

MULTIELEMENT TAXONOMY, BIOSTRATIGRAPHY,
AND PALEOECOLOGY OF LATE TRIASSIC
CONODONTS FROM THE MAMONIA COMPLEX,
SOUTHWESTERN CYPRUS

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MULTELEMENT TAXONOMY, BIOSTRATIGRAPHY, AND
PALEOECOLOGY OF LATE TRIASSIC CONODONTS
FROM THE MAMONIA COMPLEX, SOUTHWESTERN CYPRUS

BY



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A thesis submitted to the School of Graduate
Studies in partial fulfillment of the
requirements of the degree of

Master of Science

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Newfoundland

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ABSTRACT

The Mamonia Complex, situated in the southwest of Cyprus, is an allochthonous assemblage composed of Triassic to Cretaceous sediments, Triassic mafics, and subordinate metamorphics, which have been juxtaposed against the Troodos Complex (an ophiolite suite). The Complex has been subdivided into two groups: the Ayios Photios Group, a wholly sedimentary assemblage recording continental margin sedimentation, and the Dhiarizos Group, a predominantly igneous assemblage recording continental margin volcanism and associated sedimentation.

The Triassic strata of the Ayios Photios Group has been further subdivided into the following formations: the Vlambouros Formation, representing a transition from shallow- to deep-water flysch sedimentation within a subsiding basin, and the Marona Formation, characterized by pelagic limestones deposited along portions of the margin not receiving clastic sediments. Likewise, the Dhiarizos Group contains the following Triassic sedimentary units: the Petra tou Romiou Formation, representing reef and shelf sedimentation, and the "Kholetria Member", characterized by limestones occupying interstitial regions within associated submarine volcanics. The sedimentary, igneous and metamorphic rocks of the Mamonia Complex record the Early Mesozoic construction, and subsequent Late Cretaceous destruction, of a passive continental margin.

All four of the Triassic sedimentary units of the Mamonia Complex yielded conodonts. Forty-seven of the ninety-eight processed samples yielded in excess of 4700 conodonts. Multielement taxonomic study of these specimens has allowed

the recognition of thirty species. Five multielement genera (*Chirodella*, *Cornudina*, *Cypridodella*, *Misikella*, and *Neogondolella*) are revised on the basis of their multielement nature. The genus *Misikella* contains only one recognized species, *Misikella longidentata*; all other species previously referred to *Misikella* are now assigned to the new (unnamed) multielement genus New Genus A. Two other new unnamed genera are described.

Four Late Triassic conodont zones are recognized: the *Neogondolella communisti* morphotype A Zone (tentatively), and the *Epigondolella abneptis*, *Epigondolella spatulata*, and Upper Bidentata assemblage zones; suggestive of latest Carnian to late Norian age. The distribution of conodonts in the three recognized depositional environments suggests that at least some Late Triassic conodonts were nektic in habit.

(KEY WORDS: Conodonts, Triassic, Norian, Cyprus, Mamonia Complex.
Multielement Taxonomy, Biostratigraphy, Paleoecology)

Dedication

To Lorena R. Brake

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Chapter 1

Introduction

1.1. Location and General Geology

The island of Cyprus is situated in the northeast of the Mediterranean Sea (Fig. 1-1), and covers an area of about 9,250km².

Cyprus can be divided into four, arcuate, roughly east-west trending geologic zones (Fig. 1-2). These are: the Kyrenia Range, the Mesaoria Plain, the Troodos Complex, and the Mamonia Complex.

The rocks of the Kyrenia (or Pentadactylos) Range, which record passive continental margin sedimentation and volcanism, lie on a basement of Permian limestone (Robertson and Woodcock, 1980). Gravity and magnetic data show that Troodos-type (ophiolite) material extends beneath the Mesaoria Plain, but give no indication of its presence below the Kyrenia Range (Aubert and Baroz, 1974).

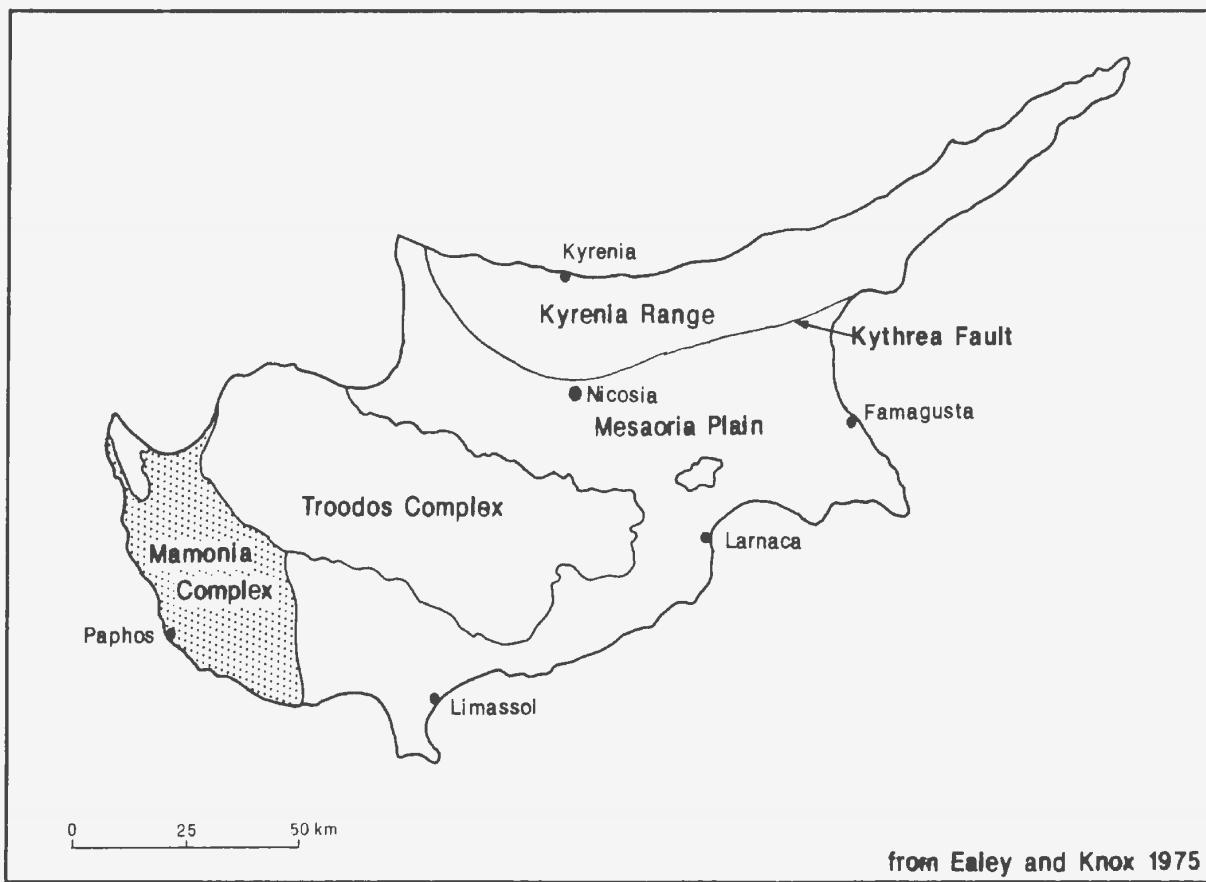
The volcanism of the Kyrenia Range, which began after the major Maastrichtian (Upper Cretaceous) folding of Cyprus and the emplacement of the Mamonia Complex (Baroz, 1980), is associated with subduction and substantial strike-slip movement along the Kythrea Fault (Rocci *et al.*, 1980).

The Mesaoria Plain is underlain by a succession of Upper Cretaceous to Pleistocene deep- to shallow-water strata which record the post-tectonic sedimentary history of the Troodos massif.



Figure 1-1: Location of Cyprus in Eastern Mediterranean, and its position relative to other areas with ophiolite complexes. See text for discussion of labelled regions.

Figure 1-2: Outline map of the geology of Cyprus.



The Troodos Complex, which forms the backbone of Cyprus, occupies an area of about 3000km² in the central region of the island. There are also two small inliers, Troulli and Akamas Peninsula, to the east and west, respectively. The present structure of the Troodos Complex is a westnorthwest-eastsoutheast elongated dome, complicated to the south by the Arakapas Fault (Robertson and Woodcock, 1980). The northwest flank of the complex is gently dipping and little deformed, whereas the south and southwest flanks exhibit steeper dips and are locally cut by subhorizontal thrusts. A complete and undeformed ophiolite sequence is present and ranges downwards from pillow lavas through a sheeted dyke complex, cummulate gabbros and peridotites, to tectonized hartzburgite (Gass, 1980).

The age of the Troodos ophiolite has been given as Late Cretaceous (Campanian) (Gass, 1980). There are no clear magnetic reversals indicated in the complex (Vine *et al.*, 1973), which is consistent with formation during a Late Cretaceous period of normal magnetization (Robertson and Woodcock, 1980).

It is accepted by most workers that the Troodos Complex was formed at some form of Late Cretaceous spreading axis. The dyke trends are predominantly north-south, and would have been originally east-west prior to the Late Cretaceous-Early Tertiary 90° anticlockwise rotation of Cyprus (to be discussed below, page 18). Chilled margin statistics (fabric orientations of chilled margins in sheeted dyke complexes), and these dyke trends, are consistent with the suggestion that the ophiolite belonged to the southern flank of the spreading zone (Kidd and Cann, 1974).

Although there is agreement concerning the spreading axis origin for the complex, there is currently some confusion as to the exact nature and setting of this axis. A variety of settings have been proposed for the origin of the Troodos ophiolite. These include:

1. An island-arc volcano (Miyashiro, 1973).

2. A back-arc basin setting (Freund *et al.*, 1975).

3. Supra-subduction zone volcanism (Moores *et al.*, 1984).

An interesting feature of the sediments of the Alpine-Mediterranean belt is the similarity of facies which existed throughout much of the Mesozoic Tethyan region (Waldron, 1984b). Calon (pers. comm., 1987) reports almost identical facies types in a belt from Cyprus to Oman. One of the more characteristic deep-water pelagic facies of the Tethyan belt is the Hallstatt facies, which often documents the earliest occurrence of ocean-floor deposition (Bernoulli and Jenkins, 1974). This facies is typically a condensed grey to pink micritic limestone, often containing pelagic bivalves (*Halobia* spp. or *Daonella* spp.). The Hallstatt facies is also of interest to this study because although it is generally poor in macrofossils, conodonts are almost ubiquitous (Krystyn, 1980). Stratigraphically, the Hallstatt facies spans the time from the late Anisian to the late Norian.

The depositional environment for the Hallstatt facies is interpreted to have been on sheltered submarine highs, likely horst blocks, in water depths as shallow as 50m (Zankl, 1971; Marcoux, 1978; Bernoulli and Jenkins, 1974). Waldron (1984a) and Robertson and Woodcock (1981b) report that texturally, the micritic, *Halobia* bearing limestones are closely comparable with deep-water peri-platform oozes around the Bahamas described by Schlager and James (1978).

1.1.1. The Mamonia Complex

The Mamonia Complex, an allochthonous, highly deformed sequence of rocks of Triassic to Cretaceous age, is located in the southwestern corner of Cyprus. The stratigraphic scheme of the complex used in this study follows that of Swarbrick and Robertson (1980) (Fig. 1-3), which is a revision of previous schemes by Henson *et al.* (1949) and Lapierre (1975).

STRATIGRAPHY OF THE MAMONIA COMPLEX – SW CYPRUS

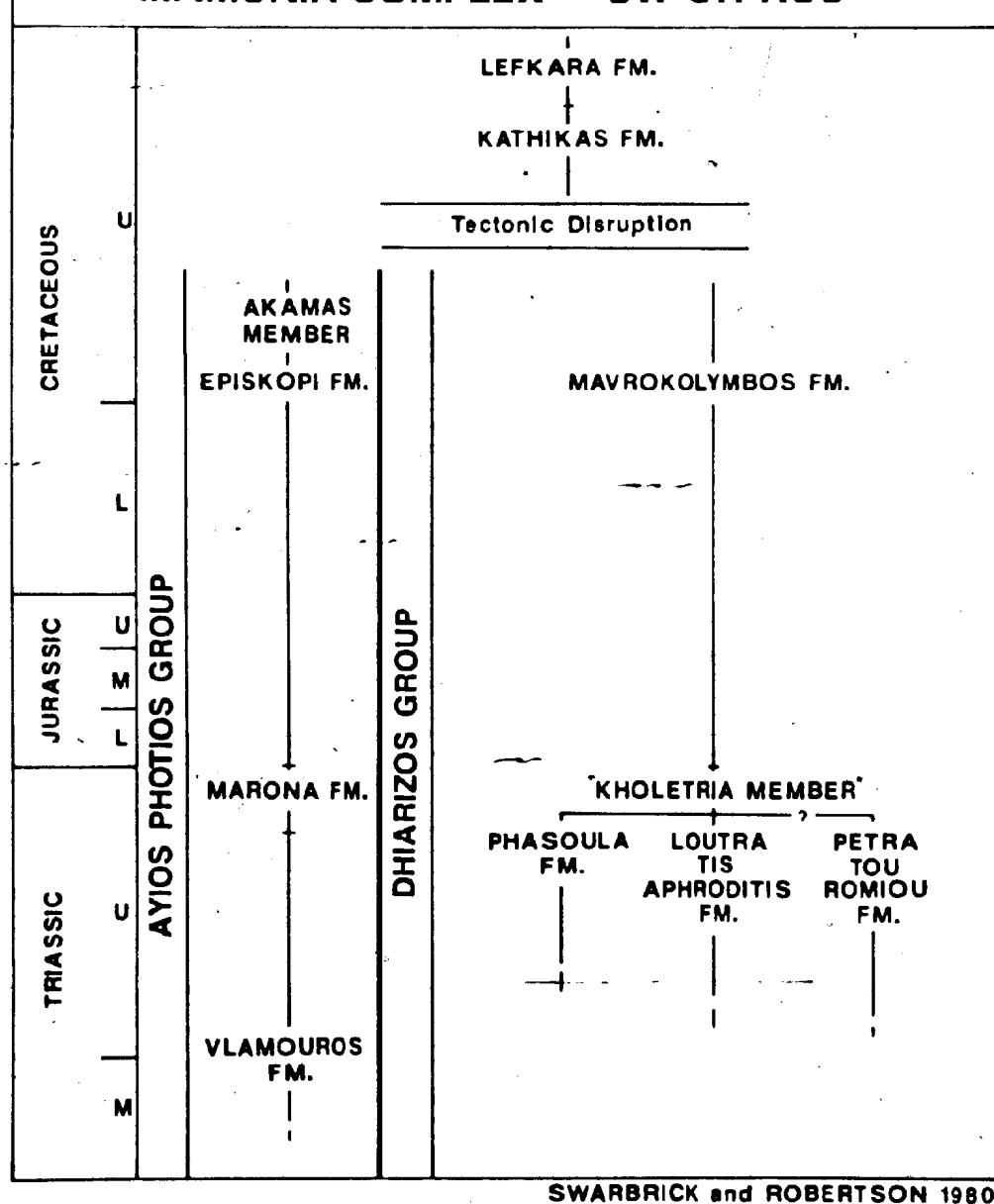


Figure 1-3: The stratigraphic classification of Mesozoic rocks of southwestern Cyprus (after Swarbrick and Robertson, 1980).

Following Swarbrick and Robertson (1980), the Mamonia Complex may be subdivided as follows:

1. a wholly sedimentary group, the Ayios Photios Group.
2. an igneous-sedimentary group, the Dhiarizos Group.
3. the Aya Varvara Formation; a series of serpentinite sheets and slivers associated with the rocks of the Dhiarizos Group. Swarbrick (1980) has proposed that the serpentinites were intruded up strike-slip faults along which the Troodos and Dhiarizos Group rocks were juxtaposed in the Late Cretaceous.
4. the Kathikas Formation; an olistostrome melange composed of rocks of the Mamonia Complex, with rare Troodos-derived material, strewn in a matrix of Upper Cretaceous red argillaceous silt. This formation is interpreted to have been formed as a series of debris flows, postdating the main emplacement of the Mamonia Complex (Robertson and Woodcock, 1979; Swarbrick, 1980).
5. the Lefkara Formation; a sequence latest Cretaceous and early Cenozoic pelagic chalks and marls which blanket the whole of southern Cyprus.

The rocks of the Mamonia Complex are similar to those of the Antalya Complex of Turkey and of the Baer-Bassit and Hatay areas of Syria (Robertson and Woodcock, 1980, 1981a; Robertson and Dixon, 1984). Those of the Antalya Complex are the most comparable, but are much thicker (exceeding 2000m) than those of the Mamonia. This relationship will be outlined in more detail in the section discussing the depositional model and geologic history (page 14).

The following descriptions of the stratigraphic units of the Ayios Photios and Dhiarizos Groups are based on field and petrographic data as well as on observations made by Swarbrick and Robertson (1980).

1.1.1.1. The Ayios Photios Group

The Ayios Photios Group is a Middle Triassic to Lower Cretaceous sedimentary sequence which has been divided into three formations: the Vlambouros, Marona, and Episkopi formations. The group is highly deformed and bears a thrust-fault relationship with the structurally underlying Dbiarizos Group. The thickness of the group is unlikely to have exceeded 200m.

The basal formation of the group, the Vlambouros Formation (Fig. 1-4, of Middle to Late Triassic age) is a sequence of quartzose sandstones, siltstones, and mudstones, with volumetrically subordinate calcirudites, calcarenites, and calcilutites. The original maximum thickness is unlikely to have exceeded 50m. Plant material is common in the green sandstones. Sedimentary structures such as graded bedding, cross-bedding, and flute and groove casts suggest deposition by turbidity currents. The composition of the sandstones is predominantly medium- to fine-grained quartz with minor feldspar; that of the calcarenites is predominantly ooids, skeletal debris and intraclasts.

Overlying the Vlambouros Formation is the Marona Formation, of Late Triassic age, up to 30m in thickness. This formation comprises grey, fine-grained, partially recrystallized and silicified micritic limestones, in part, of Hallstatt-type facies, interbedded with grey mudstones, pink siltstones, and shale. The limestones are stylolitic and contain numerous radiolaria and pelagic bivalve filaments (*?Halobia* spp.).

The Episkopi Formation, of Jurassic age, comprises the remainder of the group, and may reach 120 metres in thickness. The sequence consists of siltstones, calcilutites, and radiolarian mudstones with subordinate calcarenites, calcirudites, and calcilutites. Occurring in the upper portion of the Episkopi Formation is the Akamas Member, composed of yellow to orange, medium- to coarse-grained, quartztic sandstones (present as allochthonous blocks up to 40m in diameter).



Figure 1-4: Outcrop photograph of the Vlambouros Formation at sample REV-4-18m. Bed overturned. Note flute casts in middle background (white arrows).

The Ayios Photios Group sediments record the evolution of a passive continental margin. The Vlambouros and Marona formations represent essentially contemporaneous sedimentation in a rift environment. Erosion of a metamorphic hinterland produced the sediments of the Vlambouros Formation which were deposited by turbidity currents into the newly created ocean (Swarbrick, 1980; Swarbrick and Robertson, 1980). The sediments of the Marona Formation record deposition in areas which received little or no terrigenous sediments. Progressive deepening of the margin in the Jurassic promoted the deposition of deep-water sediments.

The Ayios Photios Group sediments occur in deformed, fault-bounded thrust sheets, within which the stratigraphical and structural organization is more coherent (Robertson and Woodcock, 1979, 1980). Even within single sheets, however, the more competent portions of the sequence are commonly disrupted to form slabs and blocks isolated within the less competent material. Sheet contacts are normally gradational rather than sharp.

While the structural styles of the group are very complicated (with zones of local inversion and conflicting fold-vergence directions), no evidence exists that the dispersion of the fold axis and axial plane measurements was caused by polyphase deformation (Robertson and Woodcock, 1979). An emplacement direction of 026° (from the present southwest) is favoured by Robertson and Woodcock (1979, 1980), who believe that the main emplacement of the Ayios Photios Group sediment sheets was by gravity sliding of sediments down a continental margin dipping to the present northeast.

1.1.1.2. The Dhiarizos Group

The Dhiarizos Group is an Upper Triassic to Upper Cretaceous sequence of volcanic and associated sedimentary rocks which can be divided into four formations: the Phasoula, Loutra tis Aphroditis, Petra tou Romiou, and Mavrokolymbos formations.

The Phasoula Formation consists of amygdaloidal or vesicular porphyritic pillow lavas intercalated with pink and grey calcilutites of the "Kholetria Member" (below; the "Kholetria Member" is placed within quotation marks as it is the name of a unit which, contrary to the stratigraphic code, is found to occur within two formations). Doleritic sills and dykes are also present. The formation may exceed 250m in thickness. A K-Ar age of 215 ± 10 Ma for the lavas has been given by Lapierre and Rocci (1976).

The Loutra tis Aphroditis Formation consists of vesicular and amygdaloidal lava breccias, volcanioclastic breccias, with subordinate volcanioclastic siltstone and manganeseiferous radiolarian mudstones of the "Kholetria Member" (below). This formation has a maximum thickness of about 75m.

Sediments in close association with the Phasoula and Loutra tis Aphroditis volcanics have been assigned to the "Kholetria Member" (Fig. 1-5), of Late Triassic age. The member includes pink and grey nodular chert-bearing calcilutites within and above pillow lavas, pink and grey calcilutites associated with manganeseiferous segregations, as well as red, thinly-bedded radiolarian cherts. This member may reach a thickness of 35m in isolated lenses.

The Petra tou Romiou Formation (see Fig. 1-6), known only as detached blocks of white, commonly recrystallized limestone, is of Late Triassic age. These blocks which show a spatial association with the volcanics and serpentinites, may be highly brecciated, and many show polished surfaces and slickensides. The principal components of the limestone are corals, algae, serpulid worm tubes, shell fragments and foraminifera tests. These blocks range in size up to about 40m in width and about 150m in length.

The Mavrokolymbos Formation, of Jurassic to Late Cretaceous age, may reach 45m in thickness. The sequence is comprised of thinly-bedded, red to green and grey, radiolarian mudstones (predominant), manganeseiferous siltstones, calcilutites, and white radiolarian siltstones.



Figure 1-5: Outcrop photograph of Phasoula Formation (pillow lavas), with interstitial limestones (white arrow) of the "Kholetria Member". Locality RNK-6-1.



Figure 1-8: Photograph of large allochthonous block of limestone of the Petra tou Romiou Formation at Episkopi village. Locality REV-2.

The Dhiarizos Group volcanics and sediments are believed to represent volcanism and sedimentation close to a continental margin (Swarbrick, 1980). The chemistry of the lavas (immobile trace element data of Pearce (1975)), is suggestive of a within-plate origin (Swarbrick, 1980; Robertson and Dixon, 1984).

The volcanics are considered to be related to crustal extension and block faulting of the Arabian-African plate (Rocci *et al.*, 1980). The reefal and shelf limestones of the Petra tou Romiou Formation were deposited in shallow water on "shelves" located on horst blocks. The pelagic "Kholetria Member" was deposited in deeper water of a more open marine environment (Swarbrick and Robertson, 1980), in close association with the volcanics.

1.1.2. Depositional Model and Geologic History

It is accepted by the majority of workers that the rocks of Cyprus (and other ophiolite complexes throughout the alpine belt) record the evolution of an ocean basin/continental margin sequence. Currently, a great deal of controversy exists as to whether these complexes represent the formation, and subsequent destruction, of one, or of more than one, ocean basin. The school of thought which advocates the "single-basin" model includes Ricou *et al.* (1984, 1986), Kazmin *et al.* (1986), and Whitechurch *et al.* (1984), while that which advocates the "multi-basin" model includes Robertson and Woodcock (1980, 1981a, 1981b, 1984), Robertson and Dixon (1984), Biju-Duval *et al.* (1977), Rocci *et al.* (1980), and Garfunkel and Derin (1984).

The key issue in this debate is the role of the so-called Calcareous Axis (a series of autochthonous carbonate platforms in southern Turkey; Fig. 1-1, page 2) during the Mesozoic (Ricou *et al.*, 1984). It could have been a small microcontinent separating two ocean basins, one to the north and one to the south ("multi-basin" model), or it could have been an integral part of the Arabian-African continent, now exposed through tectonic windows, with all ophiolitic complexes being derived from the north ("single-basin" model). The "single-

"basin" model is supported in part by similarities across strike of northern and southern outcrop belts (Ricou *et al.*, 1986) of both sediments (Ricou *et al.*, 1984) and ophiolites (Ricou *et al.*, 1984; Whitechurch *et al.*, 1984). The "multi-basin" model is supported in part by a succession consistent with a Red Sea-type of basin (Robertson and Woodcock, 1981b), evidence for a significant Mesozoic continental margin along the Egypt-Israel coastline (Garfunkel and Derin, 1984), and evidence of primary interdigititation of the Antalya Complex and the Tauride Autochthon (Waldron, 1978). In concluding their discussion Ricou *et al.* (1984) state that if there were multiple obductions ("multi-basin" model), they were so similar that they cannot be distinguished from a single one.

In conjunction with their "single-basin" model, Robertson and Woodcock (1980, 1981a) proposed a depositional model and a paleogeographic reconstruction for the Antalya Complex. With the exception of its thickness, the Antalya Complex bears a very close relationship to the Mamonia Complex. As the deformation of the Mamonia Complex is very intense, any depositional model for the complex must be consistent with existing models for related complexes. The thickness of the Mamonia, as compared to the Antalya, may be explained by a more distal position on the continental margin relative to the Antalya. Because of this, the author feels that the depositional model outlined by Robertson and Woodcock (1980, 1981a) for the Antalya is preferable for the Mamonia Complex. The following outlines the model of Robertson and Woodcock.

Prior to the Triassic this region was located south of the Paleozoic Tethys, and was part of the northern margin of Gondwanaland. During the Middle Triassic continental rifting was initiated, in association with extrusion of alkalic volcanics. Terrigenous clastic, siliceous and calcareous hemipelagic sedimentation ensued in the created rift basins. The size of these basins is debatable; they may have been quite small, on the order of several hundred kilometres wide, or even larger. Dixon and Robertson (1984) point out that the Gulf of California and the Red Sea are both thoroughly oceanic in the center, yet they are only on the order

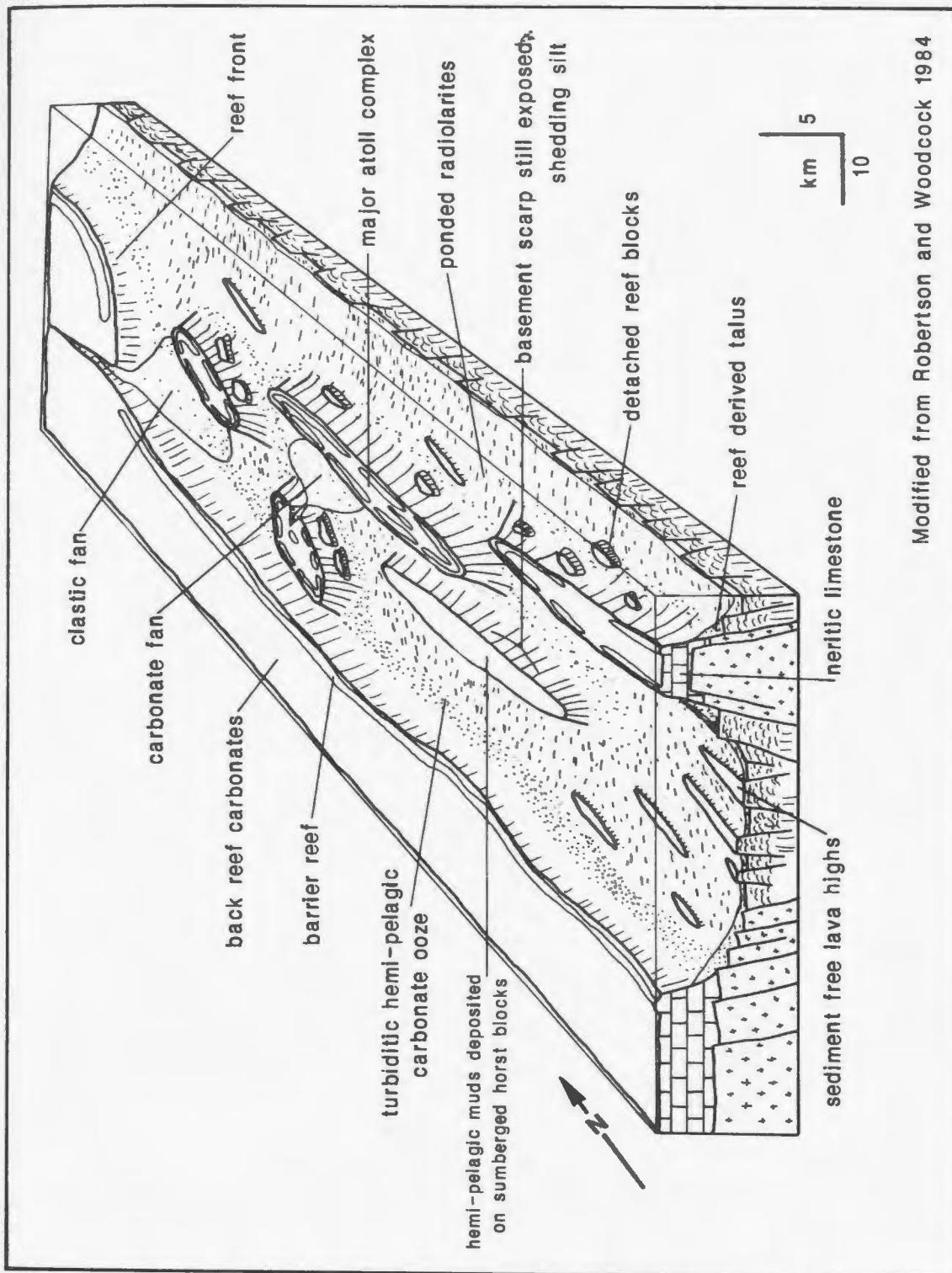
of 250km wide. Both these settings, however, are arid and have little river transport of sediments. The volume of terrigenous material in the Mamonia Complex (Vlambouros Formation) would suggest that the environment was not as arid as that of the Gulf of California or the Red Sea. Carbonate buildups, such as the Petra tou Romiou reefal limestones, are likely to have fringed horst blocks or have been situated along continental margins (Robertson and Woodcock, 1981). The end of Triassic was marked by deposition of the pelagic limestones of the Hallstatt facies (Marona Formation), reflecting an end to the terrigenous clastic input.

During the Jurassic and Early Cretaceous, relatively stable margin conditions ensued, punctuated by associated redeposition of shallow-water carbonates into the deep-water hemipelagic environment. The basin remained narrow during the Jurassic with no volcanic activity. The Late Jurassic and/or Early Cretaceous was marked by renewed uplift and subsequent deposition of the texturally mature Akamas sandstone. Rapid subsidence followed, with pelagic deposition and redeposition of platform carbonates.

The paleogeography of this period is considered by Robertson and Woodcock (1981a,1981) to have been quite complex (Figure 1-7): a small ocean basin containing numerous microcontinental slivers capped by carbonate platforms. This paleogeography, and the related facies, has been compared to that of the Bahamas (Bernoulli and Jenkins, 1974; Robertson and Woodcock, 1981a,1981b).

In the Campanian (Late Cretaceous) a belt, about 500-1500km wide, of ocean crust was formed at east-west spreading ridges offset by north-south oriented transform faults (Robertson and Woodcock, 1980). This oceanic crust is now represented by the regional ophiolite complexes (Troodos, Antalya, Hatay, and Baer-Bassit), (Figure 1-1, page 2).

An oblique northward-dipping subduction zone was initiated, and the



Modified from Robertson and Woodcock 1984

Figure 1-7: Block diagram illustrating paleogeography of the Antalya (proximal) and Mamonia (distal) complexes during Late Triassic time. Modified from Robertson and Woodcock (1984).

spreading axis and the continental margin were juxtaposed, by the end of the Maastrichtian (latest Cretaceous). At this time the Ayios Photios Group rocks were emplaced by gravity sliding down the continental margin which sloped to the southeast. The less deformed Dhiarizos Group rocks represent in part the basement rocks onto which the Ayios Photios rocks slid. Subsequent rapid uplift is shown by mass-flow deposition ofolistostrome melange (Kathikas Formation). Both groups were then juxtaposed with the Troodos Complex by strike-slip motion, possibly along a transcurrent fault system, marked by serpentinites (Ayia Varvara Formation) and high angle fault contacts (Swarbrick, 1980). Blanketing by pelagic chalks indicates that Cyprus remained in a relatively deep-water open marine setting after emplacement of all rocks.

Controversy exists as to whether the Troodos massif, and its sedimentary cover is autochthonous or allochthonous. Most Mediterranean ophiolites have been obducted onto Arabian-African platform carbonates, but this may not be the case for the Troodos and Antalya complexes (Whitechurch *et al.*, 1984). Robertson and Woodcock (1980) suggest that the Troodos massif was emplaced from an underthrusting plate onto, or against, the continental margin to the north.

Paleomagnetic evidence suggest that the Troodos massif rotated 90° counterclockwise in the Late Cretaceous-early Tertiary (Turonian-early Eocene) interval, soon after its genesis (Clube *et al.*, 1985). It has been suggested that essentially, only the island of Cyprus was rotated (Shelton and Gass, 1980; Clube *et al.*, 1985).

1.2. Previous Paleontologic Work

Previous paleontologic studies of the Mamonia Complex have been in conjunction with early stratigraphic and sedimentologic work on the complex and have dealt with pelagic bivalves, ammonoids, corals, and radiolaria. Triassic paleontologic data are listed by Henson *et al.* (1949), Pantazis (1967), and Ealey

and Knox (1975), with Jurassic work by Ealey and Knox (1975), and a Cretaceous study by Mantis (1970).

1.2.1. Previous Conodont Work

Conodonts have not been previously studied from anywhere on Cyprus. The conodonts herein described from the Mamonia Complex are of Late Triassic age, and it is this interval which will be stressed in the following brief outline of Triassic conodont studies.

A number of taxonomic papers have been of particular value to this study. Study of platform conodonts, especially *Epigondolella* has been undertaken from Bulgaria by Budurov (1972, 1976a, 1976b, 1977), from western Canada by Orchard (1983), and on a more regional scale by Kozur (1972b, 1974), Kovács and Kozur (1978), and Kozur and Mock (1972). Mosher (1968a) compared North American and European Middle and Upper Triassic faunas. One of the more comprehensive early studies undertaken was by Kozur and Mostler (1972c) of Middle and Upper Triassic faunas. Gazdzicki *et al.* (1970) studied the Norian-Rhaetian boundary in Czechoslovakia and Austria. Conodonts of Late Triassic age were described from Romania by Mirauta and Gheorghian (1975, 1978).

Conodonts have been described by a number of authors from the Mediterranean region. Early studies of the Triassic of the Mediterranean region were carried out by Huckriede (1958) and Bender and Kockel (1963) (Greece). Kristan-Tollmann and Krystyn (1975) and Onder (1984a, 1984b) studied conodonts from the Antalya Complex of Turkey. These studies report conodonts primarily of Ladinian-Carnian age. Gedik (1975, 1977) examined conodonts from other areas of Turkey and reported ages from Cambrian to Triassic. Triassic condonts have been reported from Israel (Sohn and Reiss, 1964; Huddle, 1970; Hirsch, 1972, 1975, 1977; and Hirsch and Gerry, 1974), but these are of Early and Middle Triassic age. Middle Triassic conodonts have been reported from Egypt (Eischer and Mosher, 1974), Syria (Husri and Austin, 1985), and Jordan (Bandel and Waksmundzki, 1985).

Conodont studies of the Hallstatt facies have been undertaken in Turkey (Kristan-Tollmann and Krystyn, 1975), Austria (Krystyn, 1973, 1980; Mostler *et al.*, 1978), and Yugoslavia (Cafiero and Capoa Bonardi, 1981). A regional study has also been undertaken by Mostler (1968). (The Norian faunas of these studies are quite comparable to those found in this study.)

Use of multielement conodont taxonomy is limited in Triassic conodont literature. Sweet (1970) reconstructed a number of Lower Triassic ramiform species from Pakistan. Lower and Middle Triassic reconstructions have been described by Hirsch for North America (1981), Kozur and Mostler for Hungary (1971b), and Bagnoli *et al.* for Italy (1984). Reiber (1980) described a fused conodont cluster from the Middle Triassic of Switzerland, while Ramovs (1978) and Mietto (1982) did the same from the Middle Triassic of Yugoslavia and Italy, respectively. No multielement reconstructions have been attempted anywhere for the Upper Triassic.

1.3. Purpose

The purpose of this study is threefold:

1. To study for the first time conodonts from Cyprus, specifically the Mamonia Complex, and to assign ages to the formations on the basis of conodonts.
2. To establish for the first time multielement taxonomy of Upper Triassic conodonts.
3. To compare the conodont biostratigraphic and paleoecologic data of the Mamonia Complex with studies in the Alpine belt, and to add new data to the debate on the nature of the Mamonia Complex and its regional paleogeographic setting.

1.4. Field and Laboratory Methods

1.4.1. Field Methods

Fieldwork for this study took place in June, 1985. Upon landing in Cyprus, the author travelled by car to the town of Paphos where work was based out of the Axiothea Hotel. Day trips were made by car throughout the field area. Logistical support was provided by the Cyprus Geological Survey.

As this is the first conodont study of the Mamonia Complex, it was important to sample as many different lithologies as possible. Also, samples were collected from a variety of regions within the complex in order to cover the largest possible geographic area. Samples were collected from a total of 36 localities (Figs. 1-8 to 1-13). The sample numbers may be interpreted as follows. The first letter, R, signifies the surname of the collector of the samples (Ryley). The second two letters refer to the area from which the samples were collected (eg. (R)AY = Ayios Yeoryios). The first number refers to the locality in that study area, and the last number refers to the sample at that locality. Those numbers suffixed "m" (metre) belong to measured stratigraphic sections, whereas those without the metre designation are isolated (and bear no known stratigraphic relationships to other samples). The number of samples collected at any particular locality ranged from one to thirteen, with the thickest section measuring 30m. When new lithologies were encountered isolated blocks were sampled. Each section was described in general (Appendix A), sufficient to provide basic lithologic data and to enable possible later resampling. Thin sections were cut, examined, and described for each sample (results summarized in Appendix B).

Collection of samples was complicated by three factors: Firstly, the Mamonia Complex is highly tectonized, with numerous thrust faults and complex folding. Furthermore, the sediments of the Mamonia Complex are surrounded by syn-tectonic shales. As a result, the outcrop exposure is limited and little or no

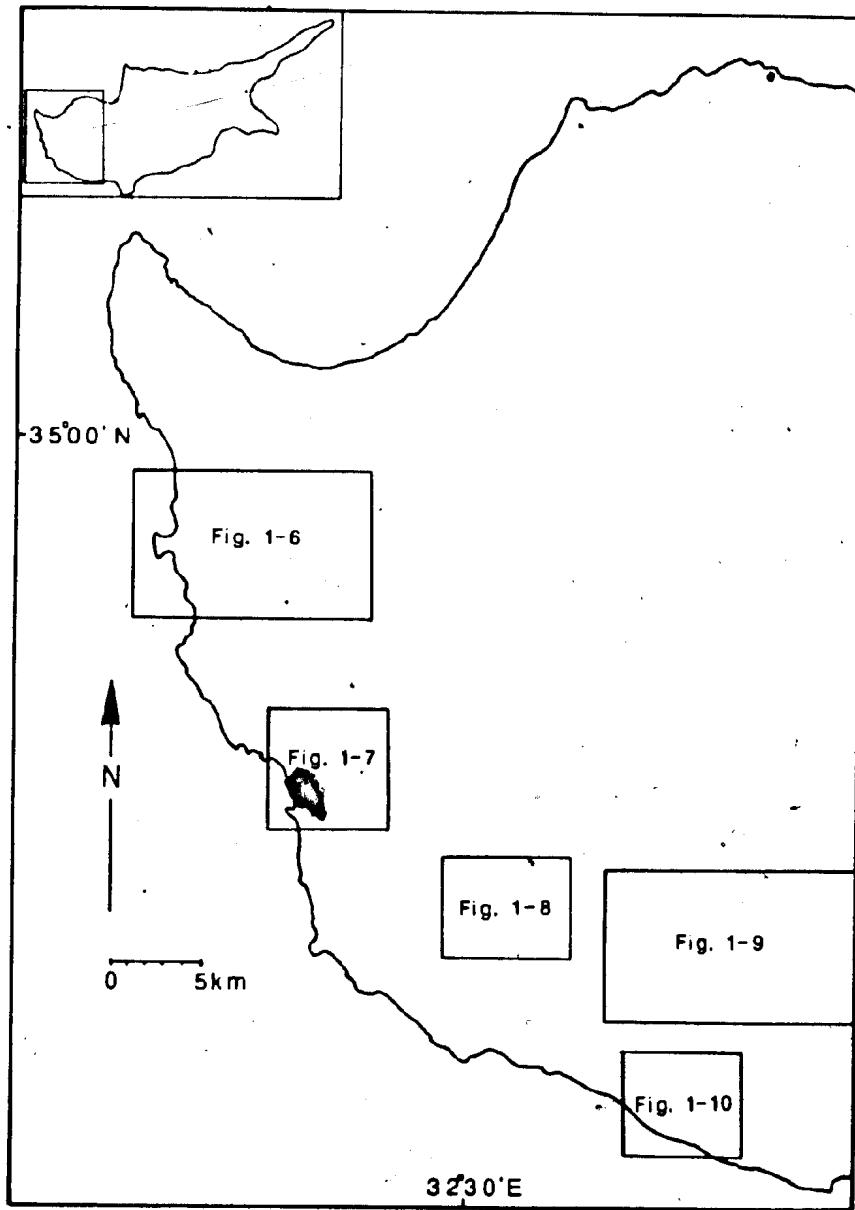


Figure 1-8: Outline map of southwestern Cyprus showing locations of succeeding sample locality maps.

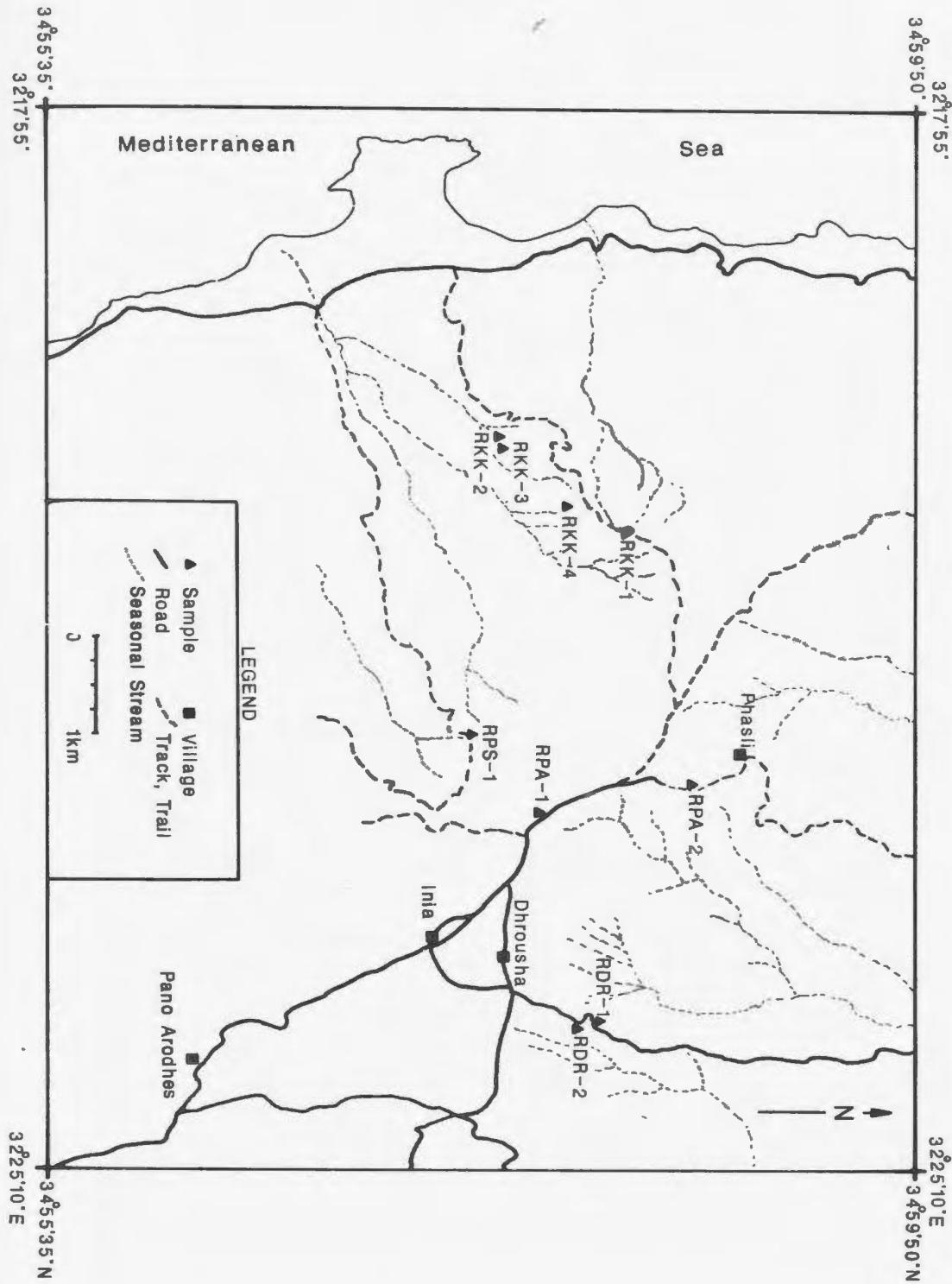


Figure 1-9: Map showing locations of collected localities in the Kryos Kolymbos region (RDR, RKK, RPA, RPS).

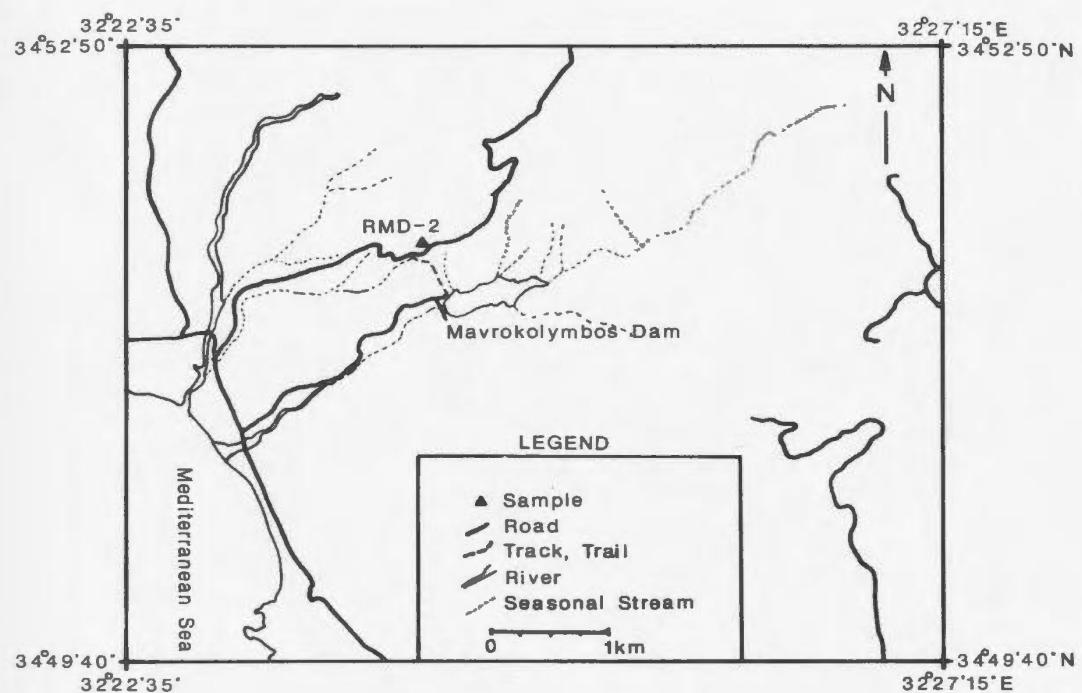


Figure 1-10: Map showing location of collected locality in the Mavrokolymbos Dam region (RMD).

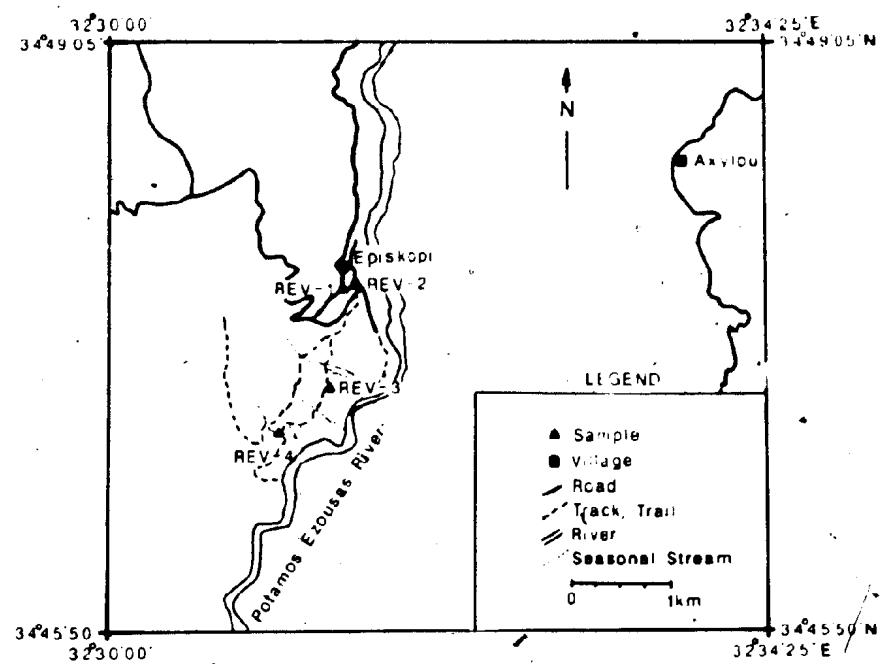


Figure 1-11: Map showing locations of collected localities in the Episkopi region (REV).

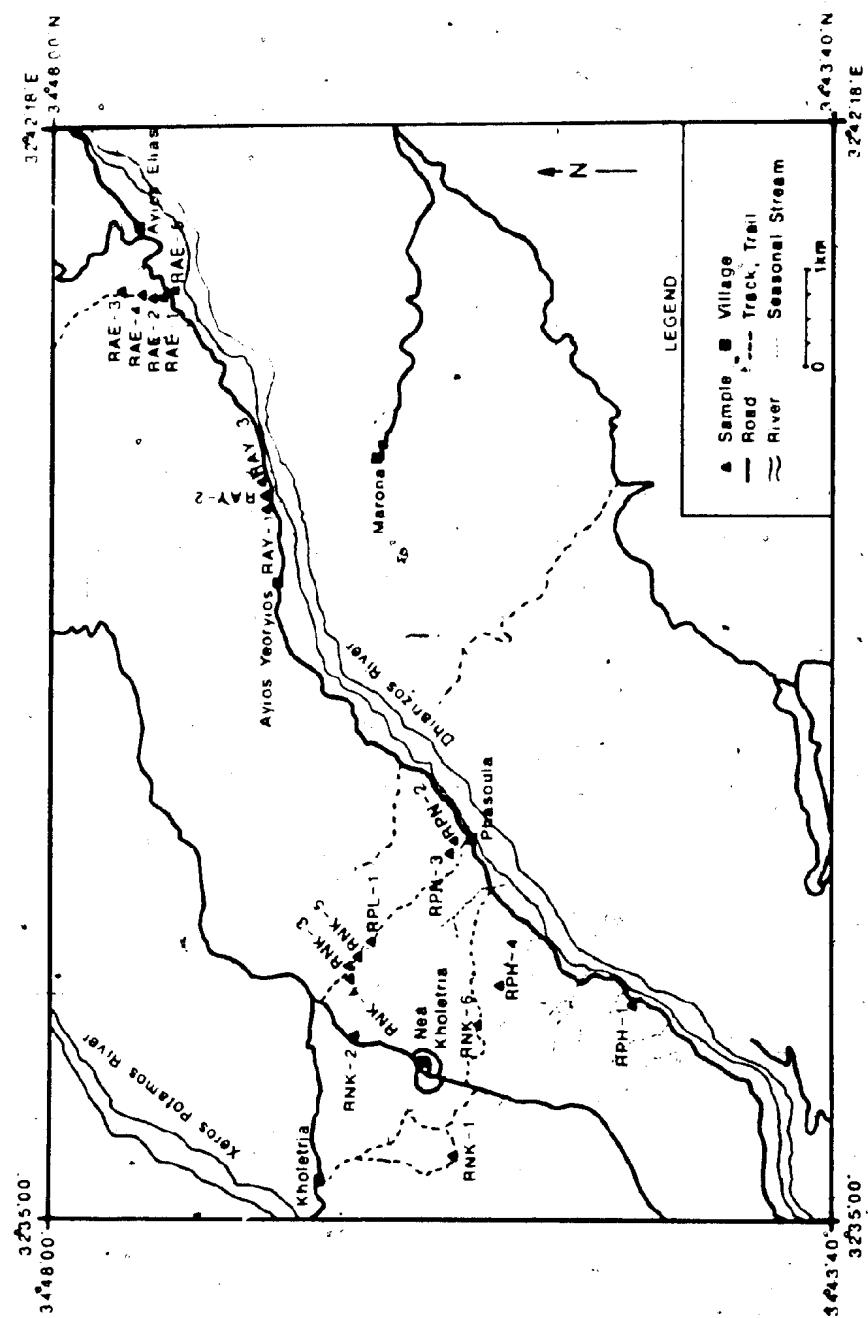


Figure 1-12: Map showing locations of collected localities in the Phasoula region (RAE, RAY, RNK, RPH, RPL).

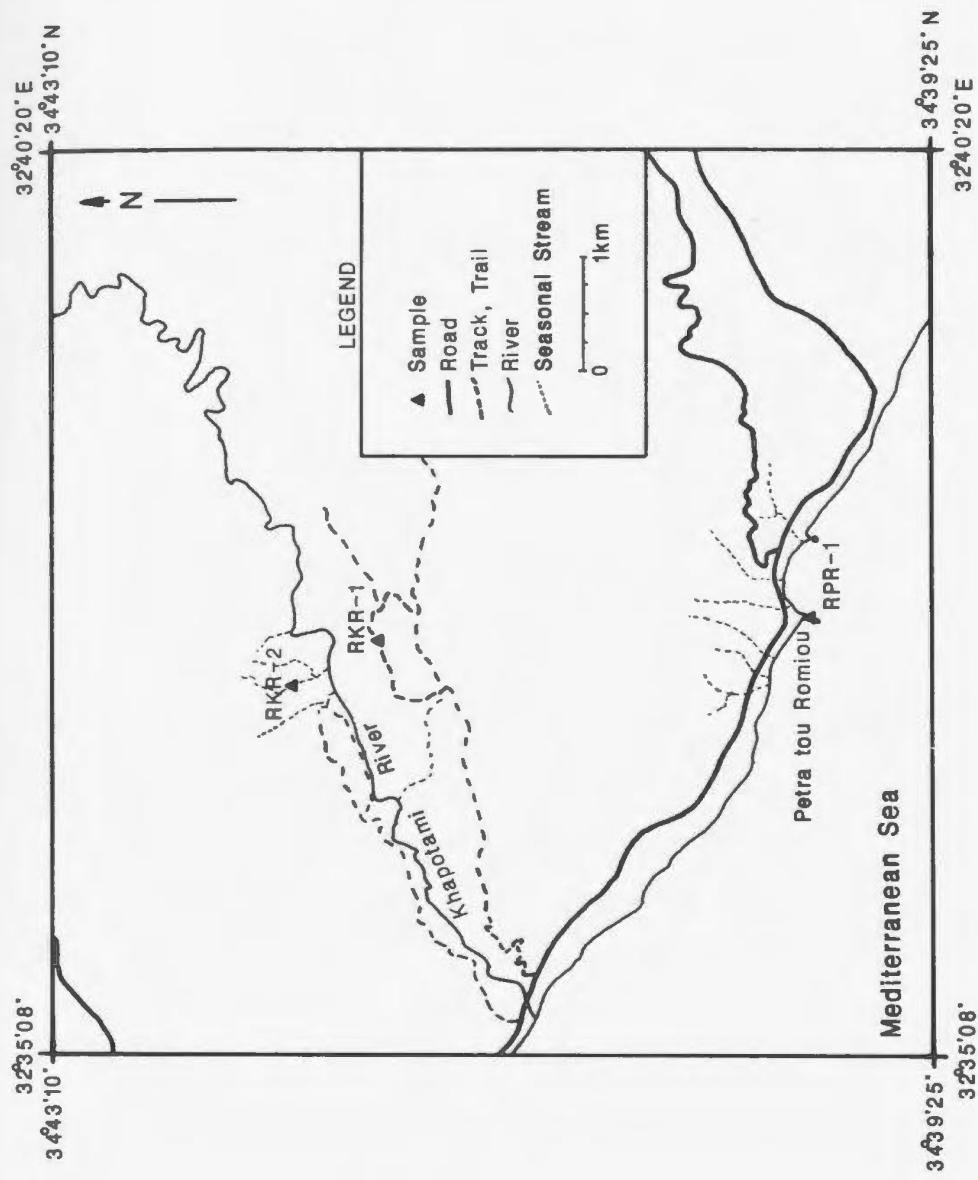


Figure 1-13: Map showing locations of collected localities in the Petra tou Romiou region (RKR, RPR).

vertical and lateral stratigraphic control exists. Secondly, the stratigraphy of the complex has not yet been completely finalized and no up-to-date geologic maps for the area exist. This makes assignment of outcrops to specific formations difficult. Lastly, it was difficult or impossible to determine the age of the sediments in the field. Only two macrofossil specimens were collected (both *Halobia* spp.). Since conodonts became extinct near the end of the Triassic, and as the total thickness of Triassic sediments in the study area does not exceed 100m, a fairly tight stratigraphic interval was targeted. Once the samples had been processed, difficulty also existed in determining if barren samples are pre-Jurassic (with the potential of yielding conodonts), or post-Triassic (with no potential whatsoever).

1.4.2. Laboratory Methods

A total of 98 samples were processed. Of these 47 (48%) yielded in excess of 4700 conodonts. Samples averaged 2kg, ranging from 1.2kg to 2.4kg. A total of 196kg of rock were processed, with a total undissolved residue of 30kg. Thus, a total of 166kg yielded an average of 28 conodonts per kg. Yields ranged from zero to about 520 conodonts per kg (Appendix D).

Samples were dissolved in 15% acetic acid. Residues were sieved through a 200 mesh ($75 \mu\text{m}$), and separated using Sodium Polytungstate at a specific gravity of 2.83. Conodonts were then picked and sorted using conventional methods. Techniques for processing and studying conodonts have recently been outlined in a volume edited by Austin (1987).

Chapter 2

Biostratigraphy and Paleoecology

2.1. Introduction

Due to the potential influence of environment on biostratigraphically significant taxa, biostratigraphy and paleoecology are two closely related disciplines. The distribution of conodont species in various environments is the framework for the following paleoecologic discussion. As such, the inferred depositional environments are important, and are first outlined. Following this, the biostratigraphy of the samples collected are discussed, including criticism of the conodont zonation used in this study. Paleoecologic interpretation of the observed conodont distribution with respect to environments follows.

2.2. Depositional Environments

As detailed paleoenvironmental analysis was not the purpose of this study, it being primarily a reconnaissance study, detailed logs were not made of the sampled sections. Furthermore, field relationships of the collected samples are, in most cases, impossible to decipher, and there exists little vertical and lateral continuity of outcrop. As a result, detailed environmental analyses were not attempted.

In this study ten lithotypes (described in Appendix C) have been assigned to three general depositional environments: pelagic, reefal, and shelf. Of these, only the pelagic and reefal environments yielded conodonts.

2.2.1. Pelagic Environment

In this study the term pelagic refers to open water environments of varying water depth, with the sediment/water interface below wave base (Scholle *et al.*, 1983). The lithotypes assigned to the pelagic environment can be divided into two groups based on the fabric of the sediments: laminated sediments (fine-grained, laminated, of deep-water origin), and turbiditic sediments (comparatively coarse-grained, showing turbiditic characteristics, of both shallow- and deep-water origin). Sediments from the two groups may be found within the same stratigraphic section.

2.2.1.1. Laminated Pelagic Sediments

Lithotypes assigned to the laminated pelagic group are: radiolarian mudstone/wackestone/packstone, calcareous chert, calcareous shale, and interpillar limestone. These have been assigned to this group based on their fine-grained, laminated nature, and the absence of any structures and faunas typical of shallow water (Wilson, 1975; Flügel, 1982; Scholle *et al.*, 1983). The sediments of this group generally lack a significant influence from terrigenous sediment sources (Scholle *et al.*, 1983).

Although, in this study, bivalve filaments were encountered only in laminated pelagic sediments, Flügel (1982) has shown that filaments are found in environments of all depths, from the subtidal to the bathyal. Filaments of the bivalve *Halobia* are very characteristic of the basinal Triassic Hallstatt facies (Flügel, 1982), as well as some non-Hallstatt facies in Western Canada (Orchard, pers. comm., 1987). Judging from the variation in oxygen content of the sediments (using presence/absence of evidence of burrowing), it is likely that a wide variety of depths are represented by the samples of this study. Water depths for Triassic pelagic facies have, however, been suggested as being as shallow as 50m (Zankl, 1971; Bernoulli and Jenkins, 1974).

These laminated pelagic sediments occur as three types:

- 1) Evenly bedded, 10-15cm thick, grey, to dark grey, calcarenite and calcilutite units.
- 2) Interbedded cherts, shales, and/or calcarenites and calcilutites. Bed thickness for cherts and limestones is generally 5-10cm; for shales, units may be up to several metres in thickness. The limestones are grey, to dark grey, in colour.
- 3) Buff-coloured limestones occupying interstitial areas in pillow lavas.

2.2.1.2. Turbiditic Pelagic Sediments

The lithotype assigned to this group is a bioclastic/lithoclastic packstone. All samples of this group have a turbiditic character. Field evidence (sole markings; Fig. 1-4, page 9) for one of the studied sections supports this interpretation, as do sedimentary structures such as crossbedding, imbrication, and graded beds, typical of Bouma divisions B and C. Textural data (moderately- to well-sorted and rounded grains) (qualitative observation; section C.5) are also supportive of a turbiditic origin.

In the field, these sediments occur as medium- to thick-bedded sandstones and shales (25cm-1m thick). Many beds are graded with scoured bases. Comparatively thin-bedded (5-15cm) sequences of shales, calcarenites and cherts also occur. The sandstones in these sequences are generally green in colour, often with plant debris, whereas the shales are typically red, and the calcarenites grey.

2.2.2. Reefal Environment

Lithotypes assigned to the reefal environment are boundstone/bafflestone and bioclastic grainstone/floatstone, and have been assigned to this environment based on their paleontologic character and petrographic fabric. The boundstone/bafflestone contains *in situ* frame-building organisms (such as scleractinian corals, serpulid worm tubes, calcisponges, and algae) and represents part of an actively growing reef environment (Flügel, 1982; James, 1983). The

bioclastic grainstone/floatstone is likely to have been deposited in a fore-reef or reef-margin environment (Enos and Moore, 1983). The presence of a micrite matrix in some samples suggests deposition below normal wave base, or in protected areas. The bioclasts in the grainstone/floatstone are identical to the faunal component of the boundstone/bafflestone lithology, suggesting that they represent part of a single reef tract.

The reefal sediments typically occur as white-coloured, isolated, massive blocks, up to 40m thick and 100m long, which appear to be brecciated and/or recrystallized, and often exhibit slickensides related to their tectonic emplacement.

2.2.3. Shelf Environment

Lithotypes assigned to the shelf environment are: whole-fossil packstone, peloidal intrasparite, and bioturbated peloidal mudstone/wackestone (Flügel, 1982; Enos, 1983).

The bioclasts of the peloidal intrasparite are moderately rounded, suggesting deposition in an agitated environment. They also possess a wide variety of clast types (intraclasts, pellets, foraminifera, echinoderm fragments, algae, bryozoa, and ooids) which are characteristic of a carbonate shelf with normal marine conditions (Flügel, 1982). The sparite cement of this lithotype is also suggestive of winnowed sediments, possibly a sand bank (Enos, 1983).

These shelf sediments are generally represented by massive white and light brown blocks, several metres in diameter, but may occur as 15-50cm irregularly bedded (occasionally siliceous) white calcarenites. The irregular bedding and the light colour is typical of shelf sequences (Wilson and Jordan, 1983).

2.2.4. Summary

The three depositional environments discussed above can be loosely related to the depositional model outlined in Section 1.1.2 and illustrated in Figure 1-7 (page 17). The laminated pelagic group includes sediments deposited in all the deep-water regions, as well as sediments deposited on submerged horst blocks (Hallstatt-type facies). They are typically deposited in deep water, though possibly as shallow as 50m, and reflect low energy, aerobic and anaerobic conditions. The turbiditic pelagic group represents sediments which are turbiditic in character and which typically have a shallow-water origin; occurring primarily in carbonate and clastic submarine fans. The reefal environment is represented by reefs occurring on the carbonate shelf area to the west, and on horst buildups. The shelf sediments are deposited in open and restricted shallow-water environments either on the carbonate platform or on horst blocks.

As the sediments of the Mamonia Complex are likely distal relative to those of the Antalya Complex, the region for which the depositional model was developed (Robertson and Woodcock, 1984), it is possible that reef and shelf sediments deposited on the carbonate platform are not represented by this study.

2.3. Biostratigraphy

The first conodont biostratigraphic zonation of the Triassic was that proposed by Sweet *et al.* (1971), who proposed twenty-two faunal assemblage zones. Of these, three were recognized in the Norian. Subsequent Upper Triassic refinements (Norian in particular) of the zonation of Sweet *et al.* (1971) were made by Kozur (1973a, 1980), Krystyn (1973, 1980), and Mostler *et al.* (1978). These zonations are based on the occurrence of species of *Epigondolella*, *Neogondolella*, and New Genus A (*Misikella* of other authors). Orchard (1983) proposed a zonation of Norian strata in western Canada based entirely on species of the genus *Epigondolella*.

The zonation to which the taxa of this study have been correlated is that

proposed by Krystyn (1980) (Fig. 2-1), which is the most refined and up-to-date zonation of Tethyan Norian strata (10 zones or sub-zones are recognized). Also, Krystyn's zonation deals with the Hallstatt facies (one of the predominant facies types found in this study) from the Salzkammergut, Salzburg, and Tyrol regions of Austria. Krystyn (1980) has suggested that this zonation may have the potential for Tethys-wide correlation.

Sweet *et al.* (1971) have pointed out the ubiquitous character of Norian conodont index species relative to older Triassic conodont faunas, which show a tendency for provincial distribution (discussed below, Section 2.4.5, page 58). Mosher (1968a) pointed out that Triassic conodonts seem to have had their greatest biostratigraphic value in the Late Triassic, where good intercontinental correlation has been obtained between Europe and western North America. This potentially allows a zonation created for the northern margin of Tethys (i.e. Austria) to be applicable to strata deposited on the southern margin (i.e. Cyprus).

However, Krystyn's zonation, based upon the occurrence of species of *Epigondolella* and *Neogondolella*, exhibits a number of potential problems. In many instances, the zonal definitions are based upon the relative abundance of certain taxa. Relative abundance of species is generally a function of paleoecology (biosfacies) and sediment accumulation rates, and should not be used to define zonations. This zonal scheme also uses the disappearance of taxa as a means of defining the base of certain zones. This, again, could be the result of paleoecology. It cannot be determined if the disappearance of a taxon is representative of an extinction event, or simply the migration of the species out of the region in question.

It should be noted that Krystyn's (1980; especially his Fig. 8, page 78) conodont zones are generally assemblage zones. The occurrence of the taxon naming the zone does not necessarily imply the identification of that zone.

Series	Stage	Substage	Ammonoid Zones Krystyn 1980		Conodont Zones Krystyn 1980	
			Marsh	II		
UPPER TRIASSIC	NORIAN	Rhaetian/ Sevanian	2	Marsh		
			1	Suessi	bidentata Zone	N. steinbergensis A. Zone*
		Aluanian	2	Columbianus		Upper Bidentata Assemblage Zone*
			1	Bicrenatus		Lower Bidentata A. Zone
			3	Magnus	spatulate Zone	Upper Postera Assemblage Zone
	Ladian	2	Paulkeli			Lower Postera A. Zone
		1	Jandianus			E. spatula Assemblage Zone*
			3	Anatropites- Boreich	primitia Zone	E. abneptie Assemblage Zone*
	CARNIAN	Tuvillian	2	Subbulatus	polygnath- iformis Zone	E. primitia A. Zone
			3			N. communisti morph.B Z
						N. communisti morph.A Z*
						Nodosa Assemblage Zone
						polygnathiformis A. Zone

Figure 2-1: Upper Carnian and Norian platform conodont zonation and its correlation with the ammonoid zonation (from Krystyn, 1980). Zones identified with reasonable certainty in the Mamonia Complex are identified by an asterisk.

Krystyn's (1980) zonation was erected for the Hallstatt Limestone in Austria. Although the Hallstatt facies one of the predominant facies types in this study, environments may be represented for which this zonation may not be valid (i.e. the reefal and shelf environments represented by the Petra tou Romiou Formation, and possibly the turbiditic pelagic sediments represented by the Vlambouros Formation). The ranges of taxa are fairly well defined in the Hallstatt facies, and other open water environments. They have not, as yet, been well documented for shallow-water environments. Krystyn's zonation has been used, however, as it is considered to be the most applicable available.

2.3.1. Correlation of Samples With Established Conodont Zonation

Of the ten zones proposed by Krystyn (1980) for the Norian, four are recognized in samples from the Mamonia Complex. Recognition of these zones is based on the occurrence of characteristic taxa in samples from continuous sections, or from certain of the isolated samples, which were collected for this study. Range charts for species which occur in stratigraphic sections are illustrated in Figures 2-2 to 2-5.

Because the available zonation is based entirely on platform taxa (species of *Epigondolella* and *Neogondolella*), samples which do not contain these taxa are difficult to assign. Also, because of the difficulty in identifying specimens of *Epigondolella* represented only by juvenile forms (*E.* spp. indet. s.f., discussed in more detail in the taxonomy section, page 97), samples containing only juvenile forms have been treated as though no diagnostic species are present.

Twenty-nine of the forty-seven conodont-yielding samples can be assigned with some certainty to specific conodont zones. Four samples have been assigned to the *Neogondolella communis* morphotype A Zone, thirteen to the *Epigondolella abneptis* Assemblage Zone, two to the *Epigondolella spatulata* Assemblage Zone, and nine to the Upper Bidentata Assemblage Zone.

REV-4-1.5m
REV-4-8m
REV-4-18m
REV-4-30m

- Chirodella sp. B
- Epigondolella bidentata s.f.
- Gen. n. A hernsteini
- Gen. n. A posthernsteini
- Neogondolella steinbergensis
- Oncodella paucidentata s.f.
- Chirodella erecta
- Gen. n. C sp. n. A
- Epigondolella posteria s.f.
- Gen. et sp. indet. G s.f.
- Gen. n. A koessenensis s.f.

Figure 2-2: Range chart for species occurring in section REV-4.

Species listed in order of first occurrence. This section is correlative with the Upper Bidentata Assemblage Zone.

Note: stratigraphic section is inverted.

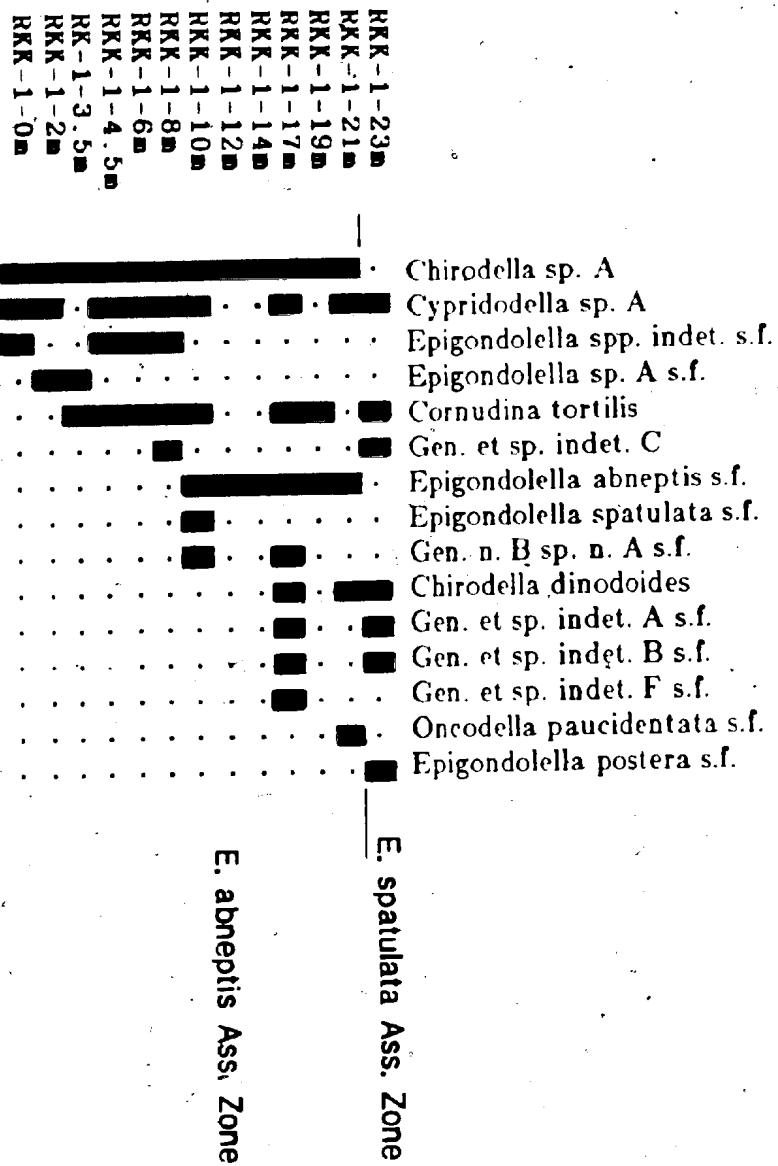


Figure 2-3: Range chart for species occurring in section RKK-1. In this section, those samples below 23m are correlative with the *Epigondolella abneptis* Assemblage Zone, while sample 23m is correlative with the *Epigondolella spatulata* Assemblage Zone. Species listed in order of first occurrence.

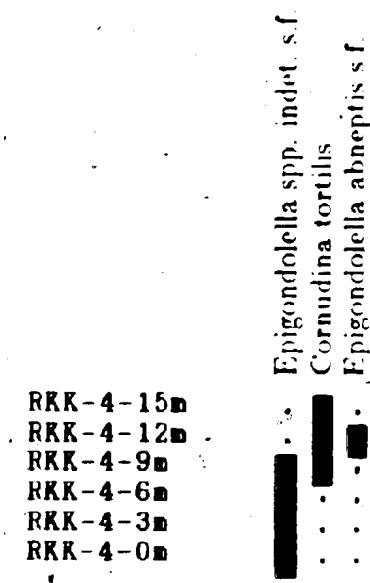


Figure 2-4: Range chart for species occurring in section RKK-4. This section is correlative with either the *Epigondolella abneptis* or the *Epigondolella spatulata* assemblage zones. Species listed in order of first occurrence.

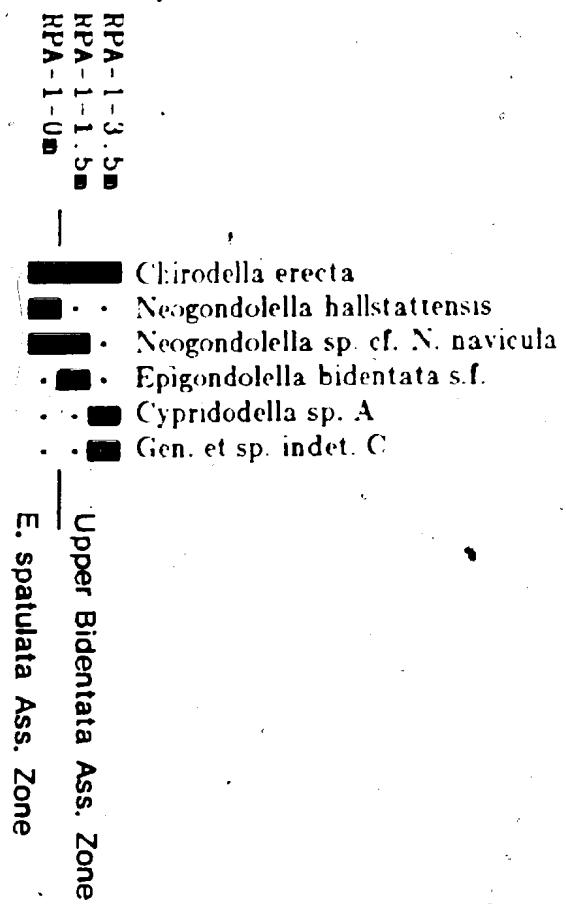


Figure 2-5: Range chart for species occurring in section RPA-1. In this section, sample RPA-1-0m is correlative with the *Epigondolella spatulata* Assemblage Zone, while the remaining samples are correlative with the Upper Bidentata Assemblage Zone. Species listed in order of first occurrence.

The interval represented by the Lower Postera, Upper Postera, and Lower Bidentata assemblage zones (an interval to which samples cannot be correlated) may be represented in section RPA-1 (Fig. 2-5). The lowermost sample in this section (RPA-1-0m) is correlative with the *Epigondolella spatulata* Assemblage Zone, while the upper two samples (RPA-1-1.5m and RPA-1-3.5m) are correlative with the Upper Bidentata Assemblage Zone. The interval between samples RPA-1-0m and RPA-1-1.5m, a red shale which was not sampled, may contain the missing zones.

Twelve samples have been assigned to the interval represented by both the *Epigondolella abneptis* and *Epigondolella spatulata* assemblage zones. The taxa used to correlate these samples with Krystyn's (1980) zonation include both the zonal guides of Krystyn and multielement ramiform species identified in this study. These samples best correlate with the upper portion of section RKK-1 (Fig. 2-3), and, as such, likely correlate with the upper portion of the *Epigondolella abneptis* Assemblage Zone (as represented in this study), or with the *Epigondolella spatulata* Assemblage Zone. Figure 2-6 illustrates the correlation between collected samples and Krystyn's (1980) Carnian-Norian conodont zonation.

Due to the absence of characteristic species, of the forty-seven samples which yielded conodonts, six (RAE-4-5m, RDR-1-1, RDR-1-2, RDR-1-3, RKR-1-17m, and REV-2-5) could not be correlated with any of Krystyn's (1980) conodont zones.

2.3.1.1. Neogondolella communisti morphotype A Zone

This zone is identified, as defined by Krystyn (1980⁷⁹), by the occurrence of specimens which are very similar, if not identical to, the index species of this zone: *Neogondolella communisti* morphotype A *sensu* Krystyn s.l.. It is recognized in four samples (REV-2-1 to REV-2-4) from a large allochthonous block of reefal limestone.

Only one other identifiable species was found to occur in this zone:

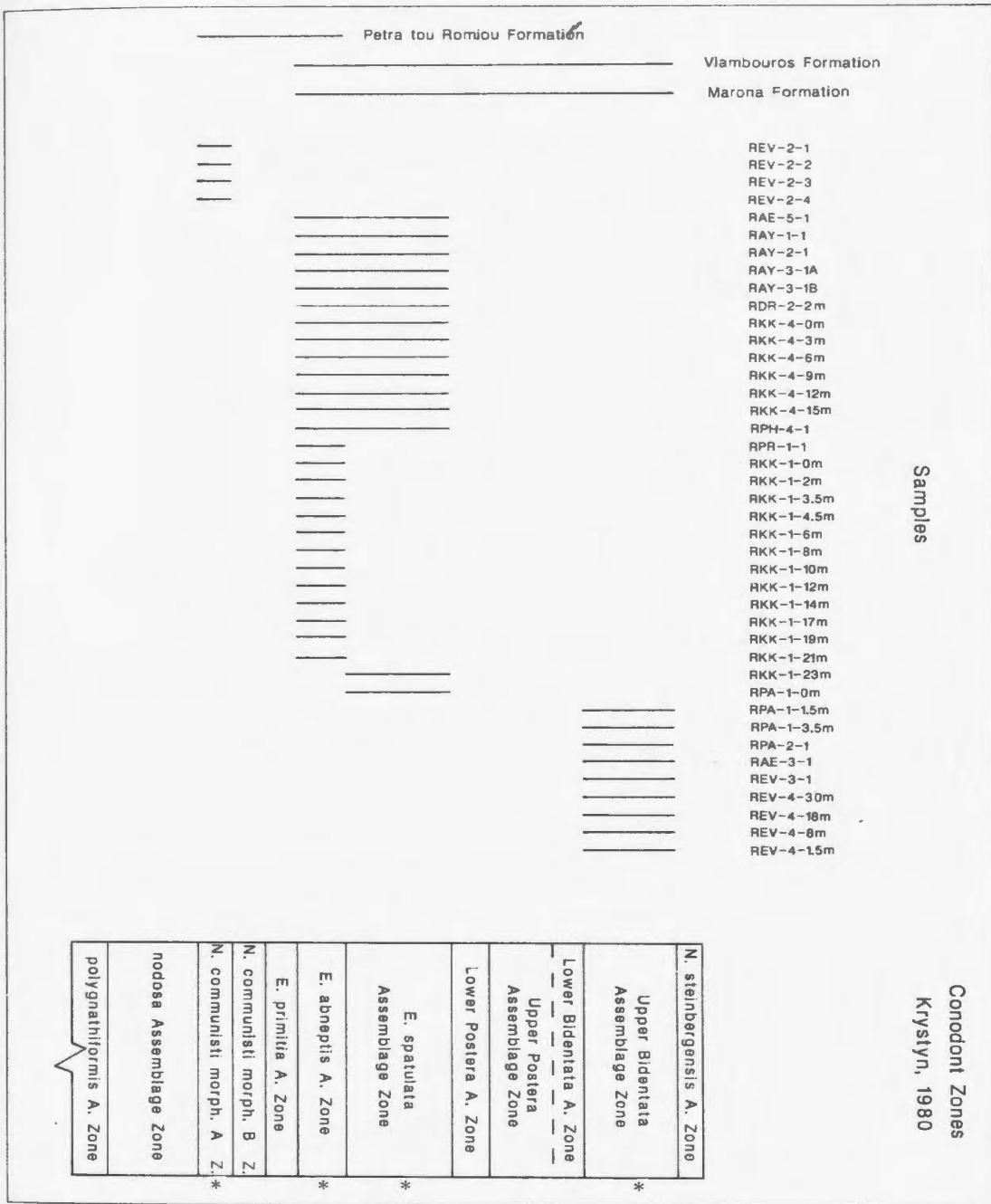


Figure 2-6: Correlation of collected conodont samples with the conodont zones of Krystyn (1980). Sampled intervals of the collected formations are also shown (does not imply exact ranges for formations). Zones identified with reasonable certainty are marked by an asterisk. For more information concerning individual samples see Appendix B.

Misikella longidentata Kozur and Mock. This species was also recovered in a sample (RAY-1-1) which can be assigned to a range of younger zones (the *Epigondolella abneptis* and *Epigondolella spatulata* assemblage zones) and, as such, is not considered characteristic of this zone.

Krystyn (1980) states that the sudden appearance of *Neogondolella navicula* in the uppermost portion of the *N. communisti* morphotype A Zone is indicative of lowermost Norian strata. Due to the absence of *N. navicula* in this study it is not possible to determine if the interval represented by this zone is uppermost Carnian or lowermost Norian.

It must be pointed out that the environment in which these taxa are found (reefal) is not the environment for which the zonation was erected (pelagic); the range of *N. communisti* s.s. in the reefal environment may be quite different from that in the pelagic environment. Hence, it is not possible to ascertain that those specimens recovered here are restricted to the *N. communisti* morphotype A Zone of Krystyn. As a result, the proposed correlation is made with reservations.

Kozur and Mock (1974a) report the occurrence of *Misikella longidentata* from lower Middle Norian strata. The presence in this study of this species in strata tentatively assigned to the uppermost Carnian or the lowermost Norian may extend the known range of the species. However, there also exists the possibility that *M. longidentata* does have a restricted range (i.e. restricted to the lower Middle Norian). If this is the case, the range of *N. communisti* s.s. in the reefal environment may be considerably greater than in the pelagic environment. In this instance, the range of *N. communisti* could be extended to the lower Middle Norian.

2.3.1.2. Epigondolella abneptis Assemblage Zone

This zone, as defined by Krystyn (1980:79), is characterized by the presence of both *Epigondolella abneptis* s.f. and *Epigondolella spatulata* s.f.. It is here represented by approximately 21m of section (samples RKK-1-0m to RKK-1-21m in section RKK-1, see Fig. 2-3, page 38), and by one isolated sample (RPR-1-1).

The following species are found to occur in this zone:

Chirodella dinodoides (Tatge)

Chirodella sp. A

Cornudina tortilis Kozur

Cypridodella sp. A

Epigondolella abneptis (Huckriede) s.f.

Epigondolella spatulata (Hayashi) s.f.

Epigondolella sp. A s.f.

Oncodella paucidentata (Mostler) s.f.

New Genus B New Species A s.f.

Gen. et sp. indet. A s.f.

Gen. et sp. indet. B s.f.

Gen. et sp. indet. C

Gen. et sp. indet. F s.f.

Epigondolella sp. A s.f. is found in the lower portion of the section assigned to this zone (RKK-1), and may allow for further refinement of the zonation at a later time when more information regarding this taxon has been accumulated.

Cypridodella sp. A is found to occur throughout this zone. Its first

appearance may have value as a zonal indicator for the *Epigondolella abneptis* Assemblage Zone. However, until the multielement taxonomy of species of *Cypridodella* is understood, and their synonymies compiled, their usefulness as zonal indicators will be limited.

This zone is recognized in rocks which can be assigned to the reefal environment and to laminated pelagic sediments.

2.3.1.3. *Epigondolella spatulata* Assemblage Zone

Two samples have been assigned to this zone, as defined by Krystyn (1980:79); one (RPA-1-0m) based on the presence of *Neogondolella hallstattensis* Mosher (whose range is restricted to this zone (Krystyn, 1980)), and the other (RKK-1-23m) because it records the first appearance of *Epigondolella postera* (Kozur and Mostler) s.f. in the stratigraphic section RKK-1 (Fig. 2-3, page 38).

The following species are found to occur in this zone:

Chirodella dinodoides (Tatge)

Chirodella erecta Mosher

Cypridodella sp. A

Cornudina tortilis Kozur and Mostler

Epigondolella postera (Kozur and Mostler) s.f.

Neogondolella hallstattensis (Mosher)

Neogondolella sp. cf. *Neogondolella navicula* (Huckriede)

Gen. et sp. indet. A s.f.

Gen. et sp. indet. B s.f.

Gen. et sp. indet. C

This zone records the first appearance of *Chirodella erecta* and

Neogondolella sp. cf. *N. navicula*, and marks the last occurrence of *Cornudina tortilis* (this is the highest interval in the Norian in which *C. tortilis* has been found to date).

Both samples assigned with certainty to this zone are from laminated pelagic sediments.

2.3.1.4. Upper Bidentata Assemblage Zone

This zone is recognized (as defined by Krystyn, 1980:80) by the presence of *Epigondolella bidentata* Mosher s.s. and *Neogondolella steinbergensis* (Mosher), with rare occurrences of *Epigondolella abneptis* s.s. and *Epigondolella postera* s.s.

The following species are found to occur in this zone:

Chirodella erecta Mosher

Chirodella sp. A

Cypridodella sp. A

Epigondolella postera (Kozur and Mostler) s.s.

Epigondolella bidentata Mosher s.s.

Neogondolella steinbergensis (Mosher)

Neogondolella sp. cf. *Neogondolella navicula* (Huckriede)

Oncodella paucidentata (Mostler) s.s.

New Genus A *hernsteini* (Mostler)

New Genus A *koessenensis* (Mostler)

New Genus A *posthernsteini* (Kozur and Mock)

New Genus A sp. cf. New Genus A *rhaetica* (Mostler) s.s.

New Genus C New Species A

Gen. et sp. indet. C

Gen. et sp. indet. D s.f.

Gen. et sp. indet. G s.f.

A number of these species are restricted to this zone, including all species of New Genus A: New Genus A *hernsteini*, New Genus A *koessenensis*, New Genus A *posthernsteini*, and New Genus A sp., cf. New Genus A *rhaetica* s.f.

Mostler *et al.* (1978) proposed a zonation for the uppermost Triassic based upon species of New Genus A (therein referred to as *Misikella*). The New Genus A fauna of this study, however, does not correlate with their zonation. All four species of New Genus A are found to occur in the Upper Bidentata Assemblage Zone, while in the zonation of Mostler *et al.* (1978), the various ranges of the species are used to define the zones. According to Mostler *et al.* (1978), New Genus A *koessenensis* and New Genus A *hernsteini* are not found to co-occur. In this study, however, they are found to co-occur in sample REV-4-8m. It should be pointed out that most of the samples containing New Genus A are from turbiditic sandstones. The difficulty in correlating these specimens with an existing zonation suggests that there may have been some reworking or stratigraphic leaking (Orchard, pers. comm., 1987) of the conodonts, although there is no other evidence (i.e. preservation condition of specimens) to support this.

Other species which are restricted to this zone are *N. steinbergensis*, *Chirodella* sp. B, New Genus C New Species A, and Gen. et sp. indet. G s.f.

Samples assigned to this zone are from laminated and turbiditic pelagic sediments.

2.3.2. Age Of Sampled Formations

Based on the correlation between the collected samples and the conodont zonation erected by Krystyn (1980), the minimum ages of the formations from which samples were collected can be estimated. The correlation between Triassic conodont zones, collected samples, and formations is illustrated in Figure 2-6 (page 42). The ages suggested for the various formations corresponds to the minimum range in age as suggested by the conodont zonation. As tops and bottoms of formations were not observed or sampled, the range in ages suggested below for the formations must be considered as absolute mimimums.

The age of the Petra tou Romiou Formation is estimated as ranging from the uppermost Tuvalian (Tuvalian 3, Carnian) to the middle Lacian (Lacian 2, Norian). The lower boundary is the base of the *N. communis* morphotype A Zone, while the upper boundary corresponds to the uppermost occurrence of *Epigondolella* sp. A s.s. (middle of *E. abneptis* Assemblage Zone). This formation was deposited in a shallow-water environment. As discussed above, the ranges of these taxa may represent ages different from those determined for the same taxa in the deep-water environment.

The age of the Marona Formation is interpreted as ranging from the middle Lacian (Lacian 2, Norian) to the top of the lower Sevatician/Rhaetian (Sevatician/Rhaetian 1, Norian). This corresponds to the range from the base of the *E. abneptis* Assemblage Zone to the top of the Upper Bidentata Assemblage Zone.

The Vlamboulos Formation is also interpreted as ranging from the middle Lacian (Lacian 2, Norian) to the top of the lower Sevatician/Rhaetian (Sevatician/Rhaetian 1, Norian), corresponding to the range from the base of the *E. abneptis* Assemblage Zone to the top of the Upper Bidentata Assemblage Zone.

None of the conodont-yielding samples collected from the Kholetria

Member* contain specimens diagnostic enough to allow correlation with Krystyn's (1980) zonation. This is due to the poor preservation of the specimens in these samples; likely related to diagenetic changes resulting from close proximity to submarine volcanism.

2.4. Paleoecology

Paleontologists must keep in mind that any fossil they study, rather than being the inanimate object that they collect, represents a once-living, complex biological system. As such, its distribution and abundance was limited by the physical, chemical, and biological factors of its environment (Laporte, 1979).

The conodontophorid animal, apart from very rare soft-part occurrences (e.g. Briggs *et al.*, 1983; Smith *et al.*, 1987), is most commonly represented by disjunct conodont elements. As conodonts are the only commonly preserved parts of the animal, paleoecologic interpretations must be based primarily on their environmental distribution (i.e. the depositional environment of the sediment from which the conodonts were extracted).

In this study, the environmental interpretations are based upon field data and petrographic analyses of samples. As such, the inferred type of substrate is one of the important characteristics of the environment which can be studied. Fortunately, the nature of the substrate correlates well with other environmental factors that are not directly recorded (Laporte, 1979), such as water energy, depth, and chemistry.

2.4.1. General Paleoecologic Models

Two major ecologic models for the conodont animal have been proposed. One model, proposed by Seddon and Sweet (1971), considers that conodontophorids were pelagic and free-swimming, and that they were ecologically depth stratified. The other (Barnes and Fahraeus, 1975; Fahraeus and Barnes, 1975) indicates a strong component of lateral segregation of faunas,

with dependance upon the physico-chemical conditions of the substrate, suggesting that most conodontophorids were benthic or nektobenthic organisms.

The environmental distribution of conodonts is likely to have been controlled by a number of factors, including the physical parameters of the water (temperature, turbidity, energy level), chemical parameters (salinity), and nutrient levels (Nicoll, 1984). Nicoll (1984) also points out that other aspects of the environment, such as benthic plant and animal communities around which the conodont animals might have lived, may have been important. Any models which attempt to fit conodonts into ecologic niches must take into account the full spectrum of controlling factors influencing the habitat of conodontophorids.

2.4.2. Triassic Studies

Mosher (1973a) recognized three groups of conodonts in the Triassic which he considered to be phylogenetically distinct and which may show ecologic preferences. Mosher's Group 2 contains species herein assigned to *Neogondolella*, *Cypridodella*, and *Chirodella*, while Group 3 is comprised solely of species of *Epigondolella*. His Group 1 conodonts (consisting of a series of form taxa not recognized in this study) are closely linked to shelf and bottom conditions, and are restricted for the most part to the Middle Triassic (a time of probable provincialism for Triassic conodonts; below, page 58). Groups 2 and 3 appear to have been less environmentally restricted.

A number of paleoecologic studies have recently been undertaken from Triassic conodonts of the western and southwestern United States (Babcock, 1976; Clark and Rosser, 1976; Clark and Hatleberg, 1983; Carey, 1984; Clark and Carr, 1984; Carr *et al.*, 1984; and Meek, 1984). These are concerned with rocks spanning most of the Triassic, and, for the most part, deal with sediments whose paleoenvironmental relationships are well understood. They also typically deal with an understood, distinctive, and widespread fauna; characteristics which are important in establishing good conodont paleoecologic models (Clark and Rosser, 1976).

The above studies make a number of observations regarding conodont distribution. Triassic conodonts have generally been found to be rare or absent in reef and shelf environments (Babcock, 1976; Carey, 1984; Meek, 1984). This is in contrast to the conodonts of other time periods (e.g. the Devonian, Silurian, and Mississippian), when conodonts were found to be common in shallow-water environments (e.g. Bultynk, 1976; Chatterton, 1976; Clark, 1981; Von Bitter *et al.*, 1986).

Triassic conodont diversity decreased basinward and shelfward from the shelf edge in the Early and Middle Triassic and appears to have been related to distance from the basin edge rather than to depth (Babcock, 1976). This suggests that there may have been greater environmental variability in the shelf edge area (Babcock, 1976; Carr *et al.*, 1984). Meek (1984) reports relatively high conodont abundances in the basinal environment of the Late Triassic. However, they are not reported from very deep basinal environments.

The distribution of conodonts in different facies is regarded as conodont biosfacies (e.g. Clark and Carr, 1984). The concept of conodont biosfacies has recently been summarized in a volume edited by Clark (1984). This volume contains four papers on Triassic conodont biosfacies, two of which deal with Upper Triassic (Norian) strata.

Carey (1984) observed that early Norian *Epigondolella* species were found in both the shallow marine (outer shelf) and deep oceanic environments. Carey takes this as evidence supporting a nektic habit for species occupying normal marine waters of greatly varying depths. Other genera whose species are interpreted to be nektic by Carey (1984) are *Neogondolella* and *Cypridodella* (both found primarily in deep-water deposits), neither of which were found to occur in the Norian.

Meek (1984), in his study of Norian strata from Nevada, found conodonts (primarily of the genus *Epigondolella*) to be nektic, active, free-moving organisms.

Species of the genus *Epigondolella* were mainly restricted to basinal sediments. However, *Epigondolella abneptis* subsp. A (*sensu* Orchard) s.l., *Epigondolella abneptis* subsp. B (*sensu* Orchard) s.l., and *Epigondolella multidentata* Mosher s.l., were also found in rocks representative of a facies intermediate between shelf and basins. *Epigondolella bidentata* was found to occur in carbonate platform sediments (Meek, 1984).

2.4.3. Paleoecologic Interpretation

The conodont species identified in this study have been plotted against the inferred depositional environments from which they were recovered (Tables 2-1 to 2-3). The taxa have been plotted against the environments for three time intervals, which distinguish three distinct periods of time: that represented by the *Neogondolella communisti* morphotype A Zone, that represented by the *Epigondolella abneptis* and *Epigondolella spatulata* assemblage zones, and that represented by the Upper Bidentata Assemblage Zone. In these environmental distribution tables, the numbers in the columns represent the number of samples yielding that species over the total number of elements recovered for that species.

Table 2-1: Table illustrating occurrence of species with respect to the environments in which they are found in the *Neogondolella communisti* morphotype A Zone. Lam.-Pel. and Turb.-Pel. refer to laminated and turbiditic pelagic sediments. Occurrence data show number of samples/number of elements recovered.

Environmental Distribution Of Conodonts In The <i>Neogondolella communisti</i> morphotype A Zone			
Species	Lam.-Pel.	Turb.-Pel.	Reefal
<i>Misikella longidentata</i>			4/25
<i>Neogondolella communisti</i> s.l.			2/7
Total Number Of Samples			4
Total Number Of Elements			32

Because of the limitations of this study, it is possible to comment only on

Table 2-2: Table illustrating occurrence of species with respect to the environments in which they are found in the *Epigondolella abneptis* and the *Epigondolella spatulata* assemblage zones. Lam.-Pel. and Turb.-Pel. refer to laminated and turbiditic pelagic sediments. Occurrence data show number of samples/number of elements recovered.

Environmental Distribution Of Conodonts In The <i>Epigondolella abneptis</i> And <i>Epigondolella spatulata</i> Assemblage Zones			
Species	Lam.-Pel.	Turb.-Pel.	Reefal
<i>Chirodella erecta</i>	1/8		
<i>Chirodella dinodoides</i>	4/181		
<i>Chirodella</i> sp. A	17/949		1/9
<i>Cornudina tortilis</i>	15/41		1/6
<i>Cypridodella</i> sp. A	13/222		
<i>Epigondolella abneptis</i> s.f.	7/38		
<i>Epigondolella postera</i> s.f.	3/79	1/7	
<i>Epigondolella spatulata</i> s.f.	4/217		
<i>Epigondolella</i> sp. A s.f.	2/22		1/20
<i>Misikella longidentata</i>	1/1		
<i>Neogondolella hallstattensis</i>	1/7		
<i>Neogondolella</i> sp. cf. <i>N. navicula</i>	1/8		
<i>Oncodella paucidentata</i> s.f.	1/1		
New Genus B New Species A s.f.	2/144		
Gen. et sp. indet. A s.f.	2/4		
Gen. et sp. indet. B s.f.	2/2		
Gen. et sp. indet. C	6/15		
Gen. et sp. indet. E s.f.	1/1		
Gen. et sp. indet. F s.f.	1/1		
Total Number Of Samples	25	1	1
Total Number Of Elements	2251	7	35

the environments in which taxa are found to occur; not on those in which they do not occur. This results from two factors. The first of these is that if a sample was found to be barren of conodonts, it was not possible to determine if this was because it is of post-Triassic age (during which time conodonts were extinct), or if it was because the sample is of pre-Jurassic age, with the potential of yielding conodonts, but deposited in an environment unfavourable to conodontophorids. On the other hand, environments may have been represented in the field from which samples were not collected for a given time-interval.

Table 2-3: Table illustrating occurrence of species with respect to the environments in which they are found in the Upper Bidentata Assemblage Zone. Lam.-Pel. and Turb.-Pel. refer to laminated and turbiditic pelagic sediments. Occurrence show number of samples/number of elements recovered.

Environmental Distribution Of Conodonts In The Upper Bidentata Assemblage Zone			
Species	Lam.-Pel.	Turb.-Pel.	Reef
<i>Chirodella erecta</i>	5/313	2/8	
<i>Chirodella</i> sp. B	2/378	3/81	
<i>Cypridodella</i> sp. A	1/7	1/28	
<i>Epigondolella bidentata</i> s.f.	3/53	3/124	
<i>Epigondolella postera</i> s.f.		2/11	
<i>Neogondolella steinbergensis</i>	2/7	4/71	
<i>Neogondolella</i> sp. cf. <i>N. navicula</i>	1/40		
<i>Oncodella paucidentata</i> s.f.	2/54	3/53	
New Genus A <i>hernsteini</i>	2/209	2/15	
New Genus A <i>koessenensis</i>	1/2	1/4	
New Genus A <i>postherneusteni</i>	2/344	3/234	
N. Gen. A sp. cf. N. Gen. A <i>rhaetica</i> s.f.	1/5		
New Genus C New Species A	2/262	1/31	
Gen. et sp. indet. C	1/1		
Gen. et sp. indet. D s.f.	1/1		
Gen. et sp. indet. G s.f.		1/1	
Total Number Of Samples	5	4	
Total Number Of Elements	1676	661	

2.4.3.1. Neogondolella communis morphotype A Zone

Conodonts indicative of this zone were recovered only from the reefal environment. In this environment, both the faunal diversity (only one or two species per sample), and the average abundance of elements, are low.

2.4.3.2. Epigondotella abneptis and Epigondotella spatulata Assemblage Zones

Both of the pelagic subenvironments, and the reefal environment, are represented by samples in this time interval. However, only one sample each for turbiditic pelagic sediments the reef environment were recorded; compared to twenty-five for laminated pelagic sediments.

In this interval, the species diversity and abundance are low in both turbiditic pelagic sediments and the reefal environment, and are high in laminated pelagic sediments.

Epigondolella postera s.f. was found to occur in both laminated and turbiditic pelagic sediments, although in less abundance in the turbiditic group.

Chirodella sp. A, *Cornudina tortilis*, and *Epigondolella* sp. A s.f. were found to occur in both laminated pelagic sediments and the reefal environment. The abundances for *Chirodella* sp. A are much higher in laminated pelagic sediments, whereas the abundances for *Cornudina tortilis* and *Epigondolella* sp. A s.f. are comparable in both environments.

2.4.3.3. Upper Bidentata Assemblage Zone

This interval has both the highest species diversity (up to ten species per sample, e.g. section REV-4, Fig. 2-2, page 37) and abundances of the intervals represented. No specimens were recovered from the reefal environment for this interval.

Ten of the sixteen recovered species are found to occur in both of the pelagic sediment types. Of these, *Chirodella erecta*, *Chirodella* sp. B, New Genus A *hernsteini*, and New Genus C New Species A are much more abundant in laminated pelagic sediments. When sample numbers and abundances are taken into consideration, the remaining species of this zone show no strong preference for environment.

2.4.4. General Observations

Table 2-4 summarizes the distribution of the species in the two environments for the total time interval represented by this study.

An important question which must be considered when interpreting these distributions is: what is the environmental origin for the conodonts in the

Table 2-4: Table illustrating occurrence of species with respect to the environments in which they are found. Lam.-Pel. and Turb.-Pel. refer to laminated and turbiditic pelagic sediments. Occurrence data show number of samples/number of elements recovered.

Environmental Distribution Of Conodonts			
Species	Lam.-Pel.	Turb.-Pel.	Reefal
<i>Chirodella dinodoides</i>	4/181		
<i>Chirodella erecta</i>	6/321	2/8	
<i>Chirodella</i> sp. A	17/949		1/9
<i>Chirodella</i> sp. B	2/378	3/81	
<i>Cornudina tortilis</i>	15/41		1/6
<i>Cypridodella</i> sp. A	14/229	1/28	
<i>Epigondolella abneptis</i> s.f.	7/348		
<i>Epigondolella bidentata</i> s.f.	3/53	3/124	
<i>Epigondolella postera</i> s.f.	3/79	3/18	
<i>Epigondolella spatulata</i> s.f.	4/217		
<i>Epigondolella</i> sp. A s.f.	2/22		1/20
<i>Misikella longidentata</i>	1/1		4/25
<i>Neogondolella communista</i> s.f.			2/7
<i>Neogondolella hallstaaffensis</i>	1/7		
<i>Neogondolella steinbergensis</i>	2/7	4/71	
<i>Neogondolella</i> sp. cf. <i>N. nivicula</i>	2/48		
<i>Oncodella paucidentalis</i> s.f.	3/55	3/53	
New Genus A <i>hernsteini</i>	2/209	2/15	
New Genus A <i>koessenensis</i>	1/2	1/4	
New Genus A <i>posthernsteini</i>	2/344	3/234	
N. Gen. A sp. cf. N. Gen. A <i>rhaetica</i> s.f.	1/5		
New Genus B New Species A s.f.	2/144		
New Genus C New Species A	2/262	1/31	
Gen. et sp. indet. A s.f.	2/4		
Gen. et sp. indet. B s.f.	2/2		
Gen. et sp. indet. C	7/16		
Gen. et sp. indet. D s.f.	1/1		
Gen. et sp. indet. E s.f.	1/1		
Gen. et sp. indet. F s.f.	1/1		
Gen. et sp. indet. G s.f.		1/1	
Total Number Of Samples	34	6	6
Total Number Of Elements	3930	668	67

turbiditic sediments. Are they from a pelagic environment or are they derived from a slope or shelf environment?

The conodonts in the turbiditic sediments are as well preserved as any others recovered in the study, possibly suggesting that they were not incorporated into a turbidity current and subject to possible abrasion, and that they may have been derived from a pelagic environment.

In the Upper Bidentata Assemblage Zone (Table 2-3, page 54), where the laminated and turbiditic sediments are equally represented, the correlation of species is quite high between the two; ten of the sixteen species are found in both sediment types. In those instances where species are not found in both type of sediments, they are usually not well represented (usually much less than forty specimens per sample, and usually occurring in only one sample). This suggests that either the conodonts lived in essentially the same environment (pelagic, with the conodonts from the turbiditic sediments being derived predominantly from the pelagic environment), or that they occupied a nektic mode of life in both deep- and shallow-water environments. With the available data it is not possible to determine which of these models is the most plausible.

For the interval represented by the *Epigondolella abneptis* and *Epigondolella spatulata* assemblage zones (see Table 2-2, page 53), all species found in the reefal environment were also found in laminated pelagic sediments. This suggests that some species did range from the reefal to the pelagic environments, and is suggestive of a nektic mode of life for these taxa.

Only one species, *Neogondolella communisti* s.f., was not found to occur in the pelagic environment; significantly, no pelagic sediments yielding conodonts of this age were sampled. This is of interest as it most typically occurs in a pelagic environment.

On average, abundances are the lowest in the reefal environment and

highest in laminated pelagic sediments. The diversity is, however, highest in turbiditic pelagic sediments. Babcock's (1976) observation that conodont diversity was highest at the shelf edge might suggest that these turbiditic sediments may have been derived from a shallow-water source.

Due to the limited environmental distribution of conodonts in this study, it is not possible to observe any changes in environmental preference through time for species or genera, as has been observed by other workers (e.g. Carey, 1984; Meek, 1984).

2.4.5. Provincialism

Most studies indicate that conodonts showed strong provincialism three times during their known stratigraphic range; in the Ordovician, the Devonian, and the Pennsylvanian-Permian (Charpentier, 1984). For the Triassic, Charpentier (1984) found the Early and Late Triassic faunas to be cosmopolitan, and offered little support for provincialism in the Middle Triassic.

However, provincialism for the Triassic (especially the Middle Triassic) has been supported by Mosher (1968a), Hirsch (1972), Kozur and Mostler (1972b), and Budurov *et al.* (1983, 1985). Mosher (1968a) found that for the Late Triassic, provincialism (Alpine and North American provinces) was represented more by an absence of European ramiform species in North America than by differences in the platform species present. (Orchard (pers. comm., 1987) reports that there are no typical *E. spatulata* and no *N. hallstattensis* in North America, and that *E. multidentata* is missing from Tethyan strata (supported by this study).) Budurov *et al.* (1983, 1985) recognized only a cosmopolitan fauna during the Early and Late Triassic, the Tethyan-Pacific "province", corresponding to the Alpine and North American provinces of Mosher (1968a), including the present territories of Europe, Asia, western and southwestern North America, and the arctic regions (Budurov *et al.*, 1985). However, during the Middle Triassic, they recognize the Germanic and Balkanide provinces in addition to the Sephardic "Realm" (fauna) of the Tethyan-Pacific "province".

Conodont provincialism has been used by a number of authors (e.g. Marcoux, 1979; Gedik, 1981) in an attempt to determine the direction, and distance, of thrusting of allochthonous units in the Mediterranean region. Marcoux (1979) suggested that the rocks of Cyprus and Baer-Bassit were thrust from the north, supporting this with evidence of Tethyan litho- and biosfacies in these regions. Gedik (1981) recognized two different faunal provinces in the Triassic of Turkey: the Mediterranean (Sephardic) and the Asiatic (Tethyan-Pacific). Gedik uses this as evidence to support a northerly origin for the nappes of the Middle Tauride Belt, and an autochthonous nature for what are interpreted to be Arabian Platform shelf deposits.

A problem with using conodont provincialism to determine the origin of nappes is that the period for which the provincialism was in effect in this area is quite limited; the maximum extent of the Sephardic "Realm" (fauna) occurred during Ladinian and Early Carnian (Hirsch, 1981). Thus, if Upper Triassic faunas are collected only from the Tethyan region, as is the case in this study, no evidence can be supplied regarding the origin of the rock units in question; there being no distinct provincialism in effect for Upper Triassic Tethyan conodont faunas.

Marcoux's (1979) suggestion of a northerly origin for Cypriot strata, based on the "Tethyan nature" of the fauna, cannot be supported or refuted by the finds of this study (Marcoux does not state which group of organisms shows a "Tethyan nature"). Regardless of their origin, if the rocks are of Late Triassic age, as is suggested by the finds of this study, the conodont fauna would have a Tethyan character. There is no evidence found in this study to support a southerly or a northerly origin, based purely on faunal resemblances.

Hirsch (1976) shows that the Middle Triassic Antalya Complex faunas are Sephardic in nature. The Sephardic fauna is restricted geographically to the southern shore of the Middle Triassic Tethys, specifically in the region of what is now Israel. This would suggest a southerly origin for the nappes in question.

If the Mamonia Complex is a distal equivalent to the Antalya Complex, as is believed, then it is likely that it was not thrust from the north (single-basin model), but was formed on the southern margin of Tethys.

2.5. Summary

The samples collected in this study have been correlated with the conodont zonation proposed by Krystyn (1980). Four of his ten zones can be recognized in samples collected from the Mamonia Complex: the *Neogondolella communisti* morphotype A Zone (tentatively), and the *Epigondolella abneptis*, *Epigondolella spatulata*, and Upper Bidentata assemblage zones. Krystyn's (1980) zonation has its limitations (there is likely to have been a strong paleoecologic overprint, as well as condensation and mixing of faunas), but has been used in this study because it is the most applicable zonation available. The *Neogondolella communisti* morphotype A Zone is recognized only tentatively, as the environment recorded in this study for this interval (reefal) is different from that in which it was defined (pelagic). The Lower Postera, Upper Postera, and Lower Bidentata assemblage zones may be represented in an unsampled shale interval approximately 1.5m thick.

Based on characteristic conodont faunas, minimum ages can be assigned to three of the four Triassic sedimentary units in the Mamonia Complex. The Petratou Romiou Formation can be assigned to uppermost Tuvalian (Karnian) to middle Lacian (Norian) age. Both the Vlambouros and Marona formations can be assigned to middle Lacian (Norian) to lower Rhaetian/Sevatican (Norian) age.

Of the four depositional groups recognized in this study, three yielded conodonts. Based on the similarities between faunas of the reefal environment and the laminated and turbiditic sediments of the pelagic environment, it is likely that some of the recovered conodont species were nektic in habit. This agrees with the findings of earlier studies on Norian conodonts (Carey, 1984; Meek, 1984).

Chapter 3

Taxonomy

3.1. Introduction

Multielement apparatus reconstructions have been attempted wherever possible in this study. Methods used for reconstructing multielement apparatuses have been outlined by Klapper and Phillip (1971) and Sweet and Bergström (1972), and may be summarized as follows:

1. Similarity of stratigraphic range and geographic distribution of elements.
2. Similarity in morphology of the elements and the identification of symmetry transition series.
3. Comparison with previously determined multielement species,

When multielement status cannot be proven for a species the elements are considered representative of form taxa, and are assigned the suffix s.f. (*sensu formo*), following Barnes and Poplawski (1973).

The terminology used for describing the "position" of an element within its respective apparatus follows the P, M, and S notation recommended by Sweet and Schönlaub (1973) and applied in the newly revised Treatise on Invertebrate Paleontology, Part W, Supplement 2. Conodonta (Robison (Ed.), 1981). In some instances however, an apparatus, or certain elements, could not be categorized in such a manner as to make use of the standard P, M, and S notation. In these cases, no locational notation is used and a descriptive terminology is used throughout the discussion of the taxon in question.

The terminology used to describe individual conodont elements follows that recommended by Sweet (*In Robison (Ed.)*, 1981).

The conodonts in this study have a Conodont Alteration Index (CAI) value of 1 (following Epstein *et al.*, 1977). Specimens for *Epigondolella* spp. indet. s.f., and *Neogondolella* spp. indet. have not been illustrated due to their juvenile, or highly fragmentary and corroded, nature.

3.2. Systematic Paleontology

Phylum CONODONTA Pander, 1856

Class CONODONTATA Pander, 1856

Order CONODONTOPHORIDA Eichenberg, 1930

GENUS CHIRODELLA Hirschmann, 1959

Type species.- *Chirodella triquetra* Tatge, 1956

Original diagnosis (Hirschmann, 1959:71): "Conodonts of hand-shape and with terminal costate cusp which is more or less bent inward." Translated from the German original by S. Pohler.

Revised diagnosis.- Apparatus consisting of digyrate ramiform elements and a symmetry-transition series of bipennate ramiform elements. Difyrate elements highly antero-posteriorly compressed and bipennate elements highly laterally compressed. Denticles long, sharp, discrete, and closely spaced. Basal cavity inverted. Symmetry-transition series possesses two end members; one bears a well-defined, downward deflected anterior process, and the other a poorly developed, straight anterior process.

Discussion.- The basis for the revised diagnosis of this genus is the multielement nature proposed above. The digyrate elements have previously been referred to *Chirodella* Hirschmann, and the bipennate elements mostly to *Neohindeodella* Kozur.

The digyrate elements are the most diagnostic; bipennate elements are generally very similar among species. The relative proportions of the different members of the symmetry-transition series may be used as criteria for species differentiation.

Within this study, an evolutionary lineage may be traced from *C. n. sp. A*, to *C. dinodooides*, to *C. erecta*, to *C. n. sp. B*. This lineage can best be observed in the evolution of the digyrate element. In three of the four species (*C. n. sp. A*, *C. dinodooides*, and *C. n. sp. B*), the orientation of the cusp, and the morphology and orientation of the long lateral process changes from an element with a straight process and straight cusp (i.e. not inwardly deflected), to an element with an arched process and an inwardly deflected cusp. *C. erecta* does not follow this pattern, as the digyrate element is much more robust, with somewhat fused denticles.

CHIRODELLA DINODOOIDES (Tatge, 1956)

Plate 1, Figures 1-5.

Synonymy.- Digyrate element.-

Metalonchodina ? dinodooides n. sp. TATGE, 1956, Pl. 6, fig. 4.

Chirodella dinodooides (TATGE). MOSHER, 1968a, p. 918, Pl. 113, fig. 1; KOIKE, 1973, p. 97, Pl. 16, fig. 30; MISIK et al., 1978, Pl. 6, fig. 7.

Chirodella triquetra gracilis n. ssp. MOSTLER, 1968, p. 180-181, Pl. 1, fig. 2.

? *Chirodella dinodooides* (TATGE). GEDIK, 1977, Pl. 14, fig. 13.

Bipennate element.-

Neohindeodella triassica aequidentata KOZUR AND MOSTLER. KOIKE, 1973, p. 107, Pl. 16, fig. 16.

Neohindeodella triassica (MULLER). MISIK, et al., 1977, Pl. 6, fig. 6.

? *Neohindeodella triassica* (MULLER). GEDIK, 1977, Pl. 4, figs. 10, 14, 15.

Description.- Digyrate ramiform element. Unit with a long downwardly deflected lateral process, and with another lateral process bearing only one denticle. Process straight, occasionally with slight arch (toward center of unit). Process height equal to denticle length. Denticles sharp, discrete, and closely spaced. Cusp and proximal denticles curved posteriorly, and inwardly. Basal cavity not apparent.

Symmetry-Transition Series.- Series composed of bipennate ramiform elements. End members bear anterior processes which are either downwardly deflected at about 80 degrees, or have no downward deflection. One form, in which anterior process is only slightly deflected (Pl. 1, fig. 3), is most commonly found. A thickening of base below cusp terminates in a point in this form. Denticles sharp, discrete, closely spaced, and increase in size distally from cusp on both processes. Unit generally planar but cusp or processes may be laterally flexed. Basal cavity not apparent.

Remarks.- The lateral process of the digyrate element of this species is similar to that of *Chirodella* n. sp. A, but the cusp is curved away from the lateral process, as well as being curved posteriorly.

Material.- 40 digyrate ramiform elements and 146 bipennate ramiform elements.

Occurrence.- Samples RDR-2-2m, RKK-1-17m, RKK-1-21m, RKK-1-23m, and RPH-4-1.

CHIRODELLA ERECTA Mosher, 1968

Plate 1, Figures 6-10.

Synonymy. - Digyrate element. -

Chirodella erecta n. sp. MOSHER, 1968a, p. 918, Pl. 113, figs. 2, 5.

Chirodella gracilis MOSTLER. MOCK, 1971, Pl. 3, figs. 12, 17; KOZUR AND MOSTLER, 1972b, p. 2-3, Pl. 13, figs. 16-26.

? *Chirodella polonica* n. sp. KOZUR AND MOSTLER, 1970, p. 429-430, Pl. 1, figs. 5-7.

Description. - Digyrate ramiform element. - Unit with one long, and one short, lateral process. Long process downwardly deflected at about 65 degrees to cusp. Base of long process very thick and extends under cusp to denticle(s) on opposite side. Denticles very closely spaced, at times partially fused. Denticles on long process parallel cusp. Denticles on short lateral process oriented about 20 degrees obliquely to cusp. Cusp and proximal denticles directed inwardly. Basal cavity not apparent.

Symmetry-Transition Series. - Series composed of bipennate ramiform elements. Anterior process may be downwardly deflected up to about 30 degrees; most commonly to about 10 degrees. Base of anterior process thickened, especially under cusp where it may have a rounded or angular outline. Denticles long, sharp, and closely spaced. Denticulation may be hindeodelloid (denticles of process vary in length). Most distal one or two denticles on anterior process generally largest on element, even larger than cusp. Denticles on anterior process directed anteriorly (but curvature is still to posterior), those on posterior, posteriorly. Basal cavity not apparent.

Remarks. - The elements of this species are more robust than those of the other three species of *Chirodella*.

Material.- 52 digrinate ramiform elements, and 277 bipennate ramiform elements.

Occurrence.- Samples REV-3-1, REV-4-1.5m, REV-4-8m, REV-4-18m, RPA-1-0m, RPA-1-1.5m, RPA-1-3.5m, and RPA-2-1.

CHIRODELLA SP. A

Plate 1, Figures 11-15.

Synonymy.- Digrinate element.

Chirodella dinodooides (TATGE). KOZUR AND MOSTLER, 1972b, p. 2, Pl. 13, fig. 15 only (*non* Pl. 1, figs. 10-13, Pl. 6, figs. 11, 12, 14-16, Pl. 8, figs. 20, 21, Pl. 15, fig. 26); KOIKE, 1981, Pl. 1, fig. 23.

Bipennate element.

Neohindeodella aequidentata KOZUR AND MOSTLER, KOIKE, 1981, Pl. 1, fig. 15.

Neohindeodella dropla SPASSOV AND GANEV, KOIKE, 1981, Pl. 7, fig. 16.

Description.- Digrinate element.- Unit with one long, downward deflected lateral process, and one denticle on opposite side of cusp. Process straight, with sharp, discrete, closely spaced denticles. Process height approximately equals one and one-half to two times denticle length. Basal cavity not apparent.

Symmetry-Transition Series.- Transition series with two forms of bipennate ramiform elements. Units differentiated on basis of orientation of anterior process and outline of base of unit. Anterior process length relatively constant throughout series. At one end of series, anterior process deflected downward at about 80 degrees. At other end, anterior process straight with thickened base. Most common forms occur with anterior process deflected at about 30 degrees. The base below the cusp may be rounded or angular. Denticles sharp, discrete, and closely spaced, increasing in size and decreasing in inclination to process.

distally from cusp. Denticles on anterior process curved posteriorly; those on posterior process straight. Basal cavity not apparent.

Remarks.- Digyrate element of this species is characteristic in possessing a straight, downward deflected lateral process, as well as a cusp oriented parallel to the process (yet still curved posteriorly).

Material.- 92 digyrate ramiform elements and 866 bipennate ramiform elements.

Occurrence.- Samples RAY-1-1, RAY-2-1, RAY-3-1A, and RAY-3-1B, RKK-1-0m, RKK-1-2m, RKK-1-3.5m, RKK-1-4.5m, RKK-1-6m, RKK-1-8m, RKK-1-10m, RKK-1-12m, RKK-1-14m, RKK-1-17m, RKK-1-19m, RKK-1-21m, RPH-4-1, and RPR-1-1.

CHIRODELLA SP. B

Plate 1, Figures 16-19.

Synonymy.- Digyrate element.

Chirodella dinodooides TATGE. MOCK, 1971, Pl. 3, figs. 20a,b.

Bipennate element.

Neohindcodella triassica praecursor KOZUR AND MOSTLER. MOCK, 1971, Pl. 3, fig. 14.

Description.- Digyrate ramiform element.- Unit bears one or two denticles on short process and a long, downwardly deflected, arched lateral process on opposite side. Cusp and denticles curved inwardly. Long process occasionally posteriorly flexed, bearing long, discrete, closely spaced, inwardly directed denticles. Basal cavity, when apparent, narrow and slit-like.

Symmetry-Transition Series.- Series composed of bipennate ramiform elements. One end member bears straight anterior process and the other an anterior process which is deflected downwards at about 45 degrees. Two forms predominate possessing anterior processes which are deflected downwards at 20 to 30 degrees. These forms have thickened base under process. One form has rounded basal margin below cusp, while the other bears angular basal margin. Denticles long, discrete, closely spaced and increase in size distally from cusp on both processes. On posterior process the denticles initially increase in size distally, then decrease in size; becoming subparallel to process. Processes of these elements possess lower region which is more hyaline than rest of unit, extends about one-third height of process, and outlines a very narrow, inverted basal cavity.

Remarks.- Digyrate element of this species is differentiated from other species of *Chirodella* by bearing both an inwardly curved cusp and a curved lateral process. The bipennate elements are also less robust than those of other species. The nature of the denticulation on the posterior process of the bipennate element is similar to that of the S elements of *Misikella longidentata* Kozur and Mock.

Material.- 74 digyrate and 385 bipennate ramiform elements.

Occurrence.- Samples REV-3-1, REV-4-1.5m, REV-4-8m, REV-4-18m, and REV-4-30m.

GENUS CORNUDINA Hirschmann, 1959

Type species.- *Cornudina breviramulis* (Tatge, 1956).

Original diagnosis (Hirschmann, 1959:44): "Conodonts with a half-round, asymmetrically bowed lower margin, more or less keeled, strongly laterally deflected, and a large cusp on the upper margin." Translated from the German original by S. Pohler.

Revised diagnosis.- Apparatus quinquimembrate (possibly seximembrate) composed of two forms of angulate pectiniform elements, and dolabrate, digyrate, and bipinnate ramiform elements. Elements typically possess basal cavities which are wide and shallow under processes, and are deeper and terminate in a pit under the cusp.

Discussion.- Sweet (In Robison (Ed.), 1981), primarily on the basis of their possible co-occurrence, considers *Cornudina* to be a possible junior synonym of *Chirodella*. In this study, species of *Cornudina* were found to co-occur with elements assignable to *Chirodella*. However in this study, each of these species is interpreted to have a distinct apparatus, and synonymy of *Cornudina* and *Chirodella* is not suggested.

Sweet (*ibidem*) also suggested the likelihood that *Cornudina* is related to *Xuniognathus* Sweet and *Cypridodella* Mosher. The apparatuses of *Cornudina* and *Cypridodella* suggested in this study are quite similar, differing primarily in the morphology of the Pb element, and in the presence of only one Sb-type elements in *Cornudina*.

CORNUDINA TORTILIS Kozur and Mostler, 1970

Plate 2, Figures 1-5.

Synonymy.- Pb element.

Cornudina tortilis n. sp. KOZUR AND MOSTLER, 1970, p. 432-433, Pl. 1, figs. 10,16,20,24; KOZUR AND MOSTLER, 1972b, p. 5-6, Pl. 1; figs. 9,14, Pl. 3, figs. 15,19,20, Pl. 4; fig. 3, Pl. 14, fig. 20; TRAMMER, 1972, Pl. 1, fig. 6 only, (non fig. 7); ZAWIDZKA, 1975, Pl. 35, fig. 5; KOIKE, 1981, Pl. 1, fig. 34; KOIKE, 1982a, p. 19, Pl. 9, fig. 3.

non Cornudina tortilis KOZUR AND MOSTLER. MIRAUTA AND GHEORGHIAN, 1978, Pl. 1, figs. 7,8,21.

Description.- Pa element.- Angulate pectiniform element with long anterior and short posterior processes. Anterior process deflected slightly laterally, bearing two to four discrete, pointed denticles. Posterior process short, with one denticle. Basal cavity shallow and wide under processes, deep under cusp.

Pb element.- Angulate pectiniform element with short processes and long cusp. Processes and cusp laterally compressed. Cusp directed posteriorly at about 45 degrees. Anterior process short with one or two denticles. Posterior process longer, with one to three denticles. Posterior process deflected laterally, and twisted about its length.

M element.- Dolabrate ramiform element with carina on concave side of cusp. Posterior process bears five anteriorly directed denticles. Cusp directed anteriorly and upward, and flexed outward. Basal cavity shallow and wide, deeper and terminating in a pit under cusp.

Sb element.- Digrate ramiform element. Cusp long, sharp, and bent

posteriorly. Outer lateral process long, bearing three denticles, and arched downward. Outer process shorter, bearing two denticles, and directed laterally and slightly to anterior. Denticles sharp and discrete. Basal cavity shallow under processes, deeper and wider under cusp.

Sc element.- Bipennate ramiform element. Anterior process long, directed downward at angle of about 60 degrees to lower margin of posterior process, bearing four sharp, discrete denticles. Posterior process bears three short denticles. Cusp erect and laterally compressed. Basal cavity shallow under processes, deeper under cusp.

Remarks.- The Pb elements of the species of *Cornudina* are all relatively similar in appearance. They are generally differentiated by the length of, and by the number of denticles on, each process. The Pb element of *C. tortilis* is typified by having a very short anterior process and a relatively short posterior process.

The recovered Pb elements of specimens of *C. tortilis* generally possess only one denticle on the anterior process, and two denticles on the posterior process. This may represent a trend within the lineage of *C. tortilis* similar to that found by Hirschmann (1959) for *C. breviramulis* (Tatge), in which specimens showed a tendency to possess fewer denticles with decreasing age.

Material.- 1 Pa (angulate), 32 Pb (angulate), 1 M (dolabrate), 3 Sb (digyrate), and 10 Sc (bipennate) elements.

Occurrence.- Samples RAY-1-1, RAY-3-1A, RAY-3-1B, RKK-1-3.5m, RKK-1-4.5m, RKK-1-6m, RKK-1-8m, RKK-1-10m, RKK-1-17m, RKK-1-19m, RKK-1-23m, RKK-4-9m, RKK-4-12m, RKK-4-15m, RPH-4-1, and RPR-1-1.

GENUS CYPRIDODELLA Mosher, 1968

Type species: *Cypridodella conslera* Mosher, 1968

Original diagnosis (Mosher, 1968a:920): "Unit possessing one large, strongly downward projecting bar surmounted by large main cusp which projects parallel or nearly parallel to bar. A secondary anterior process may or may not be present. Denticles discrete and inclined strongly to bar proximally. The inclination of the denticles decreases distally so that at the end they are near perpendicular to the bar. A small pit is commonly present beneath the main denticle; however, it may be absent, or, in the example of *C. venusta*, be enlarged to a cavity. Basal edge may be sharp or bear shallow groove. Curvature of main denticles is such as to make the long bar posterior."

Revised diagnosis.- Apparatus septimembrate; composed of angulate (Pa), digyrate (Pb,M,Sb₁,Sb₂), aiate (Sa), and bipennate (Sc) elements. Basal cavity may be deep or shallow under cusp; characteristically shallow under processes. Denticles generally long and discrete (but may be very closely spaced and thus appear partially fused).

Discussion.- This genus was originally erected by Mosher (1968a) to include species which are herein considered to represent various elements of the multielement genus described as *Cypridodella*. Sweet (In Robison (Ed.), 1981) described this genus using multielement taxonomy, but considered the apparatus to be seximembrate. *Cypridodella* is herein considered to be septimembrate, with two element types occupying the Sb position (Sb₁ and Sb₂): as opposed to the single element type in the Sb position used in Sweet's (*ibidem*) reconstruction.

Synonymy lists are very difficult to produce for species of this genus. Specimens have been illustrated which are very similar, if not identical, to those elements described below. However, in order to prove synonymy, co-occurrence of three or four of the elements is preferred (specifically the diagnostic Pa, Pb,

and M elements). This is very difficult to prove with the illustrated material. The form species *Enantiognathus ziegleri* Diebel s.f. is likely to be synonymous with the Pb element of *Cypridodella*.

CYPRIDODELLA SP. A

Plate 2, Figures 14-20.

Description.- Pa element.- Angulate pectiniform element. Anterior process downwardly deflected at angle between 25 and 45 degrees, possessing three to eight closely spaced denticles. Posterior process short with one to two denticles. Cusp straight and directed slightly posteriorly. Unit flexed slightly laterally, with both dextral and sinistral forms occurring. Denticles short, sharp, and directed upward. Basal cavity shallow and slit-like under processes.

Pb element.- Digyrate ramiform element in which one lateral process is much larger and more robust than the other. Large, robust process oriented flat on the slide, small process projects vertically and arched downward. Angle between lateral processes about 90 degrees. Denticles long, discrete, and much smaller on less robust process. Both processes may be arched and/or deflected.

M element.- Dolabrate ramiform element with posterior process oriented slightly oblique to, and almost parallel with, cusp. Denticles long, sharp, and discrete; may be as long as cusp. Basal cavity shallow and slit-like under processes.

Sa element.- Alate ramiform element with long, sharp, discrete denticles. Cusp much shorter than second or third denticle (which is very large) on posterior process. Plane of lateral processes perpendicular to posterior process. Lateral processes deflected downwards at angle of about 45 degrees. Denticles on lateral processes increase in size distally.

Sb₁ element.- Digyrate ramiform element with lateral processes of subequal length. Processes arched downwards at approximately 45 degrees. Denticles long, sharp, and discrete. Processes possess four to five denticles. Elements fragmentary.

Sb₂ element.- Digyrate ramiform element with lateral processes unequal in length. Short process bears two to three denticles; long process, five to eight. Both processes arched downwards. Long process arched strongly, and may parallel cusp. Basal cavity shallow and wide.

Sc element.- Bipennate ramiform element with long, sharp, discrete denticles. Anterior process arched downwards and deflected laterally. Both dextral and sinistral forms present. Posterior process always broken, with one to three denticles present. Anterior process bears four to ten denticles. Base of process robust. Basal cavity shallow.

Remarks.- The species concept used herein for *Cypridodella* sp. A is broad and it is possible that more than one species is present in this study. Criteria which could be used to differentiate between species include overall size and robustness, and subtle morphological differences between the Pa and M elements. However, because of the relatively low abundances, all elements assignable to *Cypridodella* are herein included in *Cypridodella* sp. A.

Material.- 22 Pa (carminate) elements, 83 Pb (digyrate) elements, 22 M (digyrate) elements, 47 Sa (alate) elements, 17 Sb₁ (digyrate) elements, 9 Sb₂ (digyrate) elements, and 52 Sc (bipennate) elements.

Occurrence.- Samples RAE-3-1, RAY-1-1, RAY-2-1, RAY-3-1A, RKK-1-0m, RKK-1-2m, RKK-1-4.5m, RKK-1-6m, RKK-1-8m, RKK-1-10m, RKK-1-17m, RKK-1-21m, RKK-1-23m, RPA-1-3.5m, and RPH-4-1.

GENUS EPIGONDOLELLA Mosher, 1968 s.f.

Type species.- *Polygnathus abneptis* Huckriede, 1958 s.f.

Original diagnosis (Mosher, 1968a:936): "The genus is characterized by the presence of node-like projections or denticles along margins of the platform and by its high and free anterior carina. Carina decreases abruptly in height posteriorly near anterior margin of platform. Keel commonly broad, bearing narrow groove down center ending in pit, which in some examples is terminal on keel; in all adult specimens it lies considerably to anterior of end of unit. Earliest ontogenetic stages show no platform development and bear a pit located terminally. Growth took place at both ends. During growth platform developed from pair of denticles, which project laterally from posterior end, and grew posteriorly."

Revised diagnosis.- No revised diagnosis given.

Discussion.- Study of the literature discussing the genus *Epigondolella* immediately illustrates the problematic nature of this genus. Confusion lies in the understanding of the systematics of, and the growth and intraspecific variability of, the genus.

The early growth stages of *Epigondolella* species resemble one another quite dramatically. Initially, elements of all species pass through a platformless stage, followed by a bidentate stage. Once the platform begins to develop, the characteristic features of each species begin to emerge. However, the unit may still resemble different growth stages of other species. This has been well illustrated in the outlines of juveniles shown by Orchard (1983).

Orchard (1983) discussed eight populations of *Epigondolella* from western Canada. For each population, he illustrated a central morphotype growth series, and a number of less common morphotypes. The range of morphologic variation exhibited by these populations is considerable, and Orchard concludes that past

interpretation of many species of *Epigondolella*, and their stratigraphic ranges, is likely to have been incorrect. The range of morphologies present within given *Epigondolella* populations make it difficult to compare specimens with those in the literature, as few authors illustrate the full range of morphologies represented in their samples. A figure illustrating the range of morphologic variation for each described species of *Epigondolella* has been provided with the discussions for each taxon (Figs. 3-1 to 3-5). It should be noted that in order to show as complete a range of variation as possible these figures illustrate specimens from more than one sample.

Within this study, five populations of *Epigondolella* are recognized. Of these, it is clear from its synonymy list that *Epigondolella abneptis* s.f. has been dealt with the most inconsistently in the literature. This is likely because of the relatively loose species concept that has been used by some authors in the past. *Epigondolella abneptis* s.f. is also the most generalized species of *Epigondolella* (Orchard, 1983), and this is likely to have had an influence on the misinterpretation of the species.

The systematics of species within the genus *Epigondolella* has been very problematical. This has been outlined by Sweet (In Ziegler, 1977) and Onder (1984b). Little progress toward finalizing the problem has been made, and most of the confusion still revolves around the synonymy of the genus. Some authors (e.g. Kovács and Kozur, 1978, 1980) continue to use *Metapolygnathus* as the senior synonym of *Epigondolella*. Following Sweet (In Ziegler, 1977) *Metapolygnathus* is herein considered to be a junior synonym of *Neogondolella* Bender and Stoppel. Other genera which are herein considered to be junior synonyms of *Epigondolella* are *Tardogondolella* Bender 1970, and *Ancyrogondolella* Budurov 1972.

Budurov (1977) attempted a revision of Late Triassic platform conodonts. He differentiated *Epigondolella* and *Metapolygnathus*, among others, on the basis of basal structure. According to Budurov (1977), *Epigondolella* possesses a loop-

like posterior termination of the keel, while *Metapolygnathus* possesses a bifurcated keel. In this study, some elements of all species of *Epigondolella* were found to possess a wide, well-developed platform, and a corresponding bifurcated keel. This suggests that keel structure is related to the development of the platform, rather than being of generic (or specific) significance.

Epigondolella is considered by Sweet (In Robison (Ed.), 1981) as being unimembrate. According to Krystyn (1980), *Epigondolella* is likely to have evolved from *Neogondolella*. *Neogondolella* is herein considered to be seximembrate (possibly septimembrate), following the suggestions of Kozur (1976) and Von Bitter (1976). The author believes that *Epigondolella* is quite possibly a multielement genus, with a similar apparatus reconstruction as that of *Neogondolella* (possibly being congeneric with *Cypridodella*). However, species of *Epigondolella* are herein identified as *sensu formo* (s.f.) because at this time it is not possible to prove a multielement nature for the genus.

Due to the similarities of the early growth stages of different *Epigondolella* species, when a sample contained only juvenile forms, those forms are identified as *Epigondolella* spp. indet..

EPIGONDOLELLA ABNEPTIS (HUCKRIEDE, 1958) s.f.

Plate 3, Figures 1,2.

Synonymy.-

Polygnathus abneptis n. sp. Huckriede, 1958, p. 156-157, Pl. 12, figs. 30-32, 33-36, Pl. 14, figs. 1,2,5,12,13,16-21,26,27,47[?],48,49[?],53,55[?],56,57[?] only (non Pl. 11, fig. 33, Pl. 14, figs. 3,14,22,51,52,54,58),

Epigondolella abneptis (HUCKRIEDE). KOZUR AND MOSTLER, 1972a, Pl. 2; figs. 9-15; KRYSTYN, 1973, Pl. 4, fig. 1 only (non figs. 2,3); ISOZAKI AND MATSUDA, 1980, Pl. 1, fig. 4; MUSHASHINO *et al.*, 1980, Pl. 3, fig. 8;

WARDLAW AND JONES, 1980, p. 900, Pl. 64, figs. 3-5,7; KOIKE, 1981, Pl. 2, figs. 26-28; ISOZAKI AND MATSUDA, 1982, p. 111-115, Pl. 1, figs. 3-6, Pl. 2, figs. 1,2 only (*non* Pl. 2, figs. 3-8); KOIKE, 1982b, p. 17, Pl. 3, figs. 1-21; SAVAGE, 1983, figs. 2A-P; ONDER, 1984, p. 89-91, Pl. 42, figs. 1-8; ORCHARD, 1987, Pl. 5.4, fig. 20 only (*non* figs. 21,22).

Epigondolella abneptis subsp. A. ORCHARD, 1983, p. 179,181, figs. 3D,E,G, 4, 7B,M,N,Y, 9A, 15D,E,F.

Epigondolella abneptis abneptis (Huckriede).- KRYSTYN, 1980, Pl. 13, figs. 8-10 only (*non* fig. 11); WANG AND DONG, 1985, p. 126-127, Pl. 1, figs. 14,15,22.

Metapolygnathus abneptis (Huckriede).- MELLO AND MOCK, 1977, Pl. 8, fig. 2; MISIK *et al.*, 1977, Pl. 7, figs. 5,6,10. YAMATO OMINE RESEARCH GROUP, 1979, text-fig. 5; BIELY AND PAPSOVA, 1983, Pl. 41, figs. 4,5;

Metapolygnathus abneptis abneptis (HUCKRIEDE). KOZUR, 1972a, Pl. 6, figs. 10-21; KOVACS AND KOZUR, 1978, p. 562-565, Pl. 3., figs. 2,3, Pl. 4, figs. 1,3; GUPTA *et al.*, 1980, p. 592, Pl. 3, fig. 1, Pl. 4, figs. 6,7,9,10; KOVACS AND KOZUR, 1980, Pl. 14, figs. 1,2; GAAL, 1982, Pl. 6, figs. 7-10.

Tardogondolella abneptis abneptis (HUCKRIEDE). MIRAUTA AND GHEORGHIAN, 1975, p. 55-56, Pl. 6, fig. 2, Pl. 8, figs. 1,2,4,6 Pl. 9, figs. 1-3.

? *Epigondolella abneptis* (HUCKRIEDE). HAYASHI, 1971, Pl. 2, figs., 1-4; HAYASHI, 1972, Pl. 1, figs. 1-3; SAKAGAMI AND WATANABE, 1972, Pl. 2, figs. 1,2,5; DURDANOVIC, 1973, Pl. 6, figs. 25a,b; BUDUROV, 1976b, p. 103, Pl. 2, figs. 22,23 only (*non* figs. 20,21); WANG AND WANG, 1976, Pl. 4, figs. 17-19. OKAMI *et al.*, 1978, Pl. 1, fig. 4; KOLAR, 1979, p. 314, Pl. 2, fig.4; KUWANO, 1979, p. 16-17, Pl. 1, figs. 1-7, Pl. 4, figs. 4,7, text-figs. 4a-e; HASHIMOTO *et al.*, 1980, text-figs. 1-4; RAFEK, 1980, p. 131, Pl. 13.1, fig. 1; SUYARI *et al.*, 1980, Pl. 1, figs 2,3; DHILLON *et al.*, 1983, Pl. 1, figs. 3,6,7; IRWIN *et al.*, 1983, Figs. 2L,M only (*non* Fig. 2G); QIU, 1984, Pl. 5, figs. 8,11.

? *Metapolygnathus abneptis* (HUCKRIEDE). MUSHASHINO *et al.*, 1979, text-fig. 3.1; BIELY AND PAPSOVA, 1983, Pl. 41, figs. 4c,5a,b.

? *Metapolygnathus abneptis echinatus* (HUCKRIEDE). MISIK *et al.*, 1977, Pl. 7, fig. 11.

? *Polygnathus abneptis* (HUCKRIEDE). BUDUROV, 1960, p. 117, Pl. 1, fig. 26.

? *Tardogondolella abneptis abneptis* (HUCKRIEDE). KOZUR AND MOSTLER, 1971a, Pl. 2, fig. 7 only (*non* fig. 9).

non Epigondolella abneptis (HUCKRIEDE, 1958). MOSHER, 1968a, p.936, Pl. 118, figs. 18-30; MOSHER, 1968b, Pl. 120, figs. 17-27; MOSHER, 1970, Pl. 110, figs. 14,15,18,20,21; SWEET *et al.*, 1971, Pl. 1, figs. 18,27; MOSHER, 1973b, Pl. 18, figs. 6,12-14,16,17; BUDUROV, 1977, p. 42-43, Pl. 1, figs. 1,2, Pl. 2, figs. 7,8; ISHIDA, 1981, Pl. 6, figs. 4-6; KOLAR-JURKOVSEK, 1982, p. 171-172, Pl. 4, figs. 3,4; KOLAR-JURKOVSEK *et al.*, 1983, p. 159-162, Pl. 1, figs. 1,2, Pl. 2, fig. 1; JURKOVSEK *et al.*, 1984, p. 320-321, Pl. 6, figs. 1-3; ORCHARD, 1987, Pl. 5.4, figs. 21,22 only (*non* fig. 20).

non Epigondolella abneptis sensu KRYSTYN (1973). CAFIERO AND CAPOA BONARDI, 1981, Pl. 58, figs. 8-12.

non Gladigondolella abneptis (HUCKRIEDE). NHODA AND SETOGUCHI, 1967, p. 232-233, Pl. 2, figs. 1-7; HAYASHI, 1968, p. 68, Pl. 2, figs. 6,7,8; NOGAMI, 1968, p. 122, Pl. 8, figs. 1-11.

non Metapolygnathus abneptis abneptis (HUCKRIEDE). GUPTA, 1983, Pl. 3, figs. 7,8, Pl. 4, fig. 3, Pl. 5, fig. 4.

non Tardogondolella abneptis (HUCKRIEDE). BENDER, 1970, p. 531, Pl. 4, figs. 29,30, Pl. 5, fig. 21; BUDUROV, 1972, p. 17, Pl. 1, figs. 1a,b.

Description.- Subsymmetric segminiplanate pectiniform element.

Carina subterminal. Free blade generally one-third to one-half unit length. Third or fourth anteriormost denticle highest. Posterior of carina, one or two subterminal nodes present on platform. Lateral ridges on free blade occur as anterior continuation of platform.

Lateral margins of platform subparallel, and bear one to four nodes or denticles. Posterior of platform largely unornamented.

Micoreticulae present over most of platform. Marginally, micoreticulae closed and well-defined, centrally, more open and less pronounced. Closed, well defined microreticulation occurs on nodes and denticles.

Keel slightly raised, terminating in loop just posterior of platform midpoint.

Remarks.- Orchard (1983) described in detail a number of populations of *E. abneptis*. The specimens herein described as *E. abneptis* s.f. compare closely with those illustrated as *E. abneptis* subsp. A s.f. by Orchard (1983). No further information can be added by this study to Orchard's coverage of *E. abneptis* s.f. populations. Figure 3-1 illustrates the range of morphologic variation exhibited by recovered specimens of *Epigondrella abneptis* s.f.

N.B.- After seeing the holotype of *E. abneptis* (of which only one-half survives) Orchard (1987, pers. comm.) doubts that *E. abneptis* can be maintained.

Material.- 348 segminate pectiniform elements.

Occurrence.- Samples RKK-1-10mm, RKK-1-12m, RKK-1-14m, RKK-1-17m, RKK-1-19m, RKK-1-21m, and RKK-4-12m.

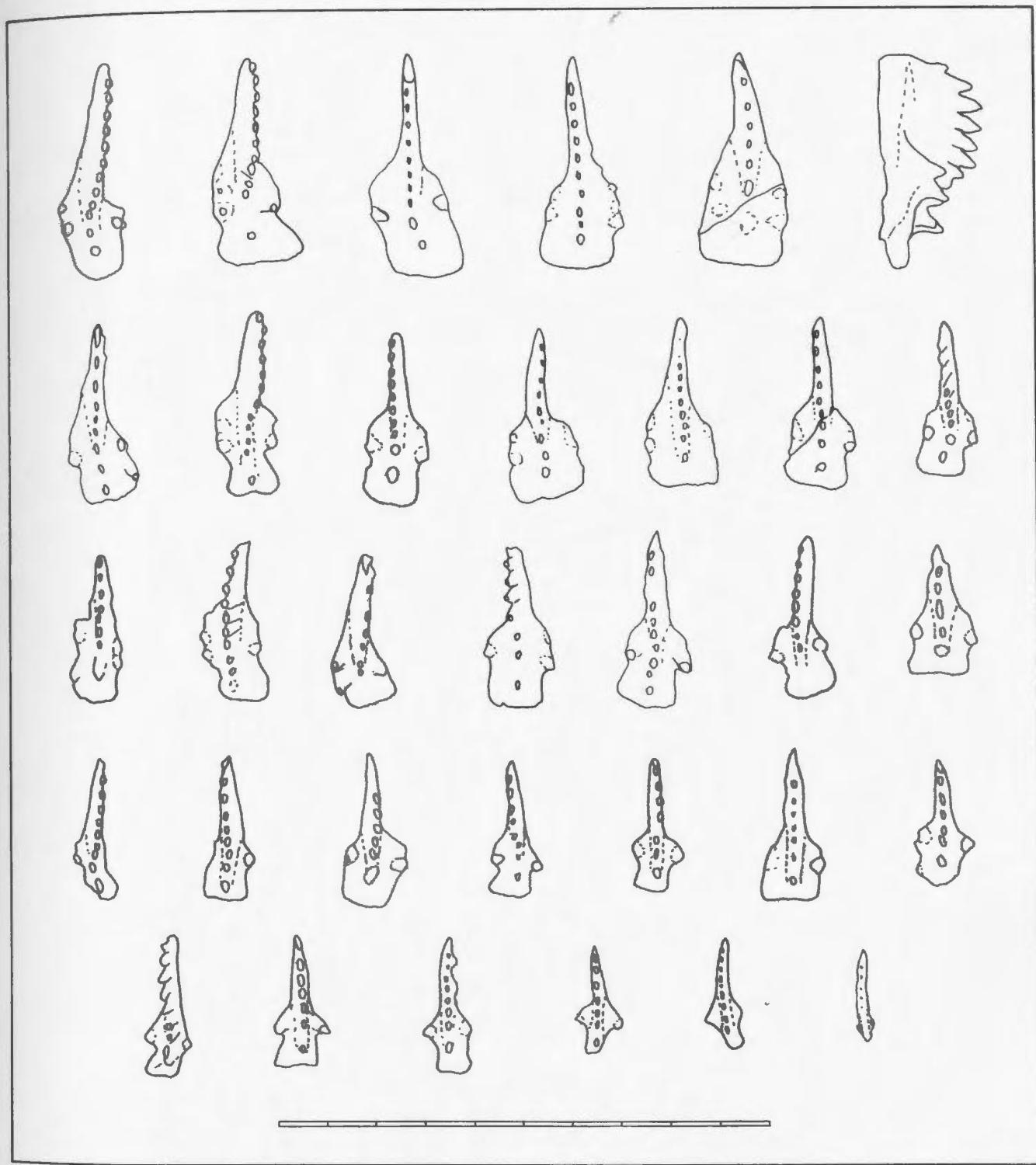


Figure 3-1: Range of morphologic variation exhibited by recovered specimens of *Epigondolella abneptis* (Huckriede) s.f. Scale bar represents 1mm.

EPIGONDOLELLA BIDENTATA, Mosher, 1968 s.t.

Plate 3, Figures 11,12.

Synonymy.-

Epigondolella bidentata n. sp. MOSHER, 1968a, p. 936, Pl. 118, figs. 31-36; MOSHER, 1968b, Pl. 120, figs. 28-33; MOSHER, 1970, Pl. 110, figs. 27,28; SWEET *et al.*, 1971, Pl. 1, fig. 30; KOZUR AND MOCK, 1972, Pl. 1, figs. 13-16; KOZUR AND MOSTLER, 1972a, Pl. 4, figs. 3-5; KRYSYNN, 1973, Pl. 5, fig. 7; MOSHER, 1973b, p. 160, Pl. 18, figs. 23,24,28; BUDUROV, 1977, p. 45, Pl. 1, fig. 7, Pl. 2, fig. 4; GUPTA, 1978, Pl. 1, figs. 1a,b; OKAMI *et al.*, 1978, Pl. 1, figs. 5-9; KOLAR, 1979, p. 314-315, Pl. 1, fig. 3, Pl. 2, fig. 2; ISOZAKI AND MATSUDA, 1980, Pl. 1, figs. 1,2; KRYSYNN, 1980, Pl. 14, figs. 1-3 only (*non* figs. 4-6); WARDLAW AND JONES, 1980, p. 900, Pl. 64, fig. 10; CAFIERO AND CAPOA BONARDI, 1981, Pl. 58, figs. 13-16; ISOZAKI AND MATSUDA, 1982, p. 117-119, Pl. 4, figs. 1-5.; IRWIN *et al.*, 1983, Fig. 2-F; ORCHARD, 1983, p. 188-189, figs. 14, 15V,W,X; BURYI, 1984, p. 42-43, Pl. 1, figs. 11,12; IGO *et al.*, 1984, Fig. 6, nos. 11,12; MEEK, 1984, Pl. 1, figs. 1-4; Orchard, 1985, Pl. 37,3, figs. 19,20; WANG AND DONG, 1985, p. 127-128, Pl. 1, figs. 1-3,26.

Metapolygnathus bidentatus (MOSHER). KOZUR, 1972a, Pl. 7, figs. 3-9,11; GAZDZICKI *et al.*, 1979, Pl. 5, figs. 10-12; KOVACS AND KOZUR, 1980, Pl. 15, fig. 1; BIELY AND PAPSOVA, 1983, Pl. 41, figs. 4a-b.

Metapolygnathus misiki n. sp. KOZUR AND MOCK, 1973, p. 11-12, Pl. 1, figs. 2a,b.

Metapolygnathus mosheri (KOZUR AND MOSTLER). GAZDZICKI *et al.*, 1979, Pl. 5, fig. 13; KOVACS AND KOZUR, 1980, Pl. 14, fig. 8.

Polygnathus abneptis n. sp. HUCKRIEDE, 1958, p. 156-157, pl.14, figs. 32,58 only (*non* pl. 14, fig. 33, pl. 12, figs. 30-36, pl. 14, figs. 1-3,5,12-14,16-22,26,27,47-57).

Tardogondolella bidentata (MOSHER). MOCK, 1971, Pl. 4, fig. 3.

cf. *Epigondolella cf. bidentata* MOSHER. ISHIDA, 1981, Pl. 7, fig. 4.

? *Epigondolella bidentata* Mosher. DHILLON et al., 1983, Pl. 1, figs. 4,5; OKAMI et al., 1978, Pl. 1, figs. 5-9.

? *Tardogondolella abneptis cf. bidentata* (MOSHER). MIRĂUTA AND GHEORGHIAN, 1975, p. 10-11, Pl. 9, fig. 4.

non *Epigondolella bidentata* MOSHER. KOIKE, 1981, Pl. 2, figs. 30,31.

Description.- Segminiplanate pectiniform element. Unit subsymmetric to asymmetric in upper view. Platform lacking, or very rudimentary, with one denticle on either side of carina.

Carina composed of long, partially fused, laterally compressed denticles. Denticles directed slightly posteriorly. Carina generally extends full length of unit. Denticles shorter, more robust, and becoming more inclined posteriorly. Carina generally straight, but may be strongly deflected laterally. Sides of free blade possess ridge-like extensions of platform; present on platformless specimens. Unit possesses one sharp, upward directed denticle on either side of carina. In well-developed platformless elements, denticles are located at midpoint of unit. Apart from two spike-like denticles, platform lacks ornamentation. When present, platform occupies posterior one-half to one-quarter of unit.

Microreticulae may be present. May occur as fine pits along platform margin, or as fine striae on lateral denticles.

Keel wide, with pit located at roughly midpoint of platform, between lateral denticles. On elements with no platform, keel continues under posterior portion of carina. On elements with platform, keel terminates posteriorly with small,

raised loop. Keel may bifurcate posteriorly in elements with well-developed platforms.

Remarks.- The criterion for recognition of this species is the presence of 2 laterally located denticles. Orchard (1983) points out that the platforms of *E. bidentata* are small, and generally slender. One specimen was recovered which possesses a well-developed platform. The keel of this element is well-developed and is bifurcated posteriorly in a manner similar to *E. abneptis* s.f. and *E. spatulata* s.f.

The diagnosis of the species has not changed since first described by Mosher (1968a). Recently, Orchard (1983) thoroughly discussed a population of *E. bidentata* s.f. recovered from western Canada. The finds of this study add little to his discussion.

Figure 3-3 illustrates the range of morphologic variation exhibited by this species.

Material.- 177 segminiplanate pectiniform elements.

Occurrence.- Samples RAE-3-1, REV-3-1, REV-4-1.5m, REV-4-30m, RPA-1-1.5m, and RPA-2-1.

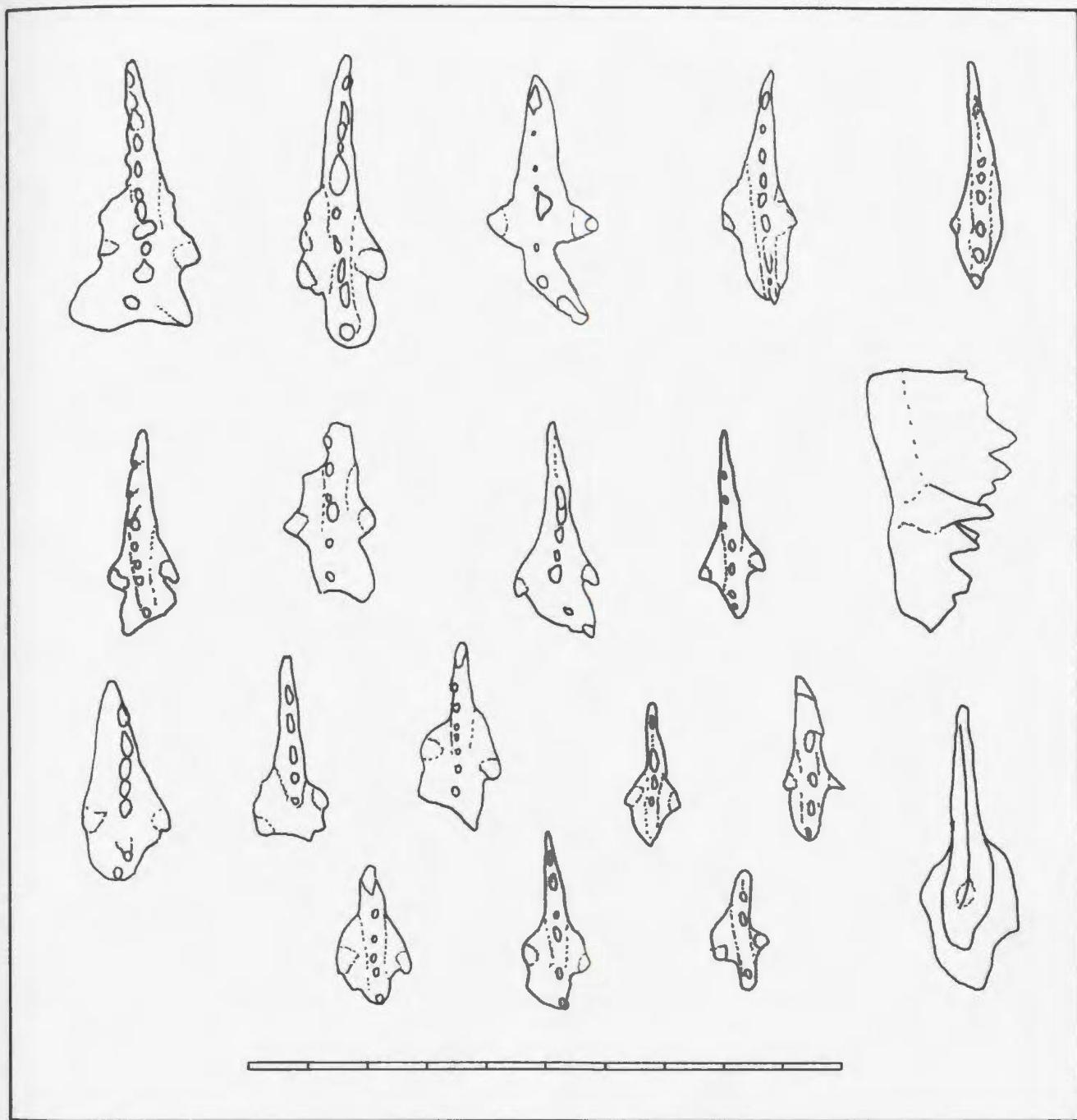


Figure 3-2: Range of morphologic variation exhibited by recovered specimens of *Epigondolella bidentata* s.f.
Scale bar represents 1mm.

EPIGONDOLELLA POSTERA (Kozur and Mostler, 1971) s.f.

Plate 3, Figures 9,10.

Synonymy:-

Tardogondolella abneptis postera n. subsp. KOZUR AND MOSTLER, 1971a, p. 14-15, Pl. 2, figs. 4-8.

Epigondolella abneptis (HUCKRIEDE). MOSHER, 1968a, p. 936, Pl. 118, figs. 20,21 only (*non* figs. 18,22-30); MOSHER, 1968b, Pl. 120, figs. 25,26 only (*non* figs. 17-24,27); SWEET *et al.*, 1971, Pl. 1, fig. 18 only (*non* fig. 27);

Epigondolella bidentata MOSHER. KOIKE, 1981, Pl. 2, figs. 30,31.

Epigondolella postera (KOZUR AND MOSTLER). KOZUR AND MOSTLER, 1972a, Pl. 4, fig. 2; KRYSYNA, 1973, p. 141, Pl. 5, figs. 5,6; BUDUROV, 1977, p. 43-44, Pl. 5, figs. 25,26; KOLAR, 1979, p. 316, Pl. 2, fig. 3; ISOZAKI AND MATSUDA, 1980, Pl. 1, figs. 6,7; KRYSYNA, 1980, Pl. 13, figs. 15-18; CAFIERO AND CAPOA BONARDI, 1981, Pl. 58, figs. 21,22; ISHIDA, 1981, Pl. 7, fig. 2; ISOZAKI AND MATSUDA, 1981, Pl. 1, figs. 6,7; ISOZAKI AND MATSUDA, 1982, p. 115-117, Pl. 3, figs. 1-9; ORCHARD, 1983, p. 186-188, figs. 11,12M,N,O,P,Q,R,S,T,15P,Q,R; BURYI, 1984, p. 41-42, Pl. 1, fig. 8-10; MEEK, 1984, Pl. 1, figs. 12-18,21,22; ONDER, 1984, p. 93-94, Pl. 25, figs. 7,8; WANG AND DONG, 1985, 128, Pl. 1, figs. 4-8,10,20,21.

Epigondolella aff. postera. ISHIDA, 1981, Pl. 7, fig. 1.

Epigondolella postera postera (KOZUR AND MOSTLER). KOZUR AND MOSTLER, 1972a, Pl. 4, fig. 1.

Epigondolella posterus hayashi n. sp. KOZUR AND MOSTLER, 1972c, p. 11-12, figs. 1a,b.

Gladigondolella abneptis (HUCKRIEDE). NOHDA AND SETOGUCHI, 1967, p. 232-233, Pl. 2, figs. 3,6 only (*non* figs. 1,2,4,5,7); NOGAMI, 1968, p. 122, pl. 8, fig. 7 only (*non*, figs. 1-6,8-11).

Metapolygnathus posterus (KOZUR AND MOSTLER). GAZDICKI *et al.*, 1979, Pl. 5, figs. 14a,b; GUPTA *et al.*, 1980, p. 593, Pl. 2, figs. 7,8, Pl. 5, figs. 1-9; KOVACS AND KOZUR, 1980, Pl. 14, fig. 7; BIELY AND PAPSOVA, 1983, Pl. 11, figs. 6a-c.

Metapolygnathus aff. posterus. GUPTA *et al.*, 1980, p. 593, Pl. 2, figs. 2-6.

Metapolygnathus posterus hayashi (KOZUR AND MOSTLER). KOZUR, 1972a, Pl. 6, fig. 22.

Metapolygnathus posterus posterus (KOZUR AND MOSTLER). KOZUR, 1972a, Pl. 6, figs. 23-25.

c.f. *Metapolygnathus zapfei* KOZUR. GAZDICKI *et al.*, 1979, Pl. 5, figs. 15a,b.

? *Epigondolella postera* (KOZUR AND MOSTLER). KOLAR-JURKOVSEK, 1982, p. 175-176, Pl. 4, figs. 1,2; DHILLON *et al.*, 1983, Pl. 1, figs. 1,2.

? *Epigondolella cf. E. postera* (KOZUR AND MOSTLER). ORCHARD, 1985, Pl. 37.2, fig. 18.

? *Epigondolella posterus hayashi* n. sp. KOZUR AND MOSTLER. KOZUR AND MOCK, 1972, p. 11-12, text-figs. 1a,b.

? *Gladigondolella abneptis* (HUCKRIEDE). HAYASHI, 1968, p. 68, Pl. 2, figs. 6,7; only (*non* fig. 8);

? *Metapolygnathus posterus* (KOZUR AND MOSTLER). MISIK *et al.*, 1977, Pl. 7, fig. 17, Pl. 8, fig. 17.

Description.- Subsymmetric segminiplanate pectiniform element.

Carina composed of ten to eleven partially fused, laterally compressed denticles. Free blade characteristically short. Fourth or fifth anteriomost denticle highest. Carina may be laterally flexed, rarely extends to posterior of unit in mature specimens. Two lateral ridges extend anteriorly along sides of carina from anterior of platform. Unit laterally compressed below ridges.

Platform moderately developed. Characteristically bears three nodes or denticles, two on one side, one on the other. Little ornamentation present apart from denticles. Platform terminates sharply at posterior, but may be rounded. Generally subsymmetric in upper view. Platform appears in growth stages with five or six anterior denticles. Lateral denticles appear first, then rest of platform.

Most specimens bear little microreticulation. Where well-developed, microreticulae are compact marginally, more faint and open on central portion of platform.

Keel narrow, with loop or bifurcation at posterior end. Lower surface smooth.

Remarks.- This taxon has recently been discussed by Isozaki and Matsuda (1982), and by Orchard (1983). This study adds little to their comments.

Figure 3-3 illustrates the range of morphologic variation exhibited by recovered specimens of *E. postera* s.s.

Material.- 97 segminiplanate pectiniform elements.

Occurrence.- Samples RAE-3-1, RAE-5-1, RAY-1-1, REV-4-8m, RKK-1-23m, and RPH-4-1.

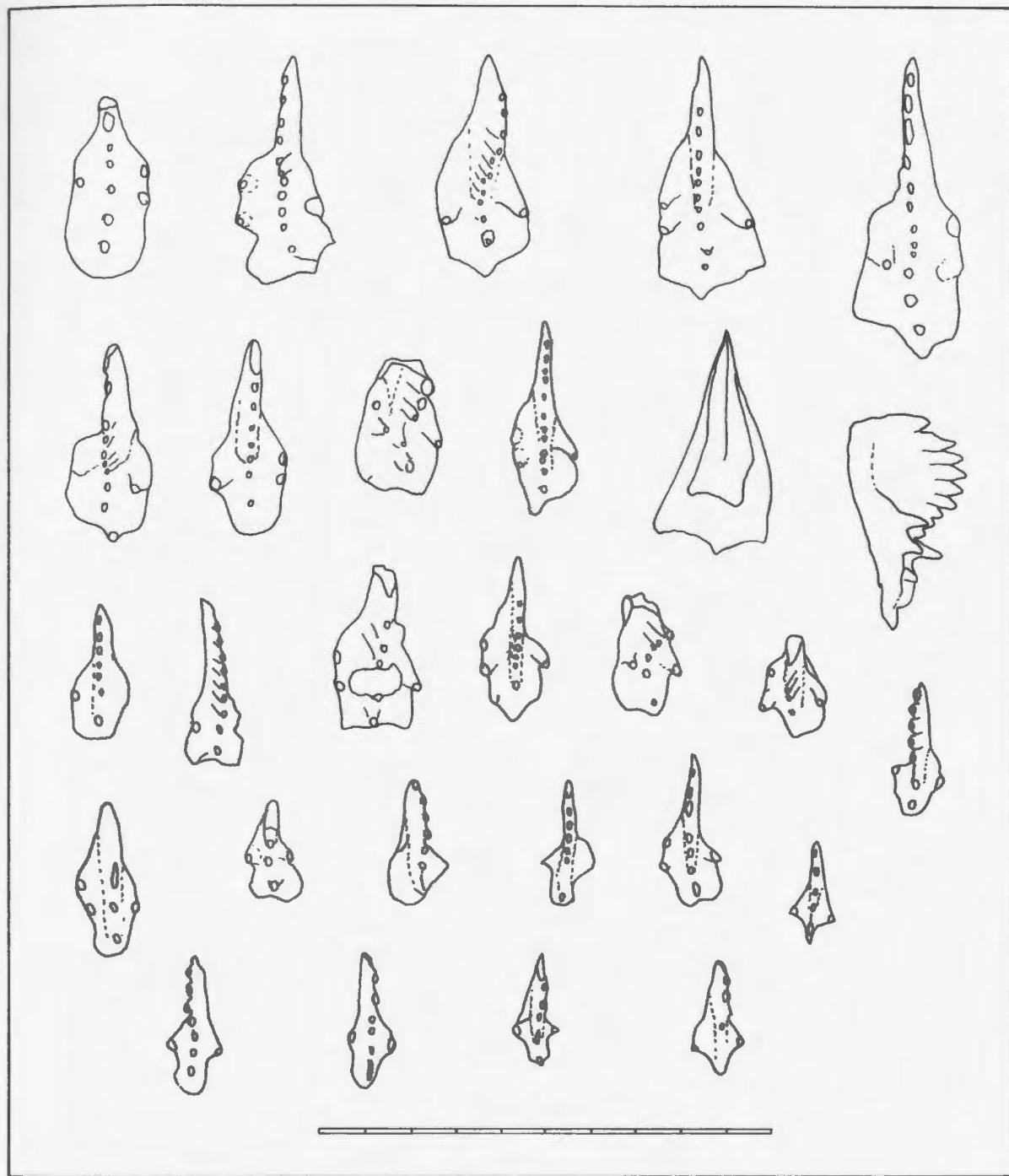


Figure 3-3: Range of morphologic variation exhibited by recovered specimens of *Epigondolella postera* s.f.
Scale bar represents 1mm.

EPIGONDOLELLA SPATULATA (Hayashi, 1968) s.f.

Plate 3, Figures 3,4.

Synonymy.

Gladigondolella abneptis var. *spatulata* var. nov. HAYASHI, 1968, p. 69, Pl. 2, figs. 5a-c.

Epigondolella abneptis (Huckriede). ISOZAKI AND MATSUDA, 1982, p. 111-115, Pl. 2, figs. 3,6-8 only (*non* Pl. 1, figs. 3-6, Pl. 2, figs. 1,2,4,5).

Epigondolella abneptis spatulata (HAYASHI). KRYSTYN, 1980, Pl. 13, figs. 12-14.

Epigondolella spatulata (HAYASHI). ISHIDA, 1981, Pl. 5, fig. 6 only (*non* Pl. 7, figs. 7,8); KOIKE, 1982b, p. 18-19, Pl. 3, figs. 22-35,41 only (*non* figs 36,40,42-46).

Epigondolella triangularis (BUDUROV). KOZUR AND MOSTLER, 1972a, Pl. 2, figs. 7,8;

Gladigondolella abneptis (HUCKRIEDE). NOHDA AND SETOGUCHI, 1967, p. 232-233, Pl. 2, fig. 5 only (*non* figs. 1-4,6,7);

Metapolygnathus abneptis spatulatus (HAYASHI, 1968). KOVACS AND KOZUR, 1978, p. 565-569, Pl. 3, figs. 4,5, Pl. 4, fig. 2. GAZDZICKI *et al.*, 1979, Pl. 5, fig. 16; GUPTA *et al.*, 1980, Pl. 2, fig. 1?, Pl. 3, figs. 2,7-9 only (*non* Pl. 3 figs. 3-6); KOVACS AND KOZUR, 1980, Pl. 14, figs. 3,4; GAAL, 1982, Pl. 6, fig. 11.

Metapolygnathus spatulatus (HAYASHI). MISIK *et al.*, 1977, Pl. 7, figs. 4,7,8,16.

Metapolygnathus spatulatus spatulatus (HAYASHI). KOZUR, 1972a, Pl. 4, figs. 4,6-8, Pl. 5, figs. 1-4;

Metapolygnathus spatulatus pseudodiebeli KOZUR. MELLO AND MOCK, 1977, Pl. 8, figs. 4,5.

Tardogondolella abneptis (HUCKRIEDE). MOCK, 1971, Pl. 4, figs. 2, 4, 6, 8, 11, Pl. 5, figs. 3, 4, 12.

? *Tardogondolella abneptis abneptis* (HUCKRIEDE). KOZUR AND MOSTLER, 1971a, Pl. 2, fig. 9 only (non fig. 7).

non *Epigondolella abneptis spatulatus* (HAYASHI). WANG AND DONG, 1985, Pl. 1, figs. 11-13, 19, 25.

non *Epigondolella spatulata* (HAYASHI). KOIKE, 1981, Pl. 2, figs. 32-36.

non *Metapolygnathus abneptis spatulatus* (HAYASHI). GUPTA *et al.*, 1980, p. 592, Pl. 2, fig. 1, Pl. 3, figs. 2-9; GUPTA, 1983, Pl. 6, fig. 1.

non *Metapolygnathus spatulatus* (HAYASHI). BUDUROV, 1977, p. 38-39, Pl. 3, figs. 7, 8, Pl. 4, figs. 5, 6 only (non Pl. 5, figs. 9-11; N.B. These are re-illustrated holotypes of Hayashi (1968), Kozur (1972), and Kozur and Mostler (1972a)); MELLO AND MOCK, 1977, Pl. 8, figs. 3, 6, 8, 9.

non *Tardogondolella abneptis spatulata* (HAYASHI). MIRAUTA AND GHEORGHIAN, 1978, Pl. 2, fig. 11.

Description.- Subsymmetric segminiplanate pectiniform element.

Carina subterminal. Free blade characteristically one-half length of unit. Third or fourth anteriormost denticle highest. Two nodes present on platform, posterior of which is subterminal cusp. Lateral ridges on free blade occur as anterior continuations of platform.

Platform spatulate. Anterior one-half to one-third of platform margin upturned, giving pinched appearance to unit, and broad spatulate posterior platform. One to four denticles or nodes on upturned portion. Posterior portion of platform largely unornamented.

Microreticulae present over whole platform; marginally, uniform and compact, centrally, more open and fine. Tips of nodes or denticles bear uniform compact microreticulae whereas sides bear open microreticulae or longitudinal striae.

Keel slightly raised, terminating in loop near platform midpoint. Posterior of loop, keel bifurcates into two postero-laterally directed, raised scars.

Remarks. - The morphologic variation observed for this species (see Fig. 3-4) compares to that illustrated by Orchard (1983) for other species of *Epigondolella*.

Material. - 217 segminiplanate pectiniform elements.

Occurrence. - Samples RAY-2-1, RAY-3-1A, RAY-3-1B, and RKK-1-10m.

EPIGONDOLELLA SP. A s.f.

Plate 3, Figures 5-8.

Synonymy.

Epigondolella spatulata (HAYASHI). ISHIDA, 1981, Pl. 5, fig. 6; Pl. 7, figs. 7,8; KOIKE, 1981, Pl. 2, figs. 32,35 only (non. figs. 33,34,36).

Metapolygnathus spatulatus (HAYASHI). Budurov, 1977, p. 38-39, Pl. 3, figs. 7,8; Pl. 4, figs. 5,6; Pl. 5, figs. 9-11 only (non. Pl. 5, figs. 12-14); MELLO AND MOCK, 1977, Pl. 8, figs. 3?,6?,8,9?.

Tardogondolella abneptis abneptis (HÜCKRIEDE). KOZUR AND MOSTLER, 1971a, Pl. 2, figs. 7,9.

Description. - Segminiplanate pectiniform element. Unit typically subsymmetrical; slightly bowed in upper view, slightly arched in lateral view.

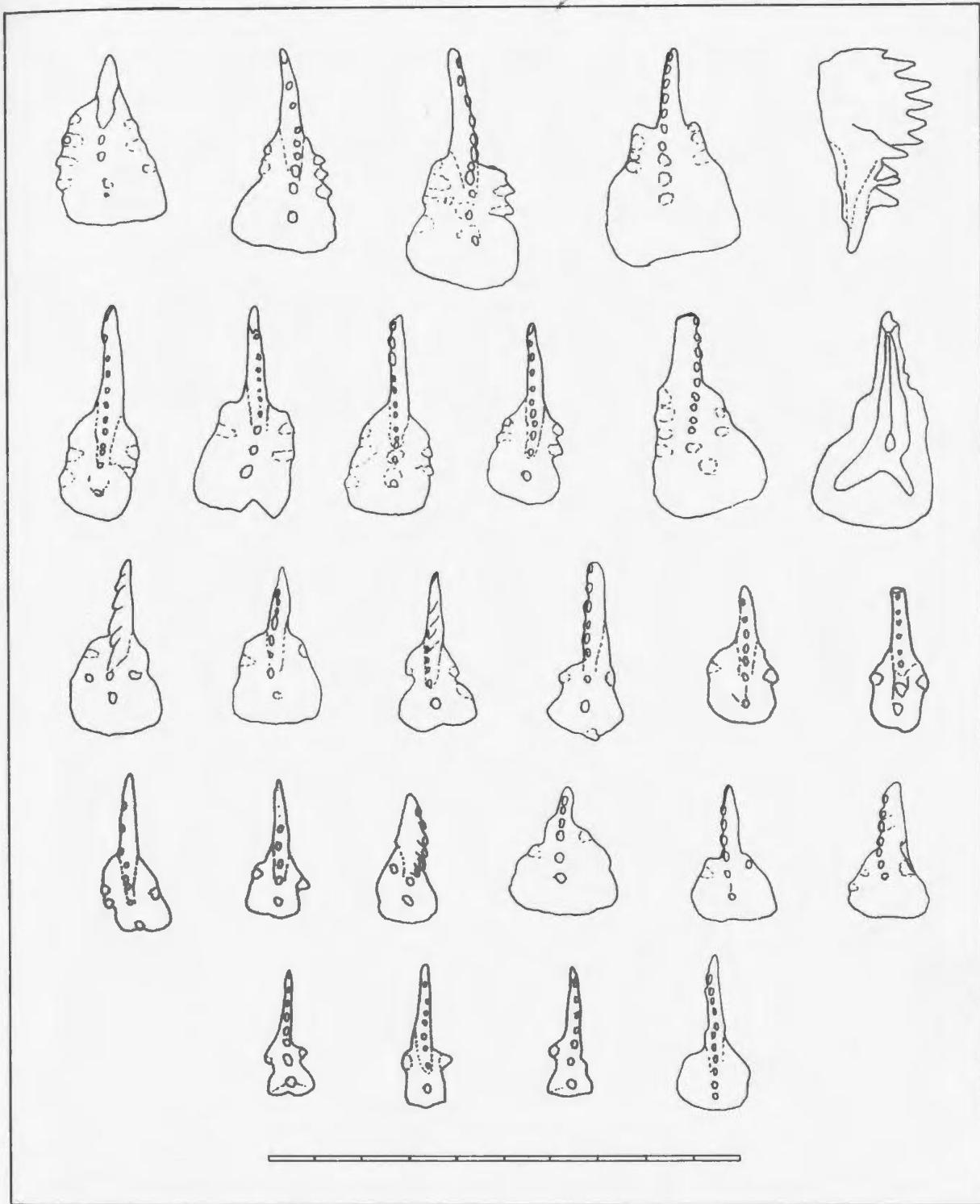


Figure 3-4: Range of morphologic variation exhibited by recovered specimens of *Epigondolella spatulata* s.f.
Scale bar represents 1mm.

Platform extends one-half to almost full length of unit. Typically spoon- to triangular-shaped in outline. Anterior end of platform tapered, posterior end squared. Platform somewhat rounded in upper view in some specimens. Anterior portion of platform more highly ornamented than posterior portion, but in some specimens may have no ornamentation. Ornamentation consists of spike-like denticles or nodes anteriorly, ridges or nodes posteriorly.

Carina high, denticles fused. Second or third anteriormost denticle highest. Carina may bifurcate posteriorly and trace bifurcation of keel. Carina terminates posteriorly in node, not reaching posterior margin.

Microreticulation is moderately open and covers the entire surface of the platform.

Apart from keel, lower surface of platform smooth. Keel increasing in width and depth from anterior to posterior. Keel bifurcates at point below posteriormost node of carina; bifurcations directed towards postero-lateral corners of unit.

Remarks.- The characteristic feature of this species is the tapered anterior margin of the platform. Significant morphologic variability (see Fig. 3-5) exists in the platform outline (spoon-shaped to subpentagonal), and in the degree to which the platform is ornamented. Two basic morphologies are recognized: 1) subpentagonal outline, with rare ornamentation on posterior of platform, and 2) spoon-shaped outline, with radiating nodes, ridges, or denticles over most of the platform.

Of the species of *Epigondolella* documented in this study, this species has the greatest degree of morphologic variation observed. Specimens which are included in this species may in fact represent more than one species. However, the number of specimens is not high, and some of the morphotypes are found to co-occur. Because of this, these morphologies are considered (tentatively) to represent intraspecific variation. —

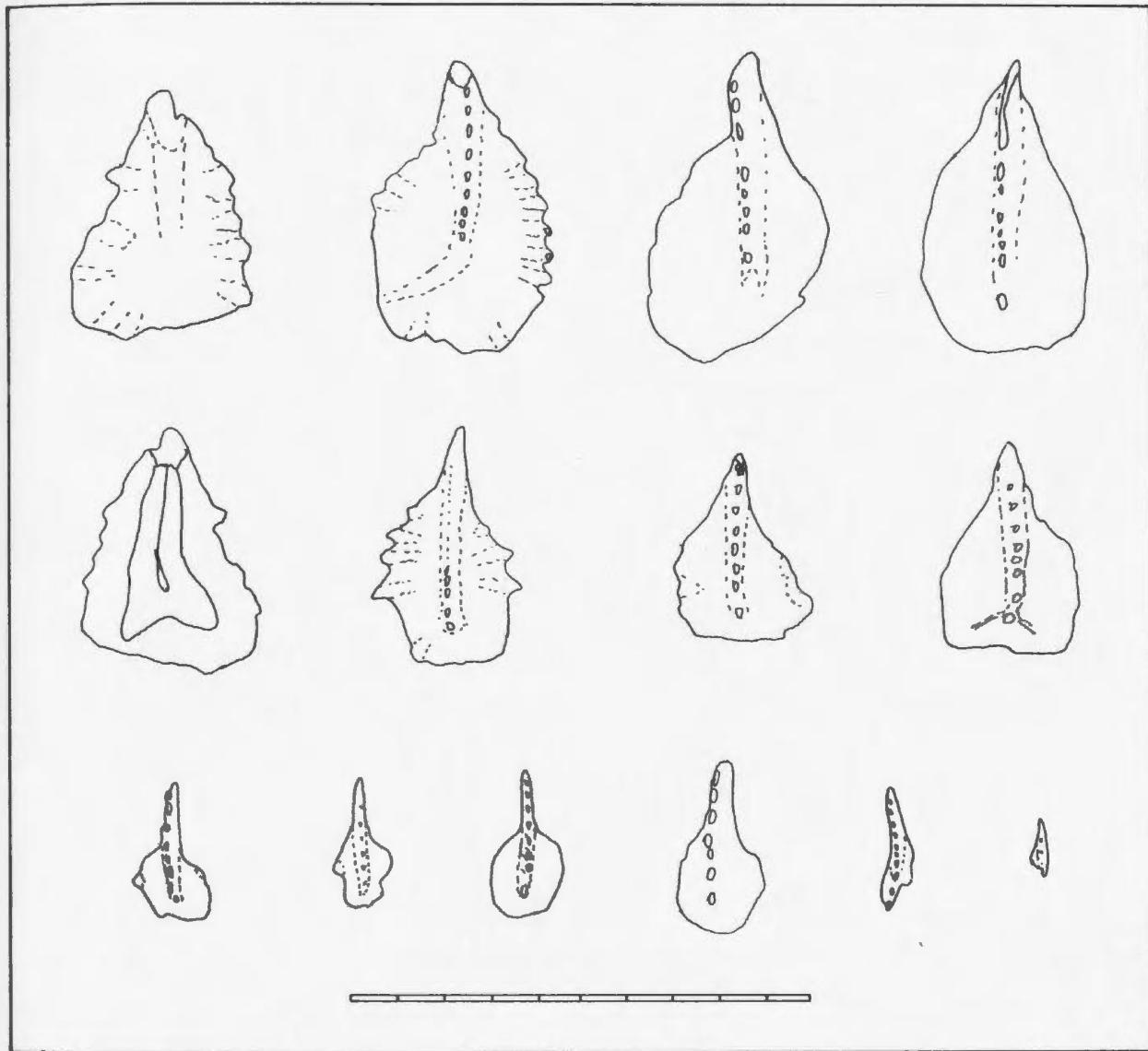


Figure 3-5: Range of morphologic variation exhibited by recovered specimens of *Epigondolella* sp. A. s.f.
Scale bar represents 1mm.

Because of the outline of the platform and the type of denticulation in some specimens, the author believes that this species may have close affinities with *E. abneptis* s.f. and *E. spatulata* s.f.

Material.- 42 segminiplanate pectiniform elements.

Occurrence.- Samples RKK-1-2m, RKK-1-3.5, and RPR-1-1.

EPIGONDOLELLA SPP. INDET. s.f.

Not Figured.

Description.- Fragmentary, corroded, and juvenile segminiplanate pectiniform elements. Platform may be triangular or rectangular in outline. Keel may bifurcate posteriorly.

Remarks.- Few non-fragmentary specimens were recovered, and these were juveniles. One juvenile fragment bears three denticles on the platform, which is suggestive of affinities with *E. postera*. However, this specimen does not have the characteristic pointed posterior margin of *E. postera*. Other less fragmentary specimens have a squared-off posterior margin, while some resemble specimens herein assigned to *E. sp. A*. Due to the fragmentary, corroded, or juvenile character of these specimens, they can not be assigned with certainty to any species of *Epigondolella*.

Material.- 33 segminiplanate pectiniform elements.

Occurrence.- Samples RDR-1-3, RKK-1-0m, RKK-4-3m, RKK-4-6m, RKK-4-9m, RKK-4-12m, and RKK-4-15m.

GENUS MISIKELLA Kozur and Mock, 1974

Type species.- *Misikella longidentata* Kozur and Mock, 1974

Original diagnosis (Kozur and Mock, 1974a:136): "Single element genus. Small growing conodonts with short, but basally strongly bowed [unit], which shows 3-8 (commonly 4-6) denticles, of which the terminal main denticle is not strongly developed (very rarely you find as a rudiment of the denticulated [process?] a small denticle behind the main denticle). The strongly flared basal cavity embraces the entire lower side of the conodont, and the flare is anteriorly clearly projecting. Basal cavity is deep, commonly cone-shaped." Translated from German original by S. Pohler and the author.

Revised diagnosis.- Tetramembrate apparatus with segminiplanate pectiniform, and alate, digrate, and bipennate ramiform elements. Pectiniform element with large, strongly reclined cusp, deep basal cavity, and widely flared basal sheath. Ramiform elements are laterally compressed with the distal denticles of the posterior process being highly fused and subparallel to process.

Discussion.- When Kozur and Mock (1974a) originally erected this genus, they cited *Misikella longidentata* as the type species. In a subsequent paper in the same journal (roughly 100 pages later, in the next issue) they cited the type species as being *Misikella hernsteini* (Mostler, 1968). Article 68a of the International Code of Zoological Nomenclature (ICZN) (Stoll *et al.*, 1961), "type by original designation", demands that *M. longidentata* be the type species for *Misikella*. With the exception of *M. longidentata*, all other species previously referred to the genus *Misikella* are herein referred to New Genus A. This is based on the difference in apparatus reconstructions herein proposed for the two genera.

MISIKELLA LONGIDENTATA Kozur and Mock, 1974

Plate 4, Figures 11-15.

Synonymy.- Pa element.

Misikella longidentata n. gen. n. sp. KOZUR AND MOCK, 1974a, p. 136-137, Pl. 1, figs. 4,5.

Sa element.-

? *Diplodella bidentata* (TATGE). KOIKE, 1982a, p. 25, Pl. 7, figs. 12-15.

Description.- Pa element.- Segminiplanate pectiniform element with partially fused denticles and large cusp. Short, sharp denticles three to five in number. Cusp large, directed posteriorly at about 35 degrees to plane of basal margin. Cusp four to five times size of denticles. Denticles of same size, except for anteriormost, which is smaller. Basal cavity deep. Basal sheath widely flared. Basal margin slightly arched (concave down).

Sa element.- Alate ramiform element. Lateral processes, bearing three denticles, bifurcate from cusp at approximately right angles. Posterior process arched, with fifteen denticles. Denticle and process height and robustness increase posteriorly, then decrease abruptly to terminate in denticles which are fused and oriented almost parallel to process. Basal cavity shallow.

Sb element.- Digyrate ramiform element with robust processes. Denticles long and sharp. One process long and arched, concave down, and the other deflected slightly downward.

Sc element.- Bipennate ramiform element with fused cusp and denticles. Cusp deflected laterally from plane of processes. Cusp and posteriormost denticles long and sharp. Denticles on posterior process increase in size posteriorly, then decrease abruptly. Distal portion of posterior process composed

of small, fused denticles oriented almost parallel to process. Anterior process short, bearing two denticles.

Remarks.- Two co-occurring variations of the Pa element are apparent; one being more robust than the other. Both are illustrated.

The morphology of the Pa element is almost identical to that of the Pa element (Sp of Von Bitter and Merrill (1980)) of *Gondolella neospaphodiiformis* Von Bitter and Merrill s.l., as described from the Virgilian (Pennsylvanian) by Von Bitter and Merrill (1980).

Material.- 12 Pa (segminiplanate) elements, 1 Sa (alate) element, 6 Sb (digyrate) elements, and 5 Sc (bipennate) elements.

Occurrence.- Samples RAY-1-1, REV-2-1, REV-2-2, REV-2-3, and REV-2-4.

GENUS NEOGONDOLELLA Bender and Stoppel, 1968

Type species (by monotypy: Bender and Stoppel, 1968:343).-

Gondolella mombergensis Tatge, 1958

Original diagnosis (Sweet, *In Ziegler*, 1973:127): 'In discussing the relationships of *Gondolella rosenkrantzi* Bender and Stoppel, Bender and Stoppel (1968) state (German): "There are, moreover, relations to *Neogondolella mombergensis* (Tatge). Differences lie in the outline of the platform, which is narrow and lancet-like in *N. mombergensis*, and in the formation of the basal furrow, which is broadened in a ring-like manner in *N. mombergensis*. In our form-species it has a triangular outline."

Revised diagnosis.- Apparatus seximembrate. Pa element segminiplanate with platform, finely to coarsely pitted on its upper surface, extending full length of element. Pb element bipennate. M element dolabrate. Symmetry-transition series composed of alate, digyrate, and bipennate elements.

Discussion.- Although Sweet (*In Ziegler*, 1973; and *In Robison* (Ed.), 1981) diagnosed *Neogondolella* as being unimembrate, the possibility of its being multimembrate has been proposed previously by Kozur (1976), and Von Bitter and Merrill (1977).

The ramiform elements herein assigned to species of *Neogondolella* share many characteristics with platform elements assigned to those species: distribution of white matter, colour, average size, similarity of cusp form, denticulation, and basal cavity, and stratigraphic co-occurrence. For these reasons both pectiniform elements and ramiform elements have been assigned to multielement species within the genus *Neogondolella*. The recovered ramiform elements were for the most part fragmentary.

Von Bitter and Merrill (1977) suggested the possibility that species of

Gondolella evolved from *Neogondolella*, rather than the reverse which has also been proposed (Clark, 1972). If this is the case, the multielement nature of *Gondolella* (Sweet, In Robison (Ed.), 1981; see especially Von Bitter, 1976) would suggest a multielement apparatus for *Neogondolella*. The ramiform elements of *N. steinbergensis* and those of *Gondolella sublanceolata* Gunnell share many characteristics (general morphology, fine striations on cusp, and basal cavity orientation). These characteristics further point out the resemblances and close relationships between the genera *Neogondolella* and *Gondolella*.

Form taxa identified by various authors as *Cratognathodus kochi* (Huckriede) s.f., *Prioniodina* sp. s.f., and *Ozarkodina tortilis* Tatge s.f., may be synonymous with ramiform elements of species of *Neogondolella*. Synonymies are very difficult to produce for the ramiform elements; in some instances ramiform elements may have been ignored in studies, and not illustrated. Also, in order to synonymize, co-occurrence must be demonstrated.

Given the septimembrate (Von Bitter, 1976) apparatus of *Gondolella* it is possible that *Neogondolella* also possessed a septimembrate apparatus, as opposed to the seximembrate reconstruction suggested herein.

NEOGONDOLELLA COMMUNISTI (Hayashi, 1968) s.f.

Plate 5, Figures 16.17.

Synonymy.

Metapolygnathus communisti gen. et. sp. nov. HAYASHI, 1968, p. 72, Pl. 3, figs. 11a-c; KOZUR, 1972a, Pl. 3, fig. 9; KOVACS AND KOZUR, 1980, Pl. 12, fig. 6 (re-illustrated holotype of Hayashi (1968)).

Metapolygnathus communisti HAYASHI morphotype A KRYSTYN, 1980, Pl. 12, figs. 8-14.

Description.- Bilaterally asymmetrical segminiplanate pectiniform element with long anterior free blade.

Carina composed of seven to ten laterally compressed, upwardly directed denticles, fused for most of their length. Carina subterminal.

Platform finely pitted with subrounded posterior margin. Mature specimens possess no nodes on platform, while juvenile specimens possess three to four nodes anteriorly, and have a constriction in platform posteriorly. Platform one-third to one-half length of unit. Lateral margin of platform upraised. Anterior margins drop steeply and form ridge along lower portion of carina. Carina constricted below ridge.

Raised keel narrow and slit-like. Pit located anterior of platform midpoint in mature specimens, but posteriorly in juvenile specimens. Posterior termination of keel loop-like, with raised bifurcation. Lower surface of platform pitted. Outline of platform when viewed laterally roughly parallels that of carina.

Remarks.- *Neogondolella communisiti* s.f. is considered by many authors to be a junior synonym of *N. polygnathiformis* (Budurov and Stefanov) s.f. (eg. Mosher, 1973; and Sweet, In Ziegler, 1973). However, the author, as do Krystyn (1980) and Kovács and Kozur (1980), herein considers *N. communisiti* s.f. to be a distinct species. A difference between the two species is the lateral outline of the platform compared to that of the carina. In *N. communisiti* s.f. the two are roughly parallel, while in *N. polygnathiformis* s.f. the trace of the platform is directed somewhat upward.

It should be noted that *N. communisiti* and *N. polygnathiformis* are not typical of *Neogondolella* and that they may be referable to another genus, possibly *Metapolygnathus*.

Krystyn (1980) reports two morphotypes of *N. communisiti*: morphotype A and morphotype B. Only one morphotype is represented by the material in this study; corresponding to morphotype A of Krystyn (1980).

Material. - 7 segminiplanate pectiniform elements.

Occurrence. - Samples REV-2-1, and REV-2-3.

NEOGONDOLELLA HALLSTATTENSIS (Mosher, 1968)

Plate 5, Figures 7,8.

Synonymy. - Pa element.

Paragondolella navicula hallstattensis n. sp. MOSHER, 1968a, p. 939, Pl. 117,
figs. 6-12; SWEET *et al.*, 1971, Pl. 1, fig. 22.

Gondolella hallstattensis (MOSHER) KOVACS AND KOZUR, 1980, Pl. 13, figs. 3-5;
KRYSYŃ, 1980, Pl. 11, fig 12.

Gondolella navicula hallstattensis (MOSHER) MOCK, 1971, Pl. 1, fig. 9, Pl. 5,
figs. 1,14.

Neogondolella navicula hallstattensis (MOSHER) MOSHER, 1973, p. 168, Pl. 20,
fig. 19; KOPKE, 1981, Pl. 2, fig. 14.

? *Gondolella navicula hallstattensis*? (MOSHER). MELLO AND MOCK, 1977, Pl.
8, fig. 15.

? *Neogondolella hallstattensis* (MOSHER). GUPTA, 1983, Pl. 2, figs. 14-17, Pl. 6,
figs. 3,4.

? *Paragondolella hallstattensis* MOSHER. GUPTA AND BUDUROV, 1981, Pl. 2,
figs. 14-17.

non Paragondolella hallstattensis MOSHER. CATALOV AND BUDUROV, 1978, p.
89-90, Pl. 3, fig. 14; BURYI, 1984b, p. 43-44, Pl. 1, figs. 16,17.

non Paragondolella navicula hallstattensis MOSHER. OKAMI *et al.*, 1978, Pl. 1,
fig. 11.

Description.- Pa element.- Segminiplanate pectiniform element with well-developed platform in mature specimens. Carina high. Denticles discrete. In juvenile forms, platform present as ridges on sides of element; does not extend to posterior of cusp. In mature forms, platform broad, surrounding posteriormost denticle. Basal cavity slit-like, shallowing anteriorly, rounded and flared at anterior end. White matter present in cusp and denticles.

Pb element.- Laterally compressed bipennate ramiform element. Anterior and posterior processes of equal length. Anterior process more robust than posterior process. Denticles sharp and discrete. Basal cavity narrow and shallow under processes, deeper and flared under cusp. White matter present in cusp and denticles.

Remarks.- Only juvenile Pa elements were recovered in this study, and resemble the juvenile forms of *Neogondolella navicula hallstattensis* illustrated by Mosher (1968a: Pl. 117, figs. 6-8). In all elements, the platform is poorly developed, and does not surround the cusp. The appearance of the denticles (discrete and less inclined than in the other species of *Neogondolella*) is characteristic of these specimens. The unit is characteristically less arched than that of other species.

The Pb element recovered is very similar to that recovered for *N. sp. cf. N. navicula*. However, the basal cavity is wider than in Pb elements of *N. sp. cf. N. navicula*. This may be a significant difference between the species, or it may just be the interspecific variability of that element.

Material.- 6 Pa (segminiplanate) elements, and 1 Pb (bipennate) element.

Occurrence.- Sample RPA-1-0m.

NEOGONDOLÉLLA STEINBERGENSIS (Mosher, 1968)

Plate 5, Figures 1-6.

Synonymy.- Pa element.-

Paragondolella navicula steinbergensis n. sp. MOSHER, 1968a, p. 939, Pl. 117, figs. 13-22.

Gondolella navicula steinbergensis (MOSHER). MIRAUTA AND GHEORGHIAN, 1975, p. 53, Pl. 6, figs. 1a,b; Pl. 7, figs. 1a,b; MIRAUTA AND GHEORGHIAN, 1978, Pl. 2, fig. 14; CAFIERO AND CAPOA BONARDI, 1981, Pl. 58, fig. 5.

Gondolella steinbergensis (MOSHER). GUPTA *et al.*, 1980, p. 588, 592, Pl. 4, figs. 1-5; KOVACS AND KOZUR, 1980 Pl. 15, fig. 2; KRYSYNA, 1980, Pl. 11, figs. 13-15;

Gondolella sp. ISOZAKI AND MATSUDA, 1980, Pl. 1, fig. 11.

Neogondolella navicula steinbergensis MOSHER. GUPTA AND RAFEK, 1976, p. 211, Pl. 1, figs. 3a,b; GUPTA, 1978, Pl. 2, figs. 1,2, Pl. 3, figs. 1,2a-c, Pl. 4, figs. 1a-c, 2a-c, Pl. 5, figs. 1a-c, 6; KOIKE, 1981, Pl. 2, fig. 25.

Neogondolella sp. indet. MEEK, 1984, Pl. 2, fig. 13 only, (non figs. 4,14-16).

Paragondolella steinbergensis MOSHER. JENKINS AND JENKINS, 1971, Fig. 5, nos. 1-8.

Paragondolella steinbergensis (MOSHER). BURZYI (*sic.*), 1984, p. 44-45, Pl. 1, figs. 13-15.

? *Gondolella steinbergensis* (MOSHER). KOLÁR-JURKOVSEK *et al.*, 1983, p. 170-171, Pl. 6, fig. 1.

Sb element.-

Lonchodina muelleri TATGE. GUPTA, 1978, p. 175-176, Pl. 5, figs. 2,3.

Prioniodina n. sp. B JENKINS AND JENKINS, 1971, Fig. 5, no. 28.

Sc element.-

Lonchodina spengleri HUCKRIEDE. GUPTA, 1978, p. 176, Pl. 5, figs. 4,5.

Description.- Pa element.- Arched segminiplanate element with low carina.

Elements generally bilaterally symmetrical. Mature specimens long and narrow. Denticles discrete, sharp, and directed slightly posteriorly. Anterior denticles higher than posterior denticles. Cusp large. White matter generally present only in cusp. Upper surface of platform, which does not extend posterior to cusp, pitted. Platform separated from carina by deep, narrow furrow. Basal cavity flared at posterior end; present as keel in anterior two-thirds of element. Basal cavity generally bilaterally asymmetrical.

Pb element.- Laterally compressed bipennate ramiform element. More robust than M or S-series elements. Slightly deflected anterior process more robust than posterior process. Cusp larger than denticles. Denticles long, sharp, and discrete, with sharp anterior and posterior margins. Basal cavity inverted and relatively deep under cusp; shallowing and extending full length of process. White matter present in cusp, rare in denticles.

M element.- Laterally compressed dolabrate ramiform element. Anterior process flexed downward. Cusp larger than denticles; both cusp and denticles are long, sharp, and discrete with sharp anterior and posterior margins. Basal cavity deep under cusp, shallow under process. White matter present in cusp.

Symmetry-transition series.- Processes laterally compressed. Cusp larger than denticles, bearing fine striations. Denticles discrete, directed upward, with sharp anterior and posterior margins. Basal cavity inverted. Deepest under cusp.

shallowing distally on processes. Tip of basal cavity pointed anteriorly. White matter present in cusp, rare in denticles.

Sa element.- Laterally compressed alate ramiform element. Lateral processes bifurcate at about 45 degrees from anterior process which has only one denticle.

Sb element.- Dipyrate ramiform element. Cusp antero-posteriorly compressed, with sharp lateral margins. Element may have costa on posterior edge of cusp.

Sc element.- Bilaterally symmetrical bipennate ramiform element. Short anterior process with one denticle.

Remarks.- The Pa element of this species closely resembles those illustrated by Mosher (1968a).

The ramiform elements of this species share characteristics with illustrated elements of *Gondolella sublanceolata* Gunnel (Von Bitter, 1976) in a number of ways. Von Bitter noted that the basal cavity is oriented at an angle to the cusp in *G. sublanceolata*. He also noted fine surface striations (visible only at high magnifications on an SEM) on the cusp. Both of these features are found on ramiform elements herein assigned to *N. steinbergensis*.

Several of the Sb elements possess a costa on the posterior face of the cusp. More Sb elements were recovered than any other ramiform type (14 versus 9, the next most abundant) and this may suggest that these costa-bearing Sb elements could be considered separately. The author considers that the presence of a costa on the Sb element would not make the element functionally different from regular Sb elements. If this element were considered to be distinct, the apparatus would be septimembrate, similar to *Gondolella*.

Material.- 43 Pa (segminiplanate) elements, 5 Pb (bipennate)elements, 1 M (dolabrate) element, 4 Sa (alate) elements, 15 Sb (digyrate) elements, and 10 Sc (bipennate) elements.

Occurrence.- Samples RAE-3-1, REV-3-1, REV-4-1.5m, REV-4-8m, REV-4-18m, and REV-4-30m.

NEOGONDOLELLA SP. CF. NEOGONDOLELLA NAVICULA (HUCKRIEDE, 1959)

Plate 5, Figures 9-13.

Synonymy.- Pa element.

cf. *Puragondolella navicula navicula* (HUCKRIEDE). MOSHER, 1968a, p. 939, Pl. 116, figs. 20-27, Pl. 117, fig. 3 only (*non* figs. 1,2,4,5); MOSHER, 1968b, Pl. 119, figs. 11-18,21 only (*non* figs. 19,20,22,23).

Description.- Pa element.- Long, narrow, arched segminiplanate pectiniform element with small accessory denticle postero-lateral to cusp. Carina high. Posteriorly directed cusp triangular, twice size of denticles. Denticles small, partially fused. Anteriormost denticle directed upwardly. Distally, denticles become inclined posteriorly. Small accessory denticle at same inclination as cusp. Accessory denticle sharp or node-like. Platform well-developed only in large specimens. On early growth stages, no platform or accessory denticle present. Postero-lateral denticle always on inner side, defining dextral or sinistral forms. Platform present as ridge from growth stage with five denticles. Platform may or may not extend around posterior portion of cusp. Platform constricted slightly just anterior of cusp. Basal cavity flared at posterior end, narrow and keel-like anterior to cusp. Local flare under accessory denticle.

Pb element.- Laterally compressed bipennate ramiform element. Slightly laterally flexed anterior process longer than posterior process (element fragmentary). Anterior process deflected downward at about 30 degrees.

Posteriorly directed denticles slightly fused. Basal cavity shallow, narrow, and slit-like.

M element.- Laterally compressed dolabrate ramiform element. Denticles and cusp subparallel. Denticles occasionally partially fused. Basal cavity shallow under process, deeper and terminating in a point under cusp. Process bears four to six denticles.

Sb element.- Digyrate ramiform element. Cusp has costa on posterior side. Denticles partially fused. Basal cavity shallow.

Sc element.- Laterally compressed symmetrical bipennate ramiform element. Basal cavity deep and pointed under cusp. Specimen fragmentary.

Remarks.- These specimens compare very closely with the platformless elements described by Mosher (1968a:939). In Mosher's description of the species, however, no mention is made of the small denticle posterior to the cusp. Mosher (*ibidem*) has illustrated specimens which appear to have this denticle. This posterior denticle may be grounds for the erection of a new species. However, this denticle may become submerged in later growth stages (Orchard, pers. comm. 1987).

The Pb element is very similar to that of *N. hallstattensis*, and is discussed in the remarks for that species.

Material.- 29 Pa (segminiplanate) elements, 2 Pb (bipennate) elements, 14 M (dolabrate) elements, 2 Sb (digyrate) elements, and 1 Sc (bipennate) element.

Occurrence.- Samples RPA-1-0m, and RPA-1-1.5m.

NEOGONDOLELLA SPP. INDET.

Not Figured

Description.- Pa element.- Fragmentary and corroded segminiplanate pectiniform element.

Carina higher at anterior than at posterior. Denticles fused for most of their length, pointed slightly posteriorly. Anterior end of carina free.

Platform widest at posterior end, tapering anteriorly. Slight constriction in platform just anterior of main denticle. Surface pitted. Platform extends posterior of main denticle.

Keel narrow and slit-like anteriorly, rounded and flared posteriorly.

Sb element.- Highly fragmentary and corroded digyrate ramiform element.

Sc element.- Fragmentary bilaterally symmetrical bipennate ramiform element..

Remarks.- Some of these Pa elements vaguely resemble those assigned to *Neogondolella navicula navicula* by many authors (Mosher 1968; 1973; Kovács and Kozur, 1980; Krystyn, 1980). Others show characteristics reminiscent of *N. polygnathiformis* s.f. and *N. communis* s.f.. However, due to the fragmentary and corroded nature of the specimens, it is not considered possible to assign them with certainty to any species of *Neogondolella*.

Material.- 15 Pa (segminiplanate) elements, 6 Sb (dogyrate) elements, and 1 Sc (bipennate) element.

Occurrence.- Sample RDR-1-3.

GENUS ONCODELLA Mosher, 1968 s.l.

Type species.- *Oncodella paudentata* (Mostler, 1968)

Original diagnosis (Mosher, 1968a:932): "Unit composed of laterally compressed bar beset with small number of widely separated and discrete, strongly inclined denticles. Anterior denticle projects initially forward then curves strongly upward and backward, giving appearance of hook or barb. Basal excavation extends entire length of unit, being largest and deepest at its anterior end."

Revised diagnosis.- No revised diagnosis given.

Remarks.- Sweet (In Robison, 1981) suggested a multielement reconstruction of a species including *Didymodella alternata* (Mosher) s.l. and *Oncodella paudentata* s.l.. *Didymodella alternata* s.l. has not been shown in the literature and in this study, to co-occur with *Oncodella paudentata* s.l., and as a result this reconstruction is considered unlikely.

ONCODELLA PAUDENTATA (Mostler) s.l.

Plate 2, Figures 6,7.

Synonymy.- dolabrate element.-

Hindeodella paudentata n. sp. MOSTLER, 1968, p. 181-182, Pl. 1, fig. 3.

Oncodella idiodentata n. sp. MOSHER, 1968a, p. 932, Pl. 114, figs. 4-6.

Oncodella paudentata (MOSTLER). SWEET *et al.*, 1971, Pl. 1, fig. 15; KOZUR AND MOSTLER, 1972b, p. 25-26, Pl. 15, figs. 6-10, 13; MOSTLER, 1978a, pl. 3, fig. 19.

? *Ligonodina* sp. HAYASHI, 1968, p. 72, Pl. 4, fig. 25.

Description.- Dolabrate element with cusp, and posterior process with two to four denticles. Cusp and denticles long, sharp, and discrete with subcircular to oval cross-sections. Inclination of denticles to process decreases posteriorly. Basal cavity shallow and wide, extends full length of process. Anteriorly, interior of basal cavity rounded. Due to lateral deflection of cusp, element may or may not be laterally symmetrical. White matter present in cusp and denticles; apices opaque, base lacks white matter.

Remarks.- One alate element was recovered which resembles the dolabrate element in all features except in possessing lateral processes. It is possible that this element represents part of an as yet unidentified multielement apparatus including *O. paucidentata* s.f.. However, this element type is under-represented, and does not co-occur with the dolabrate element. As a result, no multielement reconstruction has been attempted for *O. paucidentata* s.f.

Material.- 107 dolabrate elements (1 alate element).

Occurrence.- Samples RAE-3-1 (alate element), REV-3-1, REV-4-8m, REV-4-18m, REV-4-30m, and RKK-1-21m.

NEW GENUS A

Type species.- *Spathognathodus hernsteini* Mostler, 1968

Diagnosis.- A genus with a bimembrate apparatus, consisting of seaphate pectiniform and non-geniculate coniform elements, in which the basal cavity is typically flared and the denticles are laterally compressed and fused for most of their length.

Discussion.- Species included in New Genus A have previously been referred to the genus *Misikella* Kozur and Mock. The author has above noted (page 98) that *Misikella* has only one documented species, *Misikella longidentata* (the type species). This is further discussed under that genus. The apparatus reconstructions for *Misikella* and New Genus A are different and it is on this basis that they are considered to be distinct genera.

In previous studies the apparatus of species assigned to this genus has been considered unimembrate, composed solely of segminate pectiniform elements. In this study, however, it is considered to be bimembrate, composed of non-geniculate coniform as well as segminate pectiniform elements. Coniform elements assigned to New Genus A have not been previously illustrated in the literature. In samples with low abundance of pectiniform elements, coniform elements may be absent. This may explain why they have not previously been recognized. Skwarko *et al.* (1976) have previously suggested the possibility of a multielement apparatus for this genus (therem referred to as *Misikella*).

The assignment of both coniform and pectiniform elements to this genus is based on similarities in their basal cavities, cusp and denticles (respectively), distribution of white matter, and on their stratigraphic co-occurrence.

Sweet (*In* Ziegler, 1973) considers New Genus A (therem referred to as *Misikella*) to be a possible junior synonym of *Neospathodus* Mosher. New Genus A, however, lacks the mid-lateral ribs on the pectiniform element which are

characteristic of *Neospathodus*. Sweet (*ibidem*) also points out that species of *Neospathodus* are absent in Middle Carnian to Late Norian strata. This further suggests that New Genus A is likely to be a valid genus, distinct from *Neospathodus*. As yet, multielement apparatus reconstructions have not been proposed for *Neospathodus*; thus, comparisons with the bi-membrate apparatus of New Genus A cannot be made.

NEW GENUS A HERNSTEINI (Mostler, 1968)

Plate 4, Figures 4-6.

Synonymy. - pectiniform element.

Spathognathodus hernsteini n. sp. MOSTLER, 1968, p. 182, text-fig. 1.

Misikella hernsteini (MOSTLER). KOZUR AND MOCK, 1977a, Pl. 1, figs. 6.7; MOSTLER, 1978b, Pl. 1, figs. 10-19, Pl. 2, figs. 5-7; GAZDICKI *et al.*, 1979, Pl. 5, figs. 3-7; ISOZAKI AND MATSUDA, 1980, Pl. V, fig. 12; KOVACS AND KOZUR, 1980, Pl. 15, figs. 4-7; KRYSTYN, 1980, Pl. 14, figs. 10-12; KOIKE, 1981, Pl. 2, fig. 29; MATSUDA AND ISOZAKI 1981, Pl. 2, figs. 30a,b; ISOZAKI AND MATSUDA, 1982, Pl. 4, fig. 8; ISOZAKI AND MATSUDA, 1983, p. 66-67, Pl. 1, figs. 1-7.

Neospathodus hernsteini (MOSTLER). SWEET *et al.*, 1971, Pl. 1, figs. 2,3; KOLAR-JURKOVSEK *et al.*, 1983, p. 171-172, Pl. 7, figs. 2-3.

Neospathodus lanceolatus n. sp. MOSHER, 1968a, p. 930-931, Pl. 115, figs. 10,11 only (*non* fig. 7).

Neospathodus sp. ISOZAKI AND MATSUDA, 1980, Pl. 7, fig. 13.

Neopriponiodus sp. OKAMI *et al.*, 1978, Pl. 1, figs. 22,23.

Description.- Pectiniform element.- In upper view, element drop-shaped, flared slightly at posterior end, and bilaterally symmetrical.

In lateral view, elements show three to five denticles, fused for about one-half of their length in most specimens. Denticles laterally compressed with sharp anterior and posterior edges. Posteriormost denticle generally largest; in extreme cases may be twice the height of others. Denticles posteriorly directed, with posteriormost denticle inclined to basal margin at about 65 degrees. Anterior denticles more inclined, anteriormost may be near vertical. Apical trace of denticles either straight or convex up.

Basal cavity shallow; basal sheath not flared widely except at posterior end. Posterior basal margin rounded and flared.

Coniform element.- Non-geniculate element with laterally compressed, proclined cusp. Element has a width:height ratio of approximately 2:1.

Base of element narrowly flared. Basal cavity shallow. Slight constriction just above base related to flaring. White matter extends from apex to basal cavity.

Remarks.- New Genus *A hernsteini* is characterized by a rounded posterior margin, in contrast to New Genus *A posthernsteini* which is characterized by a slightly to strongly concave posterior margin.

The basal cavity of New Genus *A hernsteini* is much shallower than that of New Genus *A posthernsteini*. Also, the basal flare of the former is much less pronounced, and is not localized, as in the latter.

New Genus *A hernsteini* is considered to be the earliest species in the New Genus *A* lineage (Mostler *et al.*, 1978) (therein referred to as *Misikella*). In this study, it is not possible to examine the evolution of New Genus *A*, as there are too few samples.

Those elements of this species which have a very large posterior denticle may be functionally equivalent to some of the coniform elements of New Genus A *posthernsteini*. This would explain the rarity of coniform elements in this species: the large-denticled pectiniform element of New Genus A *hernsteini* may in part be replaced by the coniform element of New Genus A *posthernsteini*.

Material.- 219 pectiniform elements and 5 coniform elements.

Occurrence.- Samples REV-3-1, REV-4-8m, REV-4-18m, and REV-4-30m.

NEW GENUS A KOESSENENSIS (Mostler) s.l.

Plate 4, Figures 1-3.

Synonymy.-

Misikella koessenensis n. sp. MOSTLER, 1978b, p. 153, pl. 2, fig. 3.

Misikella hernsteini (MOSTLER). KOZUR AND MOCK, 1974a, Pl. 1, figs. 6,7.

Description.- Scaphate pectiniform element bearing small accessory denticle posterior to large main denticle. Basal cavity deep and flared. Scaphate pectiniform elements can be divided into three morphotypes: symmetrical pectiniform element, Type 1 asymmetrical pectiniform element, and Type 2 asymmetrical pectiniform element.

Symmetrical pectiniform element.- In upper view basal outline drop-shaped, with rounded end at posterior. Basal sheath flares widely. Elements typically longer than high. Length:height ratio about 4:3.

Elements have four to seven laterally compressed denticles, including small accessory denticle at posterior of element, fused for most of their length. Free portion of denticles somewhat triangular in lateral outline. Main denticle (cusp?)

directed posteriorly at angle of about 55 degrees to lower margin. Inclination of denticles to lower margin, increases anteriorly, and decreases posteriorly, from main denticle. Posterior accessory denticle generally same size as smallest anterior denticle.

Basal cavity deep; deepest at point between second and third most posterior denticles. Depth varies from between one-quarter and almost one-half element height. Lower margin straight or convex.

Type 1 asymmetrical pectiniform element.- Asymmetry of element apparent in basal outline which is modified drop-shape, characterized by swelling of outer postero-lateral corner of element and by indentation on inner postero-lateral corner. Asymmetry also defined by accessory denticle, and by postero-lateral carina on main denticle. Length:height ratio about 4:3.

Element has four large denticles inclined posteriorly at about 65 degrees to basal margin. Three anterior denticles bilaterally symmetrical. Main denticle has low, wide carina on inner side.

Small, sharp accessory denticle posterior to main denticle directed slightly to inner side. Anterior margin of accessory denticle joins posterior margin of main denticle at point about midway up element. Posterior margin of accessory denticle connects to swelling on outer postero-lateral corner of element. Postero-lateral accessory denticle on inner side.

Basal sheath flares where carina meets basal margin, and then constricts posteriorly.

Type 2 asymmetrical pectiniform element.- In outline, basal margin asymmetrically heart-shaped, with concavity in basal margin located posteriorly between two carinae. Length:height ratio about 4:3.

Denticles (four) laterally compressed and fused, for most of length. Posterior accessory denticle characteristic in having two asymmetrically located carinae. Posterior margin of this denticle deflected inwards and forms a carina. Other carina located below midway point of denticle, dropping to basal margin.

Folds created (in a similar fashion as in New Genus A *posthernsteini*) in posterior basal margin where carinae end.

Remarks.- No coniform elements were found which could be included in this species.

The holotype illustration of *Misikella koessenensis* Mostler s.l. (1978b, Pl. 2, fig. 3) resembles the symmetric pectiniform element of this species. However, the original description of the species does not, in the author's opinion, agree with the illustrated holotype: "Conodonts with denticles towering high above the basal cavity, numbering 3-5. Basal cavity wide in back and extending past the entire backside of the conodont. Basal margin stretches far past the last denticle." (Translation from the German original (Mostler, 1978b:153) by S. Pohler and the author.) They refer to the basal margin of the element as extending far past the last denticle. The orientation of their illustration is different from that used herein and is the reason for the discrepancy in the descriptions. Also, a posterior accessory denticle is therein not, as it is herein, considered an important characteristic of the species.

The differences between the above three morphotypes are quite distinct. Considering the criteria which define other species of New Genus A (posterior margin outline, etc.) it is possible that these morphotypes represent three distinct species of New Genus A. However, the scarcity of the specimens prevents such an assignment at the present.

If, however, these specimens are of the same species, this would have distinct ramifications concerning recognized species within New Genus A. In New

Genus *A koessenensis* s.l. both types of posterior margin are found: rounded (drop-shaped), and concave (heart-shaped). These are the very criteria by which the two species New Genus *A hernsteini* and New Genus *A posthernsteini* are generally differentiated. If the posterior accessory denticle is of taxonomic importance and the outline of the posterior margin a secondary feature, this would suggest that New Genus *A hernsteini* and New Genus *A posthernsteini* are conspecific. This, however, does not take into account the differences in depth of basal cavity and flare seen in New Genus *A hernsteini* and New Genus *A posthernsteini*; these features may be of greater taxonomic importance than otherwise recognized. The published stratigraphic ranges of New Genus *A hernsteini* and New Genus *A posthernsteini* overlap but are not identical, though this is not enough to disprove synonymy.

If these morphotypes are considered to represent different species, then their basal outline may be a strong enough criterion to group them with other recognized species of New Genus *A*. If this is the case, the apparatus of New Genus *A* is likely to include more element types than that which has been outlined above; elements with an accessory denticle would be grouped along with the regular pectiniform elements and the coniform elements.

Material.- 4 symmetric pectiniform elements, 1 Type 1 asymmetric pectiniform, and 1 Type 2 asymmetric pectiniform element.

Occurrence.- Samples REV-3-1, and REV-4-8m.

NEW GENUS A POSTHERNSTEINI (Kozur and Mock, 1974)

Plate 4, Figures 7-9.

Synonymy. - pectiniform element.

Misikella posthersteini n. sp. KOZUR AND MOCK, 1974b, p. 247-248, text-figs. 1-4; SKWARKO *et al.*, 1976, p. 222, text-figs. 4a-h; GAZDZICKI, 1978, p. 346, Pl. 38, figs. 1-3, Pl. 39, figs. 1-4, Pl. 40, fig. 3; MOSTLER, 1978b, Pl. 1, figs. 20-22; GAZDZICKI *et al.*, 1979, Pl. 5, figs. 1,2; ISOZAKI AND MATSUDA, 1980, Pl. 1, figs. 14,15; KOVACS AND KOZUR, 1980, Pl. 15, fig. 10; KRYSTYN, 1980, Pl. 14, figs. 7-9; GAZDZICKI AND GUPTA, 1981, text-fig. 1b; ISOZAKI AND MATSUDA, 1982, Pl. 4, fig. 9; MATSUDA AND ISOZAKI, 1982, Pl. 2, fig. 29; ISOZAKI AND MATSUDA, 1983, p. 67-69, Pl. 1, figs. 8-13, Pl. 2, figs. 1-7, Pl. 3, figs. 1-7; BURYI, 1985, fig. 4.

Misikella sp. A GAZDZICKI, 1978, p. 346-347, Pl. 40, figs. 1,2.

Neospathodus lanceolatus n. sp. MOSHER, 1968a, p. 930-931, Pl. 115, fig. 7 only, (*non* figs. 10,11).

Description. - Pectiniform element. Element segminate. Basal outline generally heart-shaped with pointed end to anterior. Elements bilaterally symmetrical. Height:length ratio about 5:6.

Laterally compressed; posteriorly directed denticles fused for most of their length. Free portion of denticles one-quarter to one-fifth total height of element. Number of denticles averages three, but may be as high as five (rare). Largest denticle located at posterior end and inclined at about 60 degrees to basal margin; inclination may be as low as 45 degrees on some elements. Anteriormost denticles inclined at greater angle than posteriormost. Apices of denticles sharp, and apical trace either straight or convex. White matter present from halfway up element to apices of denticles.

Posteriormost denticle may bear two carinae on either side of posterior furrow which deepens downward. Carinae continue to basal margin as pronounced folds. Posteriormost denticle extends past posterior margin of basal cavity by about one-third length of element.

Basal margin typically flares posteriorly to width of about one-half the element length. Basal cavity deep, usually restricted to lower one-quarter of element. Deepest portion of basal cavity located between two most posterior denticles. Basal cavity flares widely, which may be locally intensified. Posterior margin possesses a concavity located between folds created by carinae on posterior denticle. In elements where only one carina is present on posterior margin (rare), basal cavity is bilaterally asymmetrical with only one fold being present on lower base.

Coniform element.- Non-geniculate element with erect cusp. In upper view, element may be symmetrical.

Cusp laterally compressed and exhibits fine striations. Curvature of cusp consistent among elements. Cusp has length:width ratio of about 3:1.

Basal cavity deep; up to one-third the height of element. Base widely flared and may be extremely flared locally. Long axis of basal outline may not correspond to anterior-posterior direction due to localized flare.

Remarks.- The pectiniform elements in this study typically have three denticles; elements with four denticles are less common, and those with five rare. Isozaki and Matsuda (1983) incorrectly refer to *Misikella* sp. A Gazdzicki 1978 as having six denticles, and because of this have not included it in their synonymy. It is herein included as a junior synonym of New Genus *A posthermanni*.

All specimens of New Genus *A* which do not have a rounded posterior margin, and/or a small denticle posterior to the main denticle, are included in

New Genus A *posthernatéini*. This is in agreement with other authors (see Isozaki and Matsuda, 1983).

Material. 468 pectiniform elements and 110 coniform elements.

Occurrence. Samples REV-3-1, REV-4-1.5m, REV-4-8m, REV-4-18m, and REV-4-30m.

NEW GENUS A SP. CF. NEW GENUS A RHAETICA (Mostler, 1978) s.l.

Plate 4, Figure 10.

Synonymy.

cf. *Misikella rhaetica* MOSTLER, 1978b, p. 152-153, Pl. 2, figs. 1,2,4; KRYSTYN, 1980, Pl. 14, figs. 13,14.

cf. *Parvigondolella rhaetica* (MOSTLER). KOVACS AND KOZUR, 1980, Pl. 15, fig. 11.

Description. Element segminate with drop-shaped basal margin in posterior half of element.

Four to six (most common), laterally compressed denticles, fused for most of their length. Posteriormost denticle not always largest. Apical trace of denticles convex up.

Basal margin present as narrow keel in anterior third of element. Posterior two-thirds of basal cavity deep and widely flared. Posterior basal margin rounded.

Remarks. No coniform elements were found which could be attributed to this species. As a result, assignment of this species to New Genus A is *sensu formo* (s.l.).

The pectiniform elements resemble those of New Genus *A rhaetica* (Mostler) s.f. but do not have as many denticles. The basal cavity, as well as the posterior basal margin, of these specimens is very similar to those illustrated by Mostler (1978b).

The features of these specimens which most closely ally it to New Genus *A rhaetica* s.f. are the restricted basal sheath, and the relatively high number of denticles as compared to New Genus *A hernsteini*.

The rounded posterior basal margin of this species suggests a closer relationship to New Genus *A hernsteini* than to New Genus *A posthernsteini*, whereas the flare of the basal cavity indicates the reverse relationship.

Material.- 5 pectiniform elements.

Occurrence.- Sample REV-3-1.

NEW GENUS B s.s.

Type species. - New Genus B New Species A s.s.

Diagnosis. - Apparatus unimembrane. Composed of laterally flexed and compressed segminate pectiniform elements. Basal cavity shallow and flared posteriorly.

Discussion. - Species of this genus show similarities with pectiniform elements of both *Neospathodus* and New Genus A, and may be transitional between the two. No species of *Neospathodus* are known from later than the Lower Carnian, while species of New Genus A are not known to occur this low (middle Ladian) in the Norian.

NEW GENUS B NEW SPECIES A s.s.

Plate 3, Figures 13-15.

Description. - Laterally flexed segminate pectiniform element.

Blade bears five to seven laterally compressed denticles, fused for most of their length. Denticles directed slightly to posterior. Cusp terminal or subterminal. One or two (rare) denticles may be present posterior to cusp.

Basal cavity shallow and flared posteriorly. Anterior portion slit-like. Lower margin concave in lateral view at flared portion of cavity.

Remarks. - This species shows similarities with elements of species of *Neospathodus*. These include similarities in the basal cavity and margin, and denticulation. It lacks, however, the mid-lateral ridge considered characteristic of *Neospathodus* (Sweet, In Ziegler, 1973):

This species was not assigned to genus New Genus A, with which it also

shares some morphologic features, because of the shallowness of the basal cavity, the concave outline of the basal margin in lateral view, and its relatively large size. Coniform elements (Gen. et sp. indet. A s.f. and Gen. et sp. indet. B s.f.) were recovered in samples RKK-1-17m and RKK-1-23m, but their basal cavities are not similar enough to the pectiniform elements to warrant multielement status.

Material.- 144 segminate pectiniform elements.

Occurrence.- Samples RKK-1-10m and RKK-1-17m.

NEW GENUS C

Type species.- New Genus C New Species A

Diagnosis.- Apparatus seximembrate. Pa element angulate, Pb element dolabrate, M element digyrate, Sa element alate, Sb element digyrate, and Sc element bipennate. Denticles discrete, long, and laterally compressed. Basal cavity long, narrow and slit-like. Denticles and cusp finely striated.

Discussion.- The morphology of the Pa and Pb elements of this genus is quite different from that of any other genus in this study or known from the literature.

NEW GENUS C NEW SPECIES A

Plate 2, Figures 8-13.

Synonymy.- Pb element.

Neoplectospathodus muelleri KOZUR AND MOSTLER. Buryi, 1985, fig. 2.

? *Grodella hernsteinensis* KOZUR AND MOSTLER. MOSTLER, 1978b, Pl. 3, figs. 7-9.

Sc element.

? *Hindeodella (Metaprioniodus) andrusovi andrusovi* KOZUR AND MOSTLER. MOSTLER, 1978b, Pl. 3, figs. 18,20,21.

Description.- Pa element.- Angulate pectiniform element with no discernible cusp. Anterior portion arched downward at about 45 degrees to posterior basal margin (which is straight). Unit undulates laterally slightly along longitudinal axis. Denticles partially fused; becoming more so posteriorly. Denticles inclined at about 45 degrees to process axis. Base of unit less than, or

equal to, one-half height of unit. Basal cavity shallow under processes, deeper and wider under central portion of unit.

Pb element.- Dolabrate ramiform element with no discernable cusp or basal pit. Process arched downward. Denticles longer anteriorly than posteriorly, partially fused anteriorly, and discrete posteriorly. Unit longer and more gracile than Pa element.

M element.- Digyrate ramiform element with processes of unequal size. Short lateral process bears one small denticle. Long lateral process bears four to six long, discrete denticles. Cusp curved posteriorly. Unit compressed antero-posteriorly. Basal cavity shallow under processes (more apparent under large process), deeper and pit-like under cusp.

Sa element.- Alate ramiform element. Posterior process strongly arched downward, bearing ten to fifteen small, partially fused denticles. Highest denticle located mid-process. Cusp large, curved posteriorly. Lateral processes bifurcate perpendicularly, flex downward at about 50 degrees, and bear one to three small denticles. Bases of processes high. Basal cavity not apparent.

Sb element.- Digyrate ramiform element with antero-laterally directed lateral processes of unequal length. Short process (bearing two to four denticles) straight and deflected downward lightly. Long process (bearing five to seven denticles) arched downward, flexed anteriorly, and increases in size distally. Denticles discrete. Cusp has groove along posterior edge. Basal cavity not apparent.

Sc element.- Laterally compressed bipennate ramiform element. Posterior process straight, bearing five to ten posteriorly directed denticles. Anterior process more robust than posterior process, bearing three to six denticles. Anterior process deflected downwards; angle of deflection varies from 30 to 50 degrees. Basal cavity shallow.

Remarks.- As mentioned above, the morphology of the Pa and Pb elements is unlike that of any previously described species.

Material.- 15 Pa elements elements, 83 Pb elements, 46 M elements, 65 Sa elements, 20 Sb elements, and 64 Sc elements.

Occurrence.- Samples REV-3-1, REV-4-8m, and REV-4-18m.

GEN. ET SP. INDET. A s.f.

Plate 3, Figure 21.

Description.- Non-geniculate coniform element. Cusp erect and laterally compressed. Basal cavity deep: about one-third height of unit. Basal sheath widely flared and slightly asymmetric.

Material.- 4 non-geniculate coniform elements.

Occurrence.- Samples RKK-1-17m and RKK-1-23m.

GEN. ET SP. INDET. B s.f.

Plate 3, Figure 18.

Description.- Non-geniculate coniform element with accessory denticle on anterior margin. Cusp proclined. Unit laterally compressed. Basal cavity shallow under anterior portion of unit, deepening posteriorly. Basal sheath narrow anteriorly, wide posteriorly.—

Remarks.- The anterior portion of this element is broken and may represent a broken anterior process.

Material.- 2 non-geniculate coniform elements.

Occurrence.- Samples RKK-1-17m, and RKK-1-23m.

GEN. ET SP. INDET. C

Plate 3, Figures 16,17.

Synonymy.- Pa element.

Cratognathodus cuspidatus n. sp. KOIKE, 1982a, p. 20, Pl. 9, figs. 17,18.

M element.

Cypridodella pronoides (BUDIROV). KOIKE, 1982a, p. 22, Pl. 7, figs. 48,49.

Description.- Pa element.

Segminate pectiniform element. Anterior process with one or two denticles.

Cusp bears longitudinal striae. Basal cavity deep.

M element.- Digyrate ramiform element. One long, highly arched, downwardly directed lateral process, bearing two denticles, and one lateral process bearing one denticle. Basal cavity deep. Longitudinal striae on cusp.

Remarks.- These two elements likely are part of a more complete multielement apparatus, which may be related to *Cypridodella*.

Material.- 2 Pa (segminate) elements, and 14 M (digyrate) elements.

Occurrence.- Samples RAY-1-1, RAY-2-1, RKK-1-8m, RKK-1-23m, RPA-1-3.5, and RPH-4-1.

GEN. ET SP. INDET. D s.f.

Plate 3, Figure 19.

Description.- Bipennate ramiform element with long anterior and short posterior processes. Anterior process bears four discrete denticles. Posterior process exists as denticle on cusp and as extension of basal cavity. Basal cavity deep and widely flared on inner side; less so on outer side.

Remarks.- This element resembles no other in this study or in the literature.

Material.- 1 bipennate element.

Occurrence.- Sample REV-3-1.

GEN. ET SP. INDET. E s.f.

Plate 3, Figure 20.

Description.- Angulate pectiniform element with long anterior and short posterior processes. Posterior process deflected inward. Denticles irregular in size and directed upward or posteriorly. Anterior process bears four denticles; posterior, one denticle (process broken).

Remarks.- An interesting feature of this element is the irregular size of the denticles. This element may also be an aberrant Pb element.

Material.- 1 pectiniform element.

Occurrence.- Sample RAY-1-1.

GEN. ET SP. INDET. F s.f.

Plate 5, Figure 15.

Description.- Angulate pectiniform element with arched processes. Anterior process bears five posteriorly directed, sharp, closely spaced denticles. Posterior process bears two sharp denticles, not as closely spaced as those on anterior process. Cusp and denticles striated. Base of unit somewhat laterally expanded. Basal cavity shallow and wide.

Remarks.- This element shows similarities with the Pa elements of specimens illustrated for *Xaniognathus* Sweet (In Robison, 1981), but lacks the ribbed anterior process considered characteristic of that genus.

Material.- 1 angulate element.

Occurrence.- Sample RKK-1-17m.

GEN. ET SP. INDET. G s.f.

Plate 5, Figure 14.

Description.- Segminate pectiniform element. Process tapers distally. Cusp directed posteriorly at about 45 degrees. Denticles on process (four) directed upward anteriorly; becoming inclined posteriorly. Posterior denticles on process curved. Denticles sharp and closely spaced. Basal cavity deep and wide.

Material.- 1 segminate element.

Occurrence.- Sample REV-4-8m.

Chapter 4

Concluding Remarks

- Four of the ten conodont zones erected by Krystyn (1980) can be recognized in strata from the Mamonia Complex. These are the *Neogondolella communis* morphotype A Zone (recognized only tentatively), the *Epigondolella abneptis* Assemblage Zone, the *Epigondolella spatulata* Assemblage Zone, and the Upper Bidentata Assemblage Zone.
- Minimum age ranges based on conodont faunas for Triassic sedimentary units of the Mamonia Complex can be made as follows: Petra tou Romiou Formation- uppermost Tuvalian (Carnian) to middle Lacian (Norian), and Vlambouros and Marona formations- middle Lacian to middle Rhaetian/Sevatician (Norian).
- The conodont zonation of Krystyn (1980) is likely to have had a strong paleoecologic overprint. It is important for future workers to attempt to establish Triassic conodont zonations for both shallow- and deep-water environments.
- Based on the occurrence of certain taxa in both deep- and shallow-water sediments, it is likely that at least some Norian conodont taxa were nektic in habit.
- Upper Triassic conodont provincialism was characterized by a high proportion of ramiform taxa in Tethyan sediments relative to North American faunas. As a result, Upper Triassic conodont provincialism cannot be used to determine the origin of, and direction of emplacement of, allochthonous nappes in the Eastern Mediterranean region.
- Multielement species were present in the Norian, and it is likely that some of the multielement ramiform taxa were of biostratigraphic significance.

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Plates

PLATE 1

Figures 1-5 - *Chirodella dinodooides* (Tatge). 1- Posterior view of digyrate element, sample RKK-1-23m, X110, 2- Inner lateral view of bipennate element, sample RKK-1-21m, X145, 3- Lateral view of bipennate element, sample RKK-1-21m, X125, 4- Lateral view of bipennate element, sample RKK-1-21m, X200, 5- Inner lateral view of bipennate element, sample RKK-1-21m, X110.

Figures 6-10 - *Chirodella erecta* Mosher. 6- Posterior view of digyrate element, sample RPA-1-3, X170, 7- Lateral view of bipennate element, sample RPA-1-3, X125, 8- Lateral view of bipennate element, sample RPA-1-3, X130, 9- Inner lateral view of bipennate element, sample RPA-1-3, X130, 10- Inner lateral view of bipennate element, sample RPA-1-3, X145.

Figures 11-15 - *Chirodella* sp. A. 11- Posterior view of digyrate element, sample RKK-1-8m, X125, 12- Inner lateral view of bipennate element, sample RKK-1-8m, X125, 13- Lateral view of bipennate element, sample RKK-1-8m, X115, 14- Lateral view of bipennate element, sample RKK-1-8m, X85, 15- Lateral view of bipennate element, sample RKK-1-8m, X150.

Figures 16-19 - *Chirodella* sp. B. 16- Posterior view of digyrate element, sample REV-4-18m, X130, 17- Outer lateral view of bipennate element, sample REV-4-18m, X130, 18- Lateral view of bipennate element, sample REV-4-18m, X130, 19- Outer lateral view of bipennate element, sample REV-4-18m, X120.



PLATE 2

Figures 1-5 - *Cornudina tortilis* Kozur and Mostler. 1- Inner lateral view of Pb element, sample RPR-1-1, X145, 2- Inner lateral view of Pa element, sample RPR-1-1, X165, 3- Inner lateral view of Sc element, sample RPR-1-1, X175, 4- Inner lateral view of Sb element, sample RPR-1-1, X175, 5- Outer lateral view of M element, sample RPR-1-1, X120.

Figures 6,7 - *Oncodella paucidentata* (Mostler). 6- Inner lateral view of dolabrate element, sample REV-3-1, X120, 7- Posterior view of alate element, sample RAE-3-1, X200.

Figures 8-13 - New Genus C New Species A. 8- Inner lateral view of Pa element, sample REV-4-8m, X170, 9- Posterior view of M element, sample REV-4-8m, X120, 10- Inner lateral view of Pb element, sample REV-4-8m, X120, 11- Inner lateral view of Sc element, sample REV-4-8m, X85, 12- Anterior view of Sb element, sample REV-4-18m, X180, 13- Oblique inner lateral view of Sa element, sample REV-4-8m, X200.

Figures 14-20 - *Cypridodella* sp. A. 14- Inner lateral view of Pa element, sample RKK-1-17m, X100, 15- Posterior view of Pb element, sample RKK-1-17m, X85, 16- Posterior view of Sb₁ element, sample RPH-4-1, X205, 17- Posterior view of Sb₂ element, sample RPH-4-1, X140, 18- Inner lateral view of M element, sample RKK-1-17m, X125, 19- Oblique inner lateral view of Sa element, sample RKK-1-17m, X170, 20- Inner lateral view of Sc element, sample RKK-1-17m, X130.



PLATE 3

Figures 1,2 - *Epigondolella abneptis* (Huckriede) s.f.. 1- Upper view, sample RKK-1-17m, X80, 2- Inner lateral view, sample RKK-1-17m, X90.

Figures 3,4 - *Epigondolella spatulata* (Hayashi) s.f.. 3- Inner lateral view, sample RKK-1-10m, X70, 4- Upper view, sample RKK-1-10m, X70.

Figures 5-8 - *Epigondolella* sp. A s.f.. 5- Upper view, sample RPR-1-1, X65, 6- Upper view, sample RPR-1-1, X60, 7- Upper view, sample RKK-1-2m, X60, 8- Upper view, sample RPR-1-1, X60.

Figures 9,10 - *Epigondolella postera* (Kozur and Mostler) s.f.. 9- Upper view, sample RKK-1-23m, X70, 10- Inner lateral view, sample RKK-1-23m, X70.

Figures 11,12 - *Epigondolella bidentata* Mosher s.f.. 11- Inner lateral view, sample REV-4-30m, X80, 12- Upper view, sample REV-4-30m, X80.

Figures 13-15 - New Genus B New Species A. 13- Inner lateral view, sample RKK-1-17m, X230, 14- Inner lateral view, sample RKK-1-17m, X180, 15- Inner lateral view, sample RKK-1-17m, X230.

Figures 16,17 - Gen. et sp. indet. C. 16- Inner lateral view of Pa element, sample RPH-4-1, X230, 17- Posterior view of M element, sample RPH-4-1, X160.

Figure 18 - Gen. et sp. indet. B. Inner lateral view, sample RKK-1-23m, X175.

Figure 19 - Gen. et sp. indet. D. Outer lateral view, sample REV-3-1, X170.

Figure 20 - Gen. et sp. indet. E. Inner lateral view, sample RAY-1-1, X160.

Figure 21 - Gen. et sp. indet. A. Inner lateral view, sample RKK-1-23m, X170.

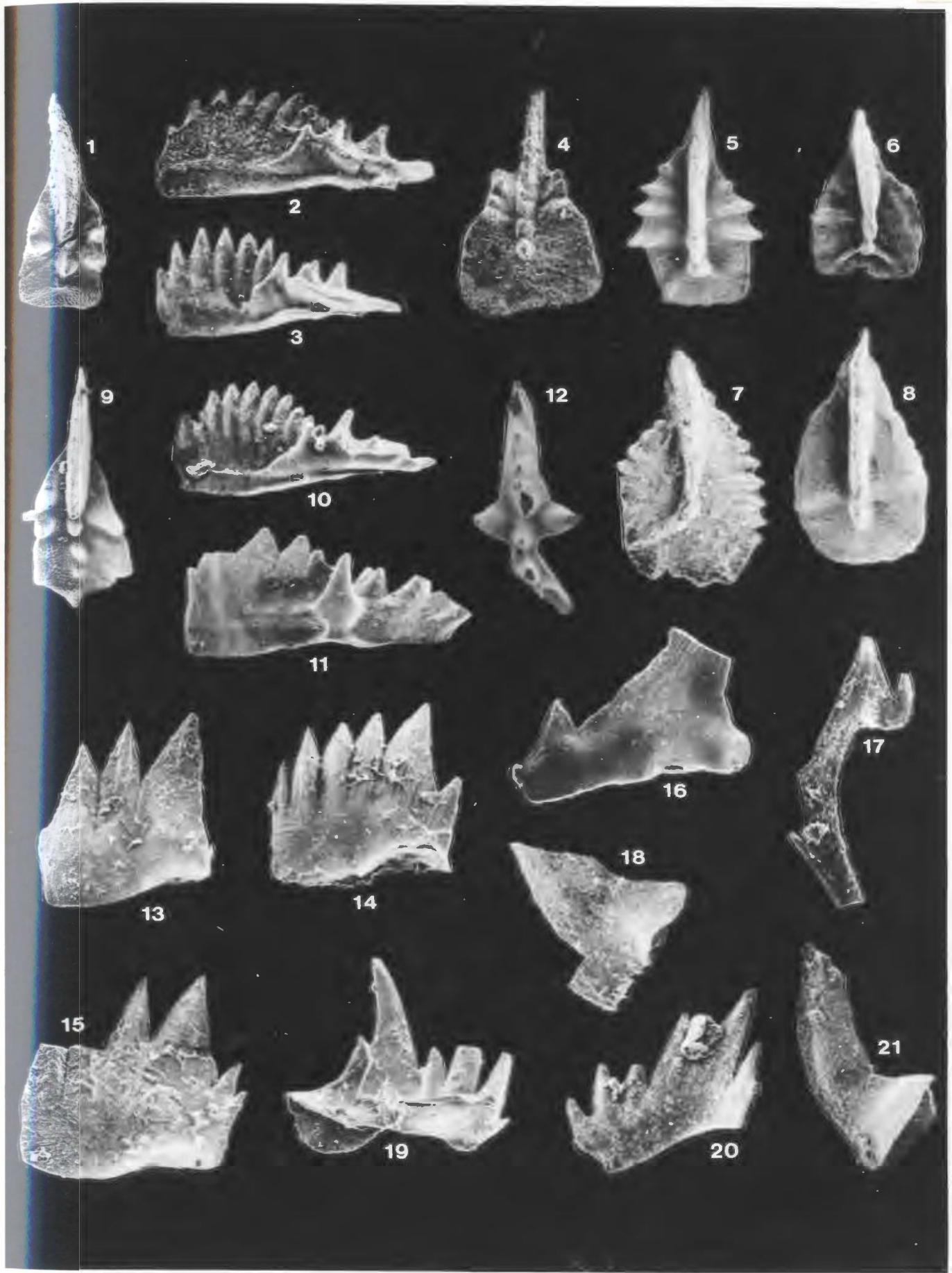


PLATE 4

Figures 1-3 - New Genus *A koessenensis* (Mostler). 1- Inner lateral view of Type 2 Asymmetric element, sample REV-4-8m, X155, 2- Inner lateral view of Type 1 Asymmetric element, sample REV-4-8m, X155, 3- Inner lateral view of Symmetric element, sample REV-4-8m, X165.

Figures 4-6 - New Genus *A hernsteini* (Mostler). 4- Inner lateral view of pectiniform element, sample REV-3-1, X215, 5- Inner lateral view of coniform element, sample REV-3-1, X240, 6- Inner lateral view of pectiniform element, sample REV-3-1, X185.

Figures 7-9 - New Genus *A posthernsteini* (Kozur and Mock). 7- Inner lateral view of pectiniform element, sample REV-3-1, X170, 8- Inner lateral view of coniform element, sample REV-3-1, X220, 9- Upper view of pectiniform element, sample REV-3-1, X150.

Figure 10 - New Genus *A* sp. cf. New Genus *A rhaetica* (Mostler) s.l., Inner lateral view, sample REV-3-1, X230.

Figures 11-15 - *Misikella longidentata* Kozur and Mock. 11- Inner lateral view of Pa element, sample REV-2-4, X105, 12- Posterior view of Sb element, sample REV-2-4, X90, 13- Inner lateral view of Pa element, sample REV-2-4, X115, 14- Inner lateral view of Sa element, sample REV-2-4, X65, 15- Inner lateral view of Sc element, sample REV-2-4, X100.

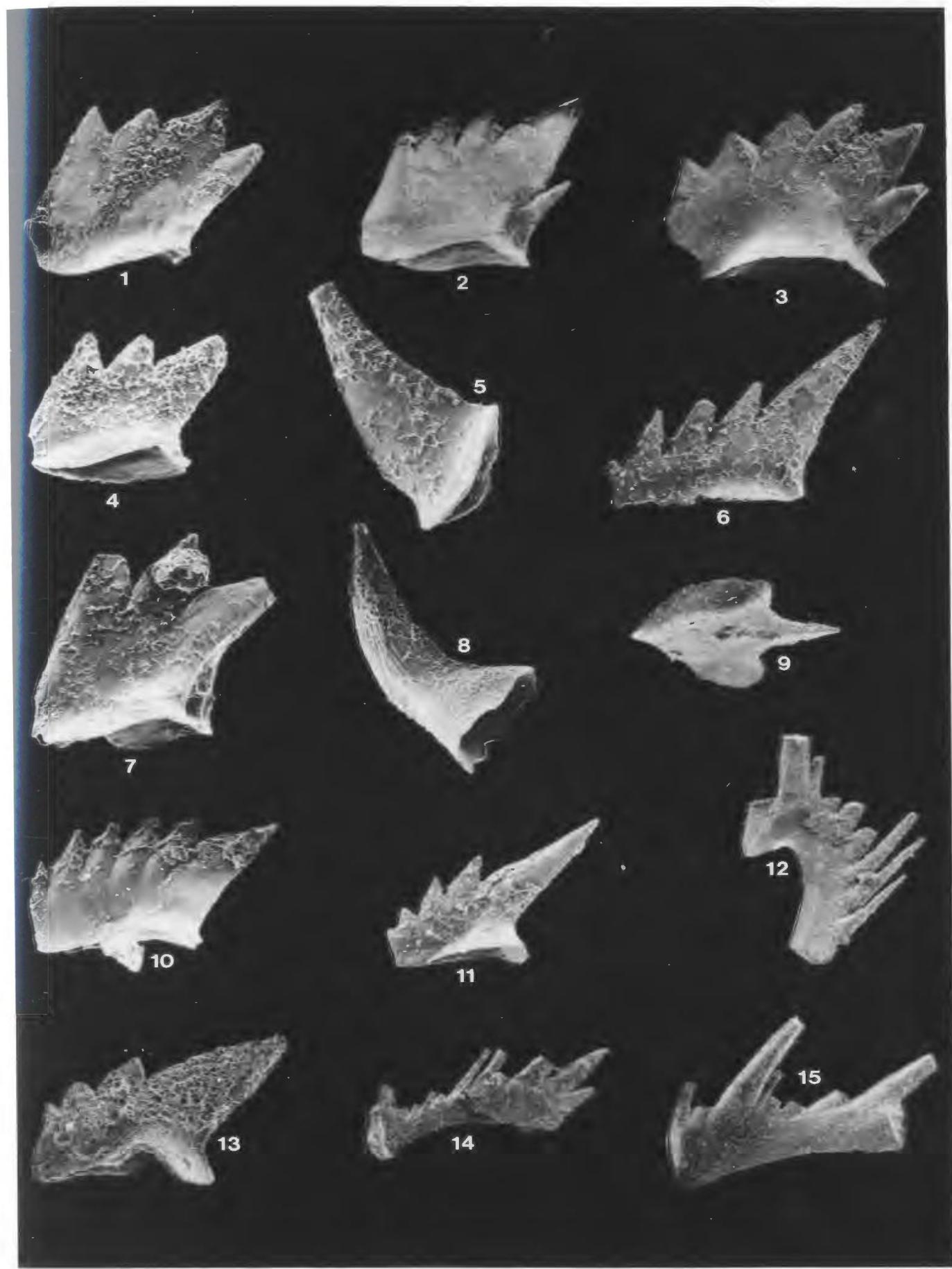


PLATE 5

Figures 1-6 - *Neogondolella steinbergensis* (Mosher). 1- Inner lateral view of Pa element, sample REV-4-30m, X75, 2- Inner lateral view of Pb element (note orientation), sample RAE-3-1, X150, 3- Inner lateral view of M element, sample RAE-3-1, X180, 4- Inner lateral view of Sa element, sample RAE-3-1, X145, 5- Posterior view of Sb element, sample RAE-3-1, X235, 6- Inner lateral view of Sc element, sample RAE-3-1, X155.

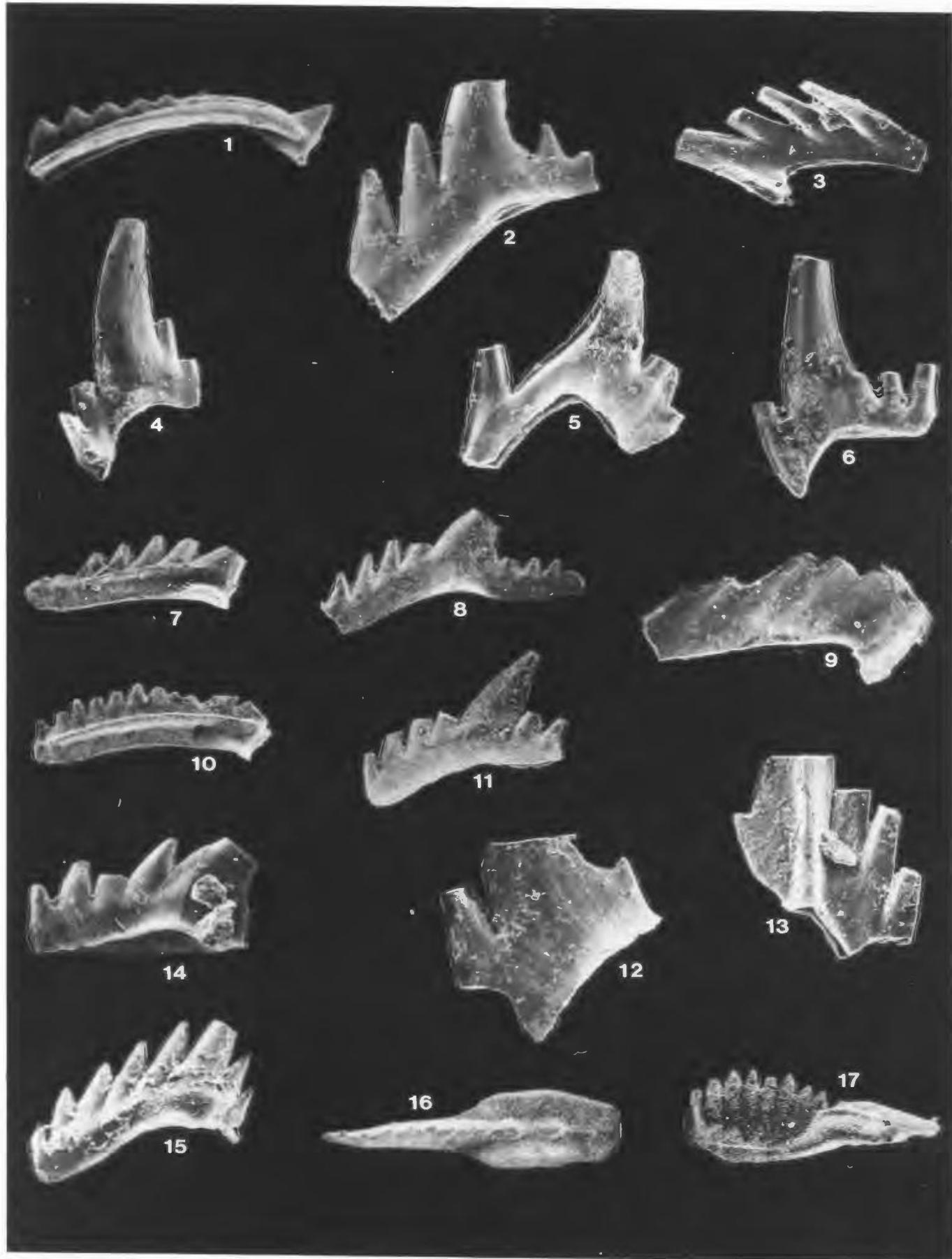
Figures 7,8 - *Neogondolella hallstattensis* (Mosher). 7- Inner lateral view of Pa element, sample RPA-1-0m, X90, 8- Inner lateral view of Pb element, sample RPA-1-0m, X125.

Figures 9-13 - *Neogondolella* sp. cf. *Neogondolella navicula* (Huckriede). 9- Outer lateral view of M element (note orientation), sample RPA-2-1, X165, 10- Inner lateral view of Pa element, sample RPA-1-1.5m, X80, 11- Inner lateral view of Pb element, sample RPA-1-1.5m, X135, 12- Inner lateral view of Sc element, sample RPA-1-1.5m, X290, 13- Posterior view of Sb element, sample RPA-1-1.5m, X245.

Figure 14 - Gen. et sp. indet. G. Inner lateral view, sample REV-4-8m, X145.

Figure 15 - Gen. et sp. indet. F. Inner lateral view, sample RKK-1-17m, X125.

Figures 16,17 - *Neogondolella communisti* Hayashi s.f.. 16- Upper view, sample REV-2-3, X85, 17- Inner view, sample REV-2-3, X70.



Appendix A

Sample Location Description

Collected localities have been given a Universal Transverse Mercator (UTM) grid reference. All grid references stated below have the prefix 36SVD, which has not been listed. Grid data have been taken from 1:50,000 topographic maps of Cyprus (Edition I-GSGS, Series 17, Sheets 16, 17, and 22), published by D. Survey, Ministry of Defence, United Kingdom, 1973, and are available from the Cyprus Geological Survey. Figure references refer to sample locality maps (Figs. 1-9 to 1-13, pages 23 to 27).

Locality- RAE-1. (Fig. 1-12). Grid Reference- 713498; Locality Description-

Outcrop situated on north side of road between Ayios Yeoryios and Ayios Elias, approximately 1 km west of Ayios Elias; Outcrop Description- Folded red shale outcrop on northwest side of road, with minor limey chert beds. Samples collected starting at northeast end of outcrop; Collected Samples- RAE-1-1, limey chert; RAE-1-2, limey chert; RAE-1-3, green limey sandstone. No recognizable stratigraphic relationship between samples; Unit- unknown.

Locality- RAE-2. (Fig. 1-12). Grid Reference- 713499; Locality Description-

Located up small track, to north of locality RAE-1, then turn right up second track after approximately 200m; Outcrop Description- Folded cherts and limestones in red shale; Collected Samples- RAE-2-1, located about 5m from north end of outcrop beside car park. 50cm thick calcarenite bed; RAE-2-2, calcilutite, located about 20m up the track on east side. No recognizable relationship between samples; Unit- unknown.

Locality- RAE-3. (Fig. 1-12). Grid Reference- 714503; Locality Description-

Approximately 100m further to northwest (past RAE-2) up track, on east side. Beds dipping about 25° to the east; Collected Samples- RAE-3-1, white calcarenite, unconformably overlying red shale; RAE-3-2, white calcarenite in red shale, located 20m down track from RAE-3-1; RAE-3-3, grey calcarenite located 2m down track from RAE-3-2; Unit- unknown.

Locality- RAE-4. (Fig. 1-12). Grid Reference- 714501; Locality Description-

Located at bend in track between localities RAE-2 and RAE-3; Outcrop Description- 11m thick strongly folded chert, limey chert, and shale sequence, within soft green siliciclastic sandstone; Samples collected from limey chert and shale units. Collected Samples- RAE-4-0m, RAE-4-1.5m, RAE-4-3m, RAE-4-5m, RAE-4-8m, RAE-4-11m; Unit- Marona Fm.

Locality- RAE-5. (Fig. 1-12). Grid Reference- 713497; Locality Description-

Located on south side of road between Ayios Yeryios and Ayios Elias, across the road from track containing localities RAE-1 to RAE-4; Outcrop Description- White calcarenite, within soft green siliciclastic sandstone; Collected Sample- RAE-5-1; Unit- Marona Fm.

Locality- RAY-1-1. (Fig. 1-12). Grid Reference- 691487; Locality Description-

Located beside road between Ayios Yeoryios and Ayios Elias, about 1km to the east of Ayios Yeoryios, to west of small streambed, about 10m north of road; Outcrop Description- 20cm thick bed of dark grey calcilutite exposed. Collected Sample- RAY-1-1; Unit- Marona Fm.

Locality- RAY-2 (Fig. 1-12). Grid Reference- 693487; Locality Description-

located about 150m to east of locality RAY-1-1, about 35m north of road; Outcrop Description- small 25cm thick outcrop of dark grey calcilutite. Collected Sample- RAY-2-1; Unit- Marona Fm.*

Locality- RAY-3 (Fig. 1-12). Grid Reference- 694488; Locality Description-

Located about 250m east of locality RAY-2, about 25m to north of road; 50m west of streambed; Outcrop Description- 3m thick unit of dark grey calcilutite (5-15cm thick beds), ?*Halobia* spp.; Collected Samples- RAY-3-1A, RAY-3-1B; Unit- Marona Fm.

Locality- RDR-1 (Fig. 1-9). Grid Reference- 455701; Locality Description- Located at roadcut between Drousha and Prodhromi, about 1.5km north of Drousha. Located on north side of road on north side of sweeping corner to east (gorge on inner side of corner); Outcrop Description- Red limestone unit bed between two pillow lava units. Top pillow lava is green, while lower is purple; Collected Samples- RDR-1-1, RDR-1-2, RDR-1-3, all from approximately same stratigraphic interval; Unit- "Kholetria Member".

Locality- RDR-2 (Fig. 1-9). Grid Reference- 456698; Locality Description- Located on northeast side of road, 200m toward Drousha from locality RDR-1, near beehives. Outcrop cannot be seen from road. Located across road from a thick outcrop of green sandstone; Outcrop Description- 2.6m thick block of white calcarenite and pink chert. 0-0.8m is chert, 0.8-2.4m is calcarenite, 2.4-2.6m is chert. Limestone and chert beds both 20-50cm thick. Cherts are highly fractured; Collected Samples- RDR-2-1m, RDR-2-2m; Unit- unknown.

Locality- REV-1 (Fig. 1-11). Grid Reference- 567505; Locality Description- Located across road from the base of the large block of white limestone at Episkopi. Collected sample is from jumble of blocks on east side of road; Outcrop Description- Sample (REV-1-1) collected from largest uncovered block of white partially recrystallized limestone; Unit- Petra tou Romiou Fm.

Locality- REV-2 (Fig. 1-11). Grid Reference- 568505; Locality Description- Large block of Petra Tou Romiou limestone at Episkopi; Outcrop Description- sample REV-2-1 collected from 5m above road level, midway between two

telephone poles at north end of outcrop; REV-2-2 collected 60m to north of REV-2-1, past fractured interval- possibly different block of limestone; REV-2-3, collected from 2m above level of road, 20m north of most southern exposure of block; REV-2-4 collected 180m from north end of exposure, about 2m above level of road; REV-2-5, collected at southern end of outcrop, about 20m above level of road; REV-2-6, collected at southern end of outcrop 40m above road level; Unit- Petra tou Romiou Fm.

Locality- REV-3 (Fig. 1-11). Grid Reference- 565-495; Locality Description- Located about 1km along track running south from Episkopi, on east side of road, past two closely spaced streams; Outcrop Description- 40cm thick dark grey calcilutite unit, within outcrop of green siliciclastic sandstone. Thin shale unit (10cm) at base of calcilutite; Collected Sample- REV-3-1; Unit- Vlambouros Fm.

Locality- REV-4 (Fig. 1-11). Grid Reference- 560-490; Locality Description- Located about 2km along track running south from Episkopi, on west side of road. Road curves to left and then right. Outcrop located on right hand portion of corner; Outcrop Description- Overturned sequence of carbonate cemented siliciclastic sandstones, calcarenites, and calcilutites dipping at 37° to N20° E. Samples collected starting at south end of outcrop (i.e. top), measured downwards from thick shale unit at top of outcrop; Collected Samples- REV-4-1.5m, REV-4-8m, REV-4-18m, REV-4-30m; Unit- Vlambouros Fm.

Locality- RKK-1 (Fig. 1-9). Grid Reference- 404703; Locality Description- Located on track to southwest of Phasli. Outcrop located on north side of track; Outcrop Description- 23m thick sequence of interbedded marls, sandy shales, and calcilutites, dipping at 45° at N30° W. Samples collected from marls and shales; Collected Samples- RKK-1-0m, RKK-1-2m, RKK-1-3.5m, RKK-1-4.5m, RKK-1-6m, RKK-1-8m, RKK-1-10m, RKK-1-12m, RKK-1-17m, RKK-1-19m, RKK-1-21m, RKK-1-23m; Unit- Marona Fm.

Locality- RKK-2 (Fig. 1-9). Grid Reference- 394692; Locality Description-

Located off track about 2km south of locality RKK-1, outcrop located about 200m to east of road down footpath; Outcrop Description- 4m thick exposure of thinly bedded (1-20cm) recrystallized calcilutite. Beds dipping 35° at N5° E; Collected Samples- RKK-2-0.5m, RKK-2-2m, RKK-2-3.5m; Unit- ?Marona Fm.

Locality- RKK-3 (Fig. 1-9). Grid Reference- 395693; Locality Description-

Located 4m above locality RKK-2, separated by a covered interval; Outcrop Description- 7m of red recrystallized (10-25cm thick bedded) calcilutite, with thin (5-10cm) interbeds of pink siliceous calcarenite; Collected Samples- RKK-3-1, collected from base of outcrop, RKK-3-2 collected from top of outcrop; Unit- ?Marona Fm.

Locality- RKK-4 (Fig. 1-9). Grid Reference- 402698; Locality Description-

Located 1km south of RKK-1, about 300m to the east of the track. Bearing from top of section to Cape Drepanum is S15° W; Outcrop Description- 30m thick outcrop of red and white cherts and recrystallized calcilutites. Outcrop unconformably overlies a green pillow lava unit. Samples collected from both pink and white units; Collected Samples- RKK-4-0m, RKK-4-3m, RKK-4-6m, RKK-4-9m, RKK-4-12m, RKK-4-15m RKK-4-18m, RKK-4-21m, RKK-23m, RKK-4-24m, RKK-4-27m; Unit- ?Marona Fm.

Locality- RKR-1 (Fig. 1-13). Grid Reference- 657394; Locality Description-

Located up track running south of, and roughly parallel to, Dhiarizos River, on south side, at entrance to Quarry; Outcrop Description- 18m of predominantly green siliciclastic sands, with minor occasional interbeds of 5-15cm thick calcilutites (increasing in volume up section). Section measured from northeast end of exposure. Sample collected at 17m (RKR-1-17m) from red-weathering, grey calcarenite bed; Unit- Vlambourou Fm.

Locality- RKR-2 (Fig. 1-13). Grid Reference- 653401; Locality Description-

Sample RKR-2-0 collected from loose block of white calcilutite located about 300m up stream bed in gorge on northern side side of the Dhirizos River; Unit- Petra tou Romiou Fm.

Locality- RMD-2 (Fig. 1-10). Grid Reference- 455581; Locality Description-

Section located about 3.5km up track from main road, on north side, at junction with track down to dam. Base of section located 100m from the road. Outcrop Description- Beds dipping 23° at N30° E. 15m thick section of 5-10cm thick beds of interbedded cherts and siliceous calcilutites. Base of section is a thin, red calcilutite bed. Collected Samples- RMD-2-0.1m, RMD-2-2m, RMD-2-3m, RMD-2-4.5m, RMD-2-1km, RMD-2-12.5m RMD-2-14m, RMD-2-14.5m; UNit- Episkopi Fm.

Locality- RNK-1 (Fig. 1-12). Grid Reference- 625468; Locality Description-

Locality on north side of track from Kholetria from Nea Kholetria, 800m from road near Nea Kholetria; Outcrop Description- 4m thick block of white recrystallized limestone, unconformably overlying purple pillowlavas. Collected Sample- RNK-1-1; Unit "Kholetria Member".

Locality- RNK-2 (Fig. 1-12). Grid Reference- 637478; Locality Description-

Roadcut 1km north of Nea Kholetria on east side of road; Outcrop Description- Roadcut consists primarily of pillow lavas. Thin units of calcilutite present up to 20cm thick; Sample RNK-2-1 collected from about 2m above road; Unit "Kholetria Member".

Locality- RNK-3 (Fig. 1-12). Grid Reference- 644479; Locality Description- On

track from north of Nea Kholetria to Phasoula. On north side of track about 300m from northwest end; Outcrop Description- Interstitial calcilutites in green (RNK-3-1) and purple (RNK-3-2) porphyritic lavas; Unit "Kholetria Member".

Locality- RNK-4 (Fig. 1-12). Grid Reference- 643479; Locality Description- Across track and slightly to west of RNK-3; Outcrop Description- Interstitial limestones in purple porphyritic pillow lavas; Collected Samples- RNK-4-1, RNK-4-2, RMK-4-3; Unit "Kholetria Member".

Locality- RNK-5 (Fig. 1-12). Grid Reference- 645478; Locality Description- Collected from loose blocks of light brown calcilutite 200m towards Phasoula from locality RNK-4; Outcrop Description- 3 blocks sampled. Samples RNK-5-5, and RNK-5-5 (largest block) from separate blocks. RNK-5-2, RNK-5-3, RNK-5-4 from same block. Block triangular in upper view, samples collected from 3 corners; Unit- Petra tou Romiou Fm.

Locality- RNK-6 (Fig. 1-12). Grid Reference- 638466; Locality Description- Sample collected from track running from south of Nea Kholetria to Phasoula. From Phasoula, travel along track which runs past limestone crusher, take first left. Samples collected 1.5km from Phasoula, on north side of track; Outcrop Description- Grey calcilutite overlying purple pillow lavas; Collected Sample- RNK-6-1; Unit "Kholetria Member".

Locality- RPA-1 (Fig. 1-9). Grid Reference- 433696; Locality Description- Section located on road between Drousha and Phasli, just north of hill with antenna on it on southwest side of road. bearing to antenna form outcrop is S20° W; Outcrop Description- Outcrop 3.5m thick consisting of thin (10cm±0 beds of dark grey calcilutite and red and cream shale units. Sample RPA-1-0m from base; 1.3m of red and cream shale, overlain by thin beds of calcilutite (sample RPA-1-1.5m). RPA-1-3.5m is collected at top of outcrop; Unit- Marona Fm.

Locality- RPA-2 (Fig. 1-9). Grid Reference- 430709; Locality Description- 800m south of Phasli on same track as RPA-1, on south side, about 50m from track; Outcrop Description - Loose block of white calcarenite; Collected Sample- RPA-2-1; Unit- unknown.

Locality- RPH-1 (Fig. 1-12). Grid Reference- 640450; Locality Description- Roadcut on northwest side of road, 3km south of Phasoula; Outcrop Description- Convex up folded sequence of cherts, shales and calcilutites. About 11m of section exposed. Basal 10m collected, top 1m very convoluted and fractured shales. Shales 1-50cm thick, cherts and limestones 1-15cm; Collected Samples- RPH-1-0m, RPH-1-2m, RPH-1-6m, RPH-1-7.5m, RPH-1-10m; Unit- unknown.

Locality- RPH-2 (Fig. 1-12). Grid Reference- 657468; Locality Description- Pillow lava outcrop on hill overlooking Phsaoula. Outcrop Description- Interstitial calcilutites from orange-rimmed pillow lavas; Collected Samples- RPH-2-1, RPH-2-2; Unit- "Kholetria Member".

Locality- RPH-3 (Fig. 1-12). Grid Reference- 656469; Locality Description- Outcrop of pillow lavas to northwest of RPH-2; Outcrop Description- Interstitial calcilutites from orange-rimmed pillow lavas; Collected Samples- RPH-3-1, RPH-3-2, RPH-3-3; Unit- "Kholetria Member".

Locality- RPH-4 (Fig. 1-12). Grid Reference- 643464; Locality Description- Track to south of Phasoula to limestone crusher, take first left, about 1.1km up track. 200m south of track on hill; Outcrop Description- Thin 20cm thick outcrop, forming top of hill, of dark grey calcilutite; Collected Sample- RPH-4-1; Unit- Marona Fm.

Locality- RPL-1 (Fig. 1-12). Grid Reference- 647477; Locality Description- 200m southeast of sample RNK-5, on north side of road; 1.7km from Phasoula, on track to just norht of Nea Kholetria; Outcrop Description- White interstitial calcilutite from purple porphyritic pillow lavas; Collected Sample- RPL-1-1; Unit "Kholetria Member".

Locality- RPR-1 (Fig. 1-13). Grid Reference- 658360; Locality Description- Sample collected from Petra tou Romiou; Outcrop Description- Large block

of white recrystallized limestone, sample RPR-1-1 collected about 1m from top of block on northnorthwest side; Unit- Petra tou Romiou Fm.

Locality- RPS-1 (Fig. 1-9). Grid Reference- 425689; Locality Description- At Y junction in track just southwest of hill with antenna; Outcrop Description- loose blocks of limestone just above a 2m thick chert outcrop; Collected Samples- RPS-1-1, RPS-1-2; Unit- unknown.

Appendix B

Sample Information

The following table provides sample information regarding those samples collected in this study. Information concerning the location of the samples is given in Appendix A. Descriptions of the lithotypes referred to are outlined in Appendix C.

Sample Information				
Sample	Lithotype	Environment	Conodonts	Formation
RAE-1-2	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	not processed	?
RAE-1-3	peloidal intrasparite	shelf	not processed	?
RAE-2-1	peloidal intrasparite	shelf	none	?
RAE-2-2	bioclastic/ lithoclastic packstone	turbiditic pelagic	not processed	?
RAE-3-1	bioclastic/ lithoclastic packstone	turbiditic pelagic	210	Marona
RAE-3-2	bioclastic/ lithoclastic packstone	turbiditic pelagic	none	Marona?
RAE-3-3	bioclastic/ lithoclastic packstone	turbiditic pelagic	none	Marona?

RAE-4-0m	calcareous chert	laminated pelagic	none	Marona
RAE-4-1.5m	calcareous chert	laminated pelagic	none	Marona
RAE-4-5m	calcareous shale	laminated pelagic	3	Marona
RAE-4-8m	calcareous shale	laminated pelagic	none	Marona
RAE-4-11m	calcareous shale	laminated pelagic	none	Marona
RAE-5-1	bioclastic/lithoclastic packstone	turbiditic pelagic	7	Vlambouros
RAY-1-1	radiolarian mudstone/wackestone/packstone	laminated pelagic	117	Marona
RAY-2-1	radiolarian mudstone/wackestone/packstone	laminated pelagic	152	Marona
RAY-3-1A	radiolarian mudstone/wackestone/packstone	laminated pelagic	145	Marona
RAY-3-1B	radiolarian mudstone/wackestone/packstone	laminated pelagic	29	Marona
RDR-1-1	sparite	laminated pelagic	2	"Kholetria Member"
RDR-1-2	calcareous chert	laminated pelagic	1	"Kholetria Member"
RDR-1-3	calcareous chert	laminated pelagic	1	"Kholetria Member"
RDR-2-1m	peloidal intrasparite	shelf	none	?

RDR-2-2m	peloidal intrasparite	shelf	2	?
REV-1-1	boundstone/ bafflestone	reef	7 none	Petra tou Romiou
REV-2-1	bioclastic grainstone/ floatstone	reef	3	Petra tou Romiou
REV-2-2	bioclastic grainstone/ floatstone	reef	1	Petra tou Romiou
REV-2-3	bioclastic grainstone/ floatstone	reef	6	Petra tou Romiou
REV-2-4	boundstone/ bafflestone	reef	20	Petra tou Romiou
REV-2-5	bioclastic grainstone/ floatstone	reef	1	Petra tou Romiou
REV-2-6	boundstone/ bafflestone	reef	none	Petra tou Romiou
REV-3-1	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	1134	Vlambouros
REV-4-1.5m	bioclastic/ lithoclastic packstone	turbiditic pelagic	33	Vlambouros
REV-4-8m	bioclastic/ lithoclastic packstone	turbiditic pelagic	316	Vlambouros
REV-4-18m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	251	Vlambouros
REV-4-30m	bioclastic/ lithoclastic packstone	turbiditic pelagic	102	Vlambouros

RKK-1-0m	calcareous chert	laminated pelagic	30	Marona
RKK-1-2m	radiolarian mudstone/wackestone/packstone	laminated pelagic	74	Marona
RKK-1-3.5m	radiolarian mudstone/wackestone/packstone	laminated pelagic	158	Marona
RKK-1-4.5m	radiolarian mudstone/wackestone/packstone	laminated pelagic	180	Marona
RKK-1-8m	radiolarian mudstone/wackestone/packstone	laminated pelagic	8	Marona
RKK-1-8m	radiolarian mudstone/wackestone/packstone	laminated pelagic	230	Marona
RKK-1-10m	radiolarian mudstone/wackestone/packstone	laminated pelagic	110	Marona
RKK-1-12m	radiolarian mudstone/wackestone/packstone	laminated pelagic	20	Marona
RKK-1-14m	radiolarian mudstone/wackestone/packstone	laminated pelagic	5	Marona
RKK-1-17m	radiolarian mudstone/wackestone/packstone	laminated pelagic	548	Marona

RKK-1-19m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	32	Marona
RKK-1-21m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	70	Marona
RKK-1-23m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	179	Marona
RKK-2-2m	calcareous chert	laminated pelagic	not processed	Marona?
RKK-2-3.5m	calcareous chert	laminated pelagic	4	Marona?
RKK-3-1	calcareous chert	laminated pelagic	none	Marona?
RKK-4-0m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	1	Marona?
RKK-4-3m	calcareous chert	laminated pelagic	1	Marona?
RKK-4-6m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	2	Marona?
RKK-4-9m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	1	Marona?
RKK-4-12m	calcareous chert	laminated pelagic	15	Marona?
RKK-4-15m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	1	Marona?

RKK-4-18m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	none	Marona?
RKK-4-21m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	none	Marona?
RKK-4-24m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	none	Marona?
RKK-4-27m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	none	Marona?
RKR-1-17m	bioclastic/ lithoclastic packstone	turbiditic pelagic	I	Vlamboulos
RKR-2-0	whole-fossil packstone	shelf	none	Patra - ton Romiou
RMD-2-0m			none	Episkopi
RMD-2-2m			none	Episkopi
RMD-2-12.5m			none	Episkopi
RMD-2-14m			none	Episkopi
RNK-2-0.5m			none	*Kholetria Member*
RNK-2-1m			none	*Kholetria Member*
RNK-3-2	interpillow carbonate	laminated pelagic	none	*Kholetria Member*
RNK-4-1	interpillow carbonate	laminated pelagic	none	*Kholetria Member*
RNK-4-2	interpillow carbonate	laminated pelagic	none	*Kholetria Member*
RNK-4-3	interpillow carbonate	laminated pelagic	none	*Kholetria Member*

RNK-5-1	bioturbated peloidal mudstone/ wackestone	shelf	none	Petra tou Romiou
RNK-5-2	bioturbated peloidal mudstone/ wackestone	shelf	none	Petra tou Romiou
RNK-5-3	bioturbated peloidal mudstone/ wackestone	shelf	none	Petra tou Romiou
RNK-5-4	bioturbated peloidal mudstone/ wackestone	shelf	none	Petra tou Romiou
RNK-5-5			none	Petra tou Romiou
RNK-6-1			none	"Kholetria Member"
RPA-1-0m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	23	Marona
RPA-1-1.5m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	160	Marona
RPA-1-3.5m	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	224	Marona
RPA-2-1	radiolarian mudstone/ wackestone/ packstone	laminated pelagic	9	?
RPH-1-0m	calcareous shale	laminated pelagic	none	?

RPH-1-6m	calcareous shale	laminated pelagic	none	?
RPH-1-7.5m	calcareous shale	laminated pelagic	none	?
RPH-1-10m	calcareous shale	laminated pelagic	none	?
RPH-2-1	interpillow carbonate	laminated pelagic	none	"Kholetria Member"
RPH-2-2	interpillow carbonate	laminated pelagic	none	"Kholetria Member"
RPH-3-1	interpillow carbonate	laminated pelagic	none	"Kholetria Member"
RPH-3-2	interpillow carbonate	laminated pelagic	none	"Kholetria Member"
RPH-4-1	radiolarian mudstone/wackestone/packstone	laminated pelagic	167	Marona
RPL-1-1	interpillow carbonate	laminated pelagic	none	"Kholetria Member"
RPR-1-1	bioclastic grainstone/floatstone	reef	35	Petra tou Romiou
RPS-1-1	bioclastic/lithoclastic packstone	turbiditic pelagic	none	?
RPS-1-2	bioclastic/lithoclastic packstone	turbiditic pelagic	none	?

Appendix C

Lithotype Descriptions

Characteristics noted during petrographic study of the collected samples include depositional fabric and texture, matrix type, clast types and their relative proportions, and detrital grains. Diagenetic features were not studied in detail, as this was beyond the scope of the project. Standard thickness thin-sections were stained with an Alizarin Red S and potassium ferricyanide solution. Polished surfaces of certain thin-sections were examined using cathode-luminescence.

The textural classification used in this study is the modification of Dunham (1962) proposed by Embrey and Klovan (1971). Description of authigenic quartz follows that outlined by Folk and Pittman (1971); microquartz refers to equant crystals less than 20 μm size, whereas megaquartz is coarser than 20 μm .

Because of the small numbers of samples available, it was not possible to perform formal microfacies analysis (e.g. see Flügel, 1972; 1982; Wilson, 1975). Instead, ten petrographically distinct lithotypes are defined.

C.1. Radiolarian mudstone/wackestone/packstone

In this lithotype, the micrite matrix averages 65%, but may reach 95%. Bioclasts present are radiolarian tests, filaments (very thin calcitic skeletal grains, which according to Flügel (1982), probably represent larval stages of mollusks), and sponge spicules. Radiolaria (predominantly spumellarians) occur in all samples and are calcite and/or chert filled. Filaments may be common. Sheltered undersides of filaments often exhibit sparry calcite cement filling

(umbrella effect). Sponge spicules (primarily monad) are rare to common in abundance (though always subordinate in volume to radiolaria). The variation in radiolarian and sponge spicule abundance defines 1cm scale parallel laminations.

Rare detrital quartz (<0.1mm) is found in some samples, and occasionally occurs as concentrated units. Silicification, often in the form of nodular chert, may be present and can be seen to cross-cut lamination. Bioturbation may be pronounced, and burrows are filled by either microsparite or a more radiolarian-rich sediment.

Neomorphic sparite is characteristic of some samples, and in these instances is the predominant component. The large neomorphic sparite crystals are often patchy and twinned, and are not interpreted to be fracture or vein fills. Neomorphic origin is indicated by the presence of inclusions with ghost fabrics and textures, such as pellets and radiolarian tests. Stylolites are common, with 0.1mm thick (average) accumulations of insoluble minerals. Samples often display calcite- and chert-filled fractures, and the latter may contain 0.1mm-sized Fe-dolomite rhombs. 32 Samples.

C.2. Calcareous chert

This lithotype is characterized by partial or total chert replacement of mudstone/wackestone. The chert is primarily microquartz and may be banded with clay impurities. The rock is frequently fractured, with fractures filled with calcite which has grown at the expense of the chert host rock. Ghosts of radiolaria and pellets may be present. Because this lithotype did yield conodonts (5 samples), some of the calcite may represent altered mudstone. 10 Samples.

C.3. Calcareous shale

This type has a matrix of unidentified clay minerals and/or micrite. Radiolaria and/or sponge spicules are present, and may be the predominant component (up to about 80% of rock). Radiolaria may be calcite or chert filled. Parallel laminations reflect variations in radiolarian/songe spicule abundance. 7 samples.

C.4. Interpillow limestone

This type is composed of two groups, one of which is composed primarily of sparite (>80%), with minor amounts of clay minerals, micrite, chert, and radiolaria. The other is characterized by a micrite matrix (>75%), with minor filaments, sponge spicules, pellets, and echinoderm fragments. None of these samples yielded conodonts. 8 samples.

C.5. Bioclastic/lithoclastic packstone

These samples are characterized by moderately- to well-rounded, and poorly- to well-sorted, clasts. Many samples show grading on a 1cm scale. Rare crossbedding and preferred orientation of clasts is seen. This lithotype may be lithoclast or bioclast dominated, and may have a matrix of micrite, chert, or clay minerals.

Lithoclast dominated samples are composed of a relatively high proportion (20-60%) of quartz lithoclasts and detrital grains, which range in size from 0.05-0.5mm, and have a micrite matrix (5-35%). Pellets and intraclasts are the predominant carbonate particles with rare foraminifera, bryozoa, echinoderm fragments, and algae. Micrite matrix ranges from 5-35% of rock volume.

Bioclast dominated samples have a low percentage (5%) of quartz grains and a cherty micrite matrix. Pellets and intraclasts are very common (20-35% and 10-30%, respectively). Echinoderm fragments are the dominant bioclast type,

with rare foraminifera, bivalve fragments, bryozoa, and ooids. Grain size averages 0.2mm.

Some other samples are characterized by a matrix of unidentified clay minerals, averaging 25% of the rock volume. Intraclasts, pellets, and echinoderm fragments are the most dominant clast types, with minor gastropods, foraminifera, algae, bryozoa, bivalves, and detrital quartz. Clasts may show preferred orientation, and some replacement by chert. 11 samples.

C.6. Boundstone/bafflestone

This lithotype is coral, calcisponge, and algae dominated, with a subordinate volume of serpulid worm tubes, which have micrite envelopes and which are often sparite filled. No detrital quartz is present, but rare void-filling microquartz is seen. Encrusting algae may impart a laminated fabric. Bioclasts are rare planispiral foraminifera and echinoderm fragments. Stromatactis fabrics with geopetal fillings are present. 3 samples.

C.7. Bioclastic grainstone/floatstone

This group is composed of varying proportions of reef-derived bioclasts in a micrite, or microspar, matrix. Bioclasts are predominantly 1cm-sized coral, sponge, and serpulid worm tube fragments, with subordinate echinoderm and bivalve fragments. Voids are filled by chert (microquartz) or fibrous calcite, and stromatactis fabrics are present. 5 samples.

C.8. Whole-fossil packstone

This lithotype is represented by only one sample. One complete gastropod (exhibiting good geopetal filling), and one complete bivalve (megalodont?) are present in this sample (bioturbated packstone). Pellets and lumps comprise the majority of the sediment, with minor ostracode shells. Detrital (windblown) quartz (0.1mm) composes <2% of the sample, but may be locally abundant.

C.9. Peloidal intrasparite

This type is a grainstone with sparite cement (5-15%). A wide variety of clast types, with an average size of 0.5mm, are present. Intraclasts and pellets are most abundant, and bioclasts include foraminifera, echinoderm fragments, algae, bryozoa, and ooids. Detrital quartz and chert are rare. The clasts are poorly- to moderately-sorted, and moderately-rounded. 4 samples.

C.10. Bioturbated peloidal mudstone/wackestone

Of the 4 samples assigned to this type, 3 are wackestone and 1 is mudstone. Pellets (10-15% of rock volume) average 0.2mm in size. Interiors of ostracodes and fenestrae (up to 10% and 15% of rock, respectively) are quartz and calcite filled, and may display geopetal fillings. Bioturbation may be very pronounced.

Appendix D

Distribution Table

The following table documents the distribution of conodont elements in each of the samples. Note: the order of the samples is not stratigraphic.



