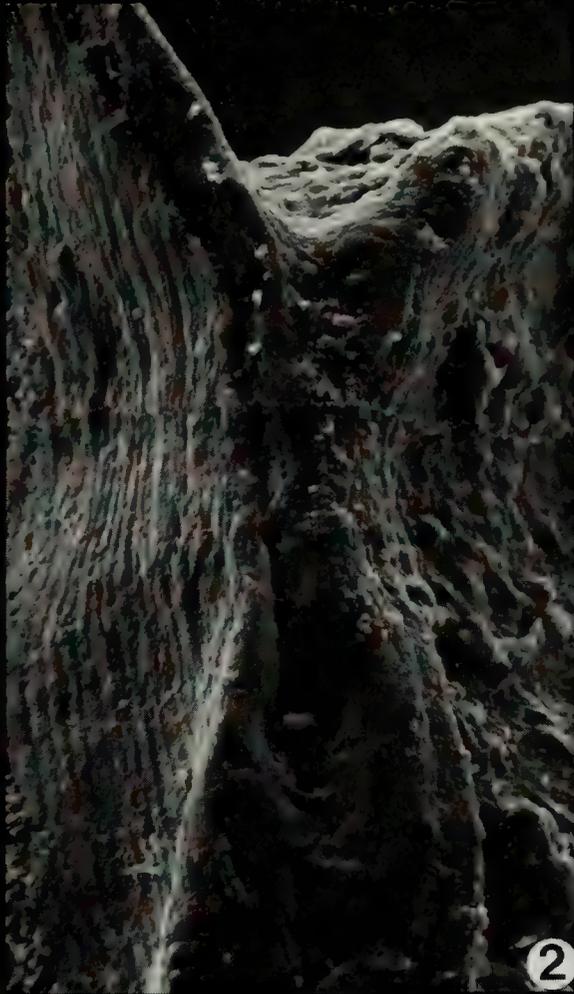
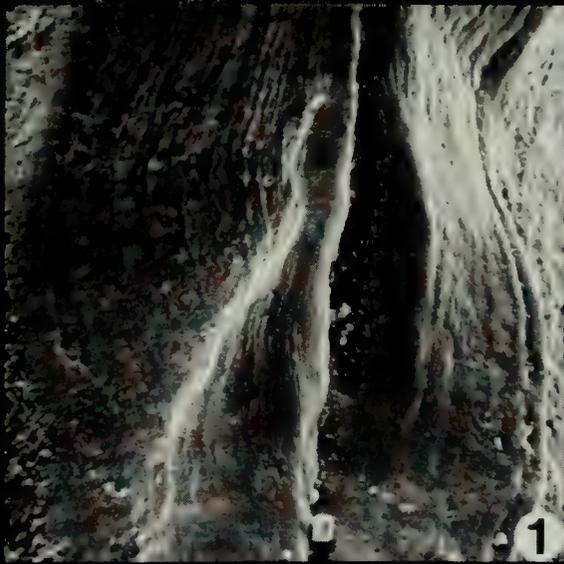


Plate 28, figs. 1–9

Mestognathus neddensis Rhodes, Austin, and Druce, 1969, type specimens, detailed upper, lower, and left lateral views, Upper D₂ Subzone, Avonian (Viséan), *locus typicus*, ?River Nedd, Breconshire, North Crop, South Wales Coalfield, United Kingdom.

Figs. 1–3. Upper views.

1. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 92.
2. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 143.
3. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 145.

Figs. 4,5,7. Lower views.

4. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 112.
5. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 182.
7. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 182.

Figs. 6,8,9. Left lateral views.

6. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, × 78.
8. Paratype (here considered *Mestognathus* sp.), BMNH X 251, × 143.
9. Paratype (here considered *Mestognathus* sp.), BMNH X 252, × 130.

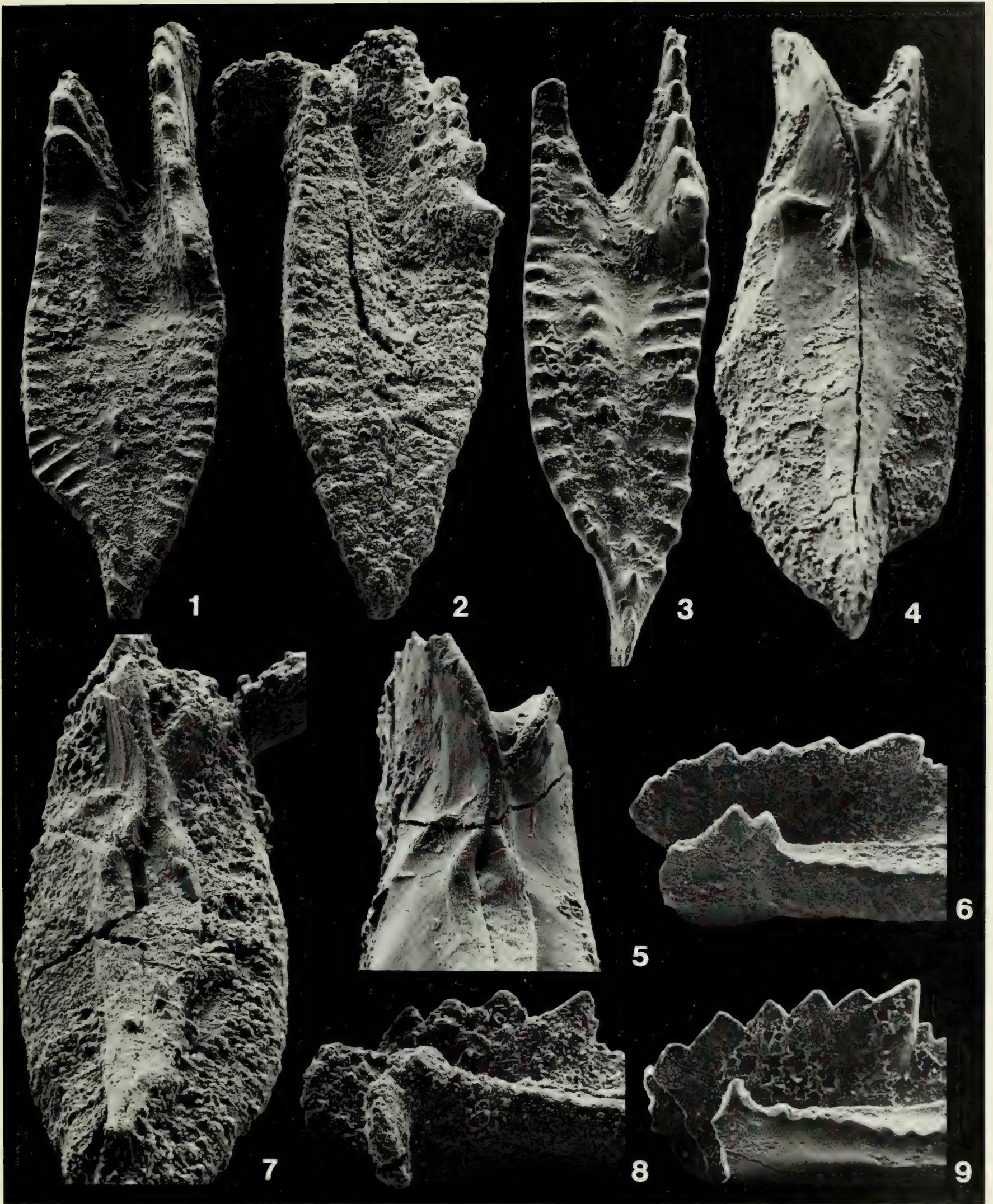


Plate 29, figs. 1–10

Mestognathus neddensis Rhodes, Austin, and Druce, 1969, type specimens, detailed lower views, Upper D₂ Subzone, Avonian (Viséan), *locus typicus*, ?River Nedd, Breconshire, North Crop, South Wales Coalfield, United Kingdom.

Figs. 1–4, 7, 8. Holotype (here considered *Mestognathus bipluti*), BMNH X 250, detailed lower views.

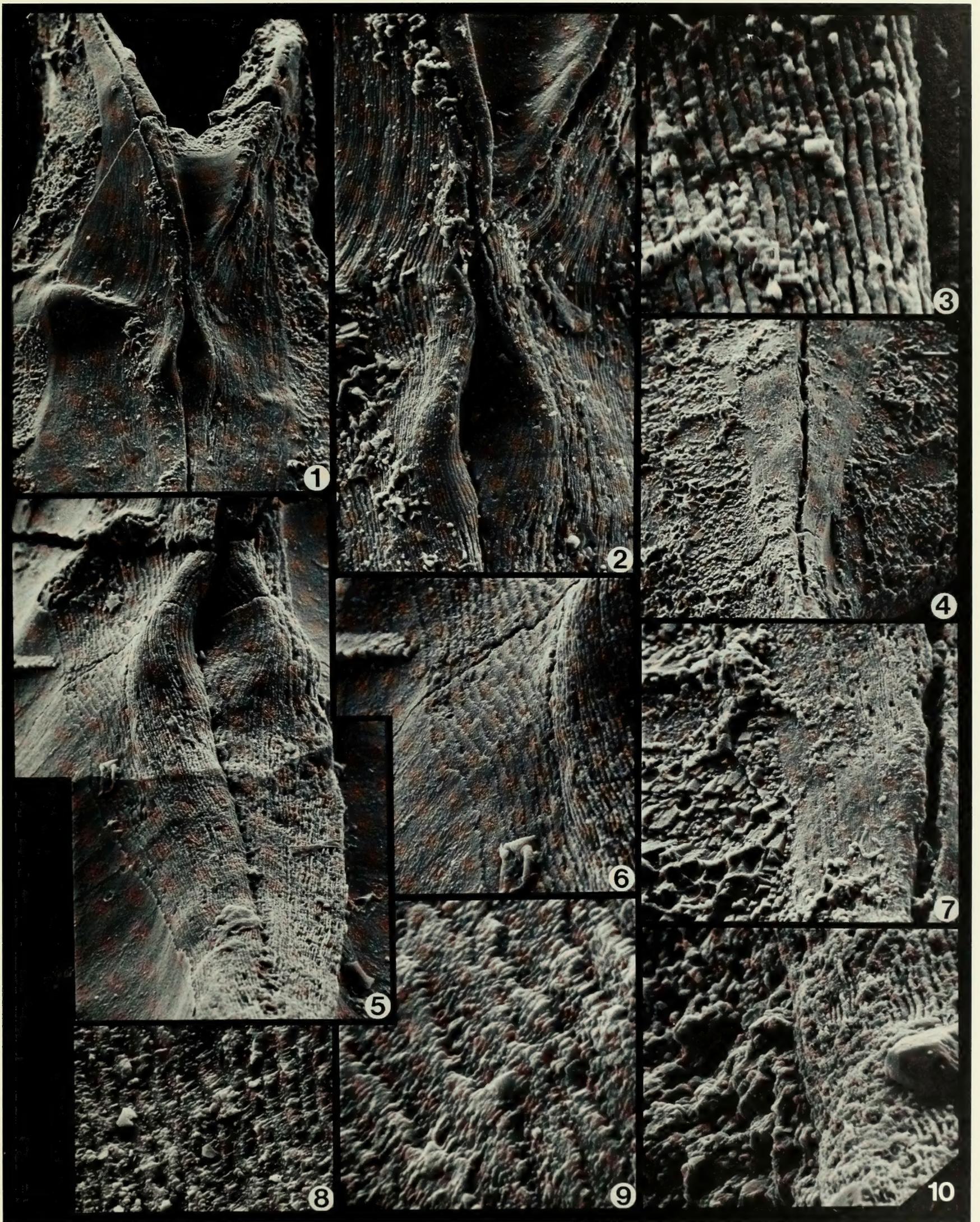
1. Broad eversion strip, basal cavity, basal groove in secondary keel, and right lower growth node, × 189.
2. Basal cavity, basal groove in secondary keel, × 474.
3. Lamellae of eversion strip adjacent to basal groove, × 1860.
- 4–7. Eversion strips, recrystallized or overgrown crimp, and basal groove, × 192, × 420, × 840, and × 480, respectively.

8. Crystallites perpendicular to and forming lamellae, × 1860.

Figs. 5, 6, 9. Paratype (here considered *Mestognathus* sp.), BMNH X 252, detailed lower views.

5. Eversion strip, basal cavity and groove, smooth crimp, and growth node, × 420.
6. Overlapping lamellae of eversion strip, smooth crimp, × 840.
9. Crystallites perpendicular to and forming lamellae, × 4200.

Fig. 10. Paratype (here considered *Mestognathus* sp.), BMNH X 251, detailed lower view, posterior end, junction between pseudokeel and recrystallized or overgrown crimp, × 840.





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