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A REVISION OF AUSTRALIAN MESOZOIC AND CENOZOIC LUNGFISH OF THE FAMILY NEOCERATODONTIDAE (OSTEICHTHYES:DIPNOI), WITH A DESCRIPTION OF FOUR NEW SPECIES

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ABSTRACT—The taxonomy of the predominantly Australian fossil dipnoan genus, *Neoceratodus,* is revised and the Recent Australian lungfish, *Neoceratodus forsteri,* and two fossil species, *Neoceratodus eyrensis* and *Neoceratodus nargun,* are redefined. Two new species of the related Tertiary genus, *Mioceratodus,* are described on the basis of tooth plates from central and northern localities in Australia. These are *Mioceratodus diaphorus* and *Mioceratodus poastrus.* A new genus, *Archaeoceratodus,* is erected to include three rare Tertiary species and one Mesozoic species. The Tertiary members of this genus are the type species, *Archaeoceratodus djelleh,* described originally as *Neoceratodus djelleh,* and two new species, *Archaeoceratodus rowleyi* and *Archaeoceratodus theganus.* The Mesozoic species is *Archaeoceratodus avus* from Triassic and Cretaceous deposits in southeastern Australia, described originally as *Ceratodus avus.* All three genera belong in the family Neoceratodontidae.

INTRODUCTION

AUSTRALIA IS noted for an extensive fossil dipnoan fauna from Mesozoic and Cenozoic deposits (Kemp, 1991a; Wade, 1931) and for one surviving species of lungfish, the Recent *Neoceratodus forsteri.* Some of the fossil descriptions are based on fragments of scale or bone, definitely dipnoan but not referable to any known species because diagnostic features are missing (Chapman, 1912; Wade, 1935; Waldman, 1971). Several taxa are known from almost complete, laterally flattened animals (Kemp, 1994; Ritchie, 1981; Wade, 1935; Woodward, 1890) that cannot be correlated with species described from tooth plates and associated jaw bones because they have poorly preserved dentitions. This is unfortunate because most Australian Mesozoic and Cenozoic dipnoans have been defined from tooth plates (Chapman, 1914; Kemp, 1982a, 1983; Krefft, 1874; White, 1925, 1926; Woodward, 1906). Only three Australian fossil species have been described from both tooth plates, or their impressions, and bones of the skull, jaws, palate, and postcranial skeleton. These are *Mioceratodus gregoryi* (*Epiceratodus denticulatus*) (Hills, 1934), *Mioceratodus anemosyrus* (Kemp, 1992a), and *Ceratodus avus* (*Sagenodus laticeps*) (Woodward, 1908).

Collections of fossil lungfish from mid-Tertiary deposits in central and northern Australia have added a new genus and two species, *Mioceratodus anemosyrus* and *Mioceratodus gregoryi* (White, 1925) to the fauna of this continent (Kemp, 1992a). In this paper, two new species, *Mioceratodus diaphorus* and *Mioceratodus poastrus,* are added to this genus, and *M. anemosyrus* and *M. gregoryi* are defined on tooth plates. Both are found in central and northern Australian mid-Tertiary deposits. Species of *Mioceratodus* have elongate tooth plates with long curving ridges and an occlusal surface with complex punctations, including a hypermineralised dentine called petrodentine (Lison, 1941). Skull bones in species of this genus are similar in number and distribution to those of *Neoceratodus forsteri,* but their shapes differ (Kemp, 1992a).

A second new genus, *Archaeoceratodus,* is described to include *Neoceratodus djelleh* (Kemp, 1982a) and two additional new species, *Archaeoceratodus theganus* and *Archaeoceratodus rowleyi,* from Tertiary localities in central and eastern Australia. The Triassic and Cretaceous species, *Ceratodus avus* (Woodward, 1906, 1908), is referred to *Archaeoceratodus.* Tooth plates of this genus are characterized by extremely short ridges and complex punctation patterns on the occlusal face of the tooth plate. No skull bones have been found associated with tooth plates referable to *Archaeoceratodus.*

The genus *Neoceratodus,* which includes the Recent Australian lungfish, *Neoceratodus forsteri,* is redefined. *Neoceratodus eyrensis,* first described as *Epiceratodus eyrensis* by White (1925), and *Neoceratodus nargun,* described originally as *Ceratodus nargun* (Kemp, 1983), are the two fossil members of this genus.

Abbreviations are as follows: AM = Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; FV = Private collection, Terry Poole, Brisbane; HMV= Hunterian Museum, Glasgow; MMF = Mining and Metallurgical Museum, Sydney; MV = Museum of Victoria, Melbourne; NTM = Northern Territory Museum, Darwin; QM = Queensland Museum, Brisbane; SAM = South Australian Museum, Adelaide; UCMP = Museum of Vertebrate Paleontology, Berkeley.

BASIS FOR TAXONOMIC DETERMINATIONS

Terminology.—Terminology used in this description follows Kemp (1991b, 1992a).

Characters.—The taxonomic diagnoses and descriptions in this paper are based on a list of characters tested on specimens of *Neoceratodus forsteri,* the Recent Australian lungfish (Kemp, 1990). Large specimens from two localities (Figures 1, 2) and four different size classes from one locality (Figure 2) were used to determine the effects of environment and development on the structure of the jaw bones and tooth plates of *N. forsteri.* The list of characters of tooth plates and jaw bones has been modified to classify the Australian fossil material on the basis of characters found to be reliable in the living species.

Relatively few of the large number of potential characters could be used for taxonomic determination (Kemp, 1990). Many characters are affected by inherent variability and dietary and environmental factors. Stage of development also causes marked changes in the structure of the tooth plate. Other characters are the same over a wide variety of species. Additional characters, like divided or intercalated ridges, result from developmental abnormalities and should not be used for taxonomic purposes. Preservation of the fossil specimens also reduced the number of useable characters.

Characters valuable at a generic level in neoceratodonts are the size of the pulp cavity, the extent of mantle dentine visible on the occlusal surface, the origin of the ridges, the position of upper tooth plates in relation to each other, the shape of the

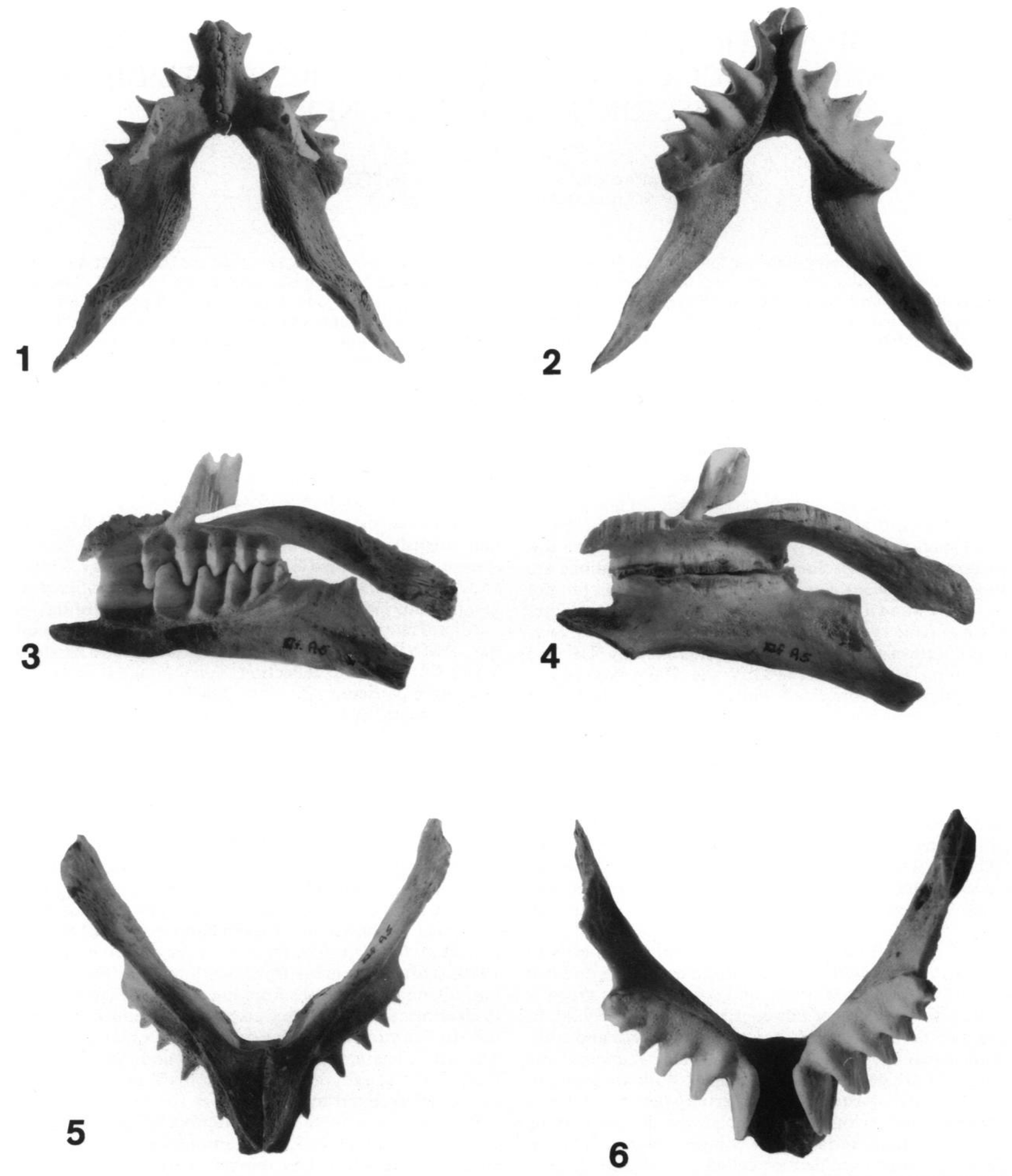


FIGURE 1—Matching upper and lower jaws of *Neoceratodus forsteri* from an adult specimen, Brisbane River (QM I 26016) showing tooth plate characters. *1*, abocclusal view of upper jaw bones; *2*, occlusal view of upper tooth plate and attached bones; *3*, labial view of tooth plates in occlusion; *4*, lingual view of tooth plates in occlusion; *5*, abocclusal view of lower jaw bones; *6*, occlusal view of lower tooth plates and jaw bones. Scale line = 2 cm.

upper and lower symphyses, the presence of the ascending pterygopalatine process, the form of the sulcus below the prearticular bone, and the presence of petrodentine sensu strictu (Lison, 1941). Characters valid at a specific level are the pattern of punctations, with or without petrodentine, on the occlusal surface, the presence or absence of a procumbent keel on the mediolingual junction, the shape of the mediolingual face of the tooth plate, the shape of ridge 1 in upper and lower tooth plates,

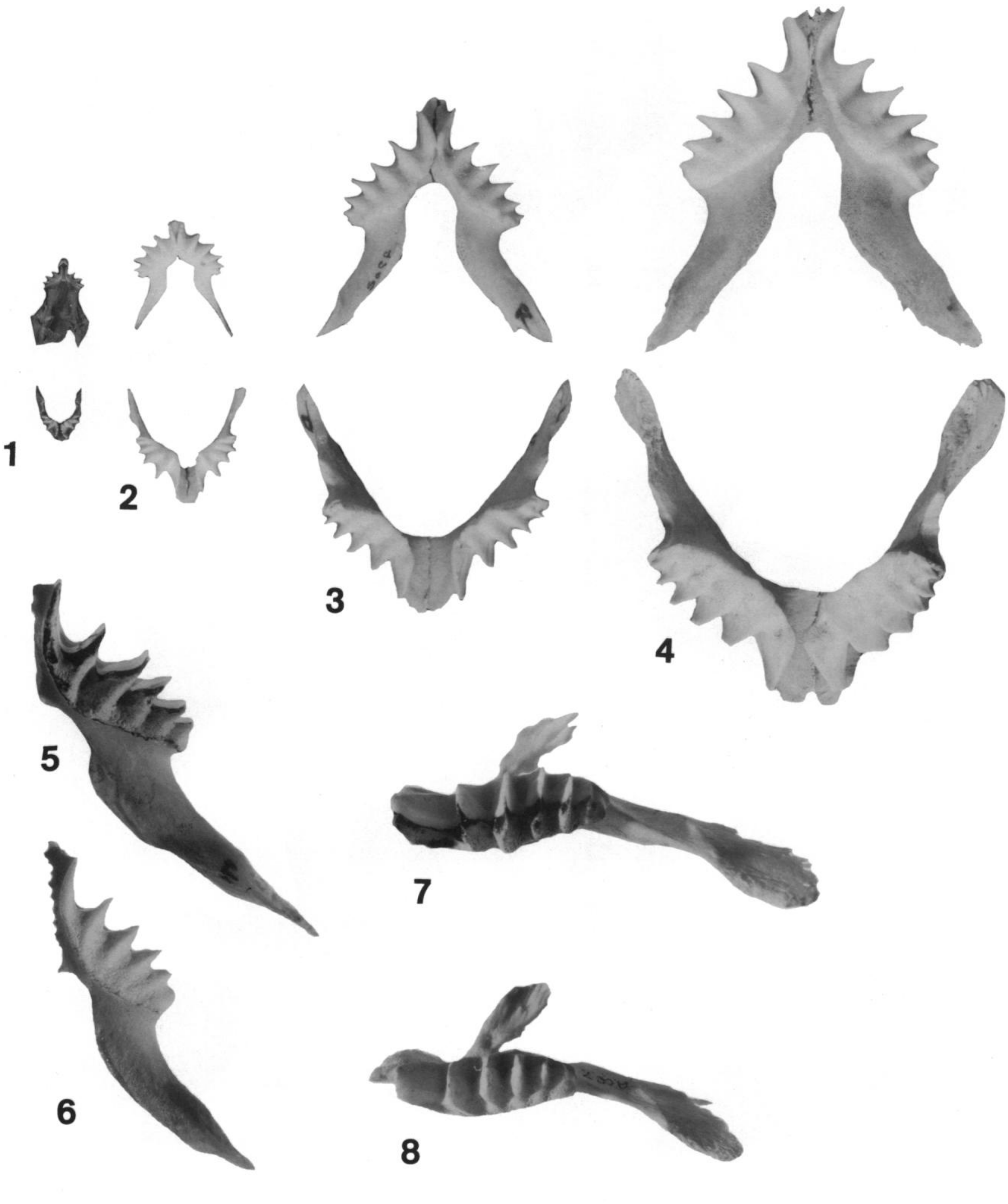
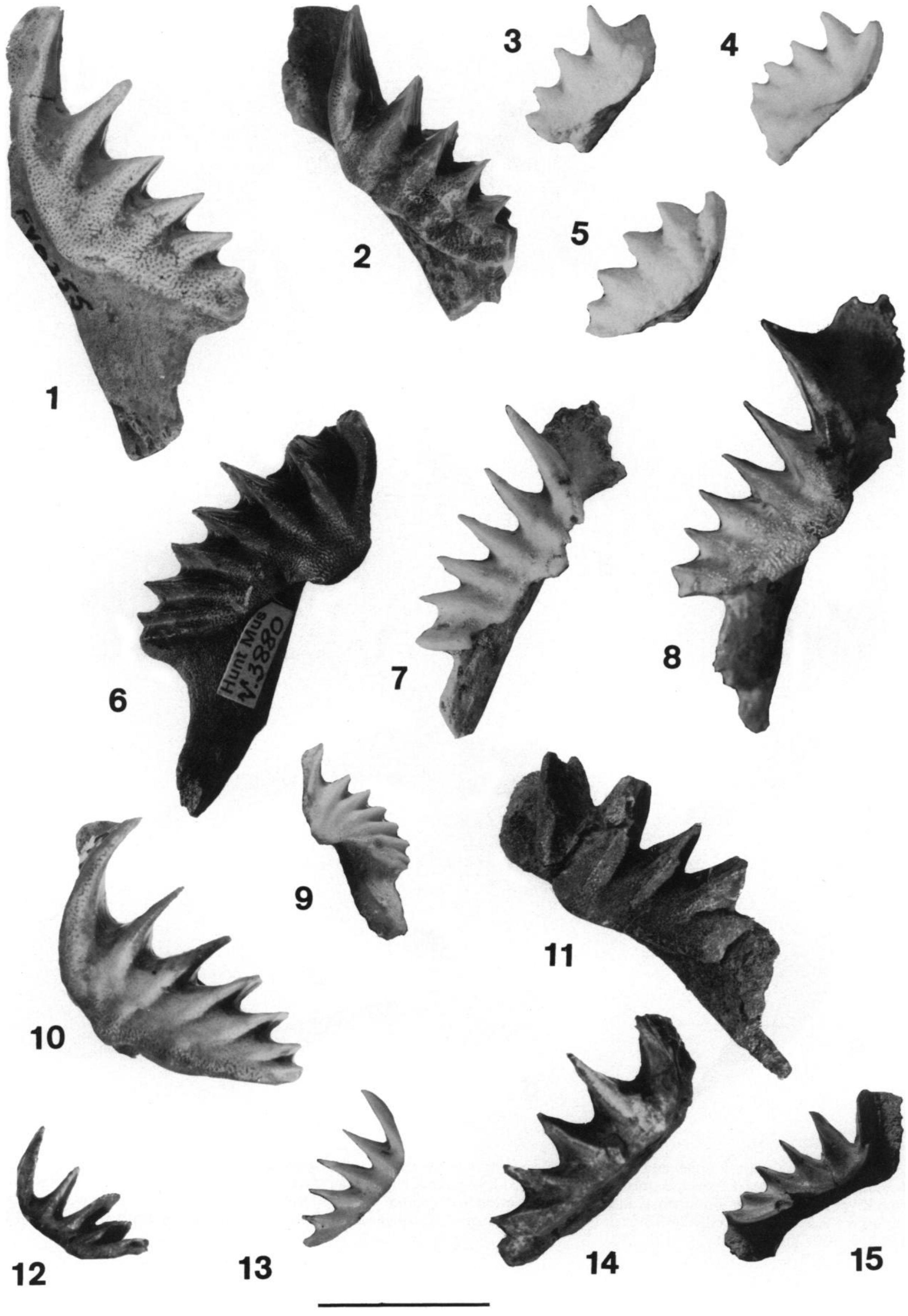


FIGURE 2—*1–4*, Occlusal views of upper and lower jaws of *Neoceratodus forsteri* from the Brisbane River to show changes with growth. *1*, minute, QM I 26002; *2*, small, QM I 25999; *3*, medium, QM I 26017; *4*, large, QM I 26014. *5–8*, upper jaws from the Enoggera Reservoir and the Brisbane River to illustrate environmental and inherent variation in *N. forsteri*. *5, 6*, occlusal views of adult upper tooth plates. *5*, QM I 26000 from Enoggera Reservoir; *6*, QM I 26018 from the Brisbane River. *7, 8*, labial views of the same adult upper tooth plates. *7*, QM I 26000; *8*, QM I 26018. Scale line = 2 cm.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and the shape of the posterior ridges in both. In addition, the relationship of the first ridge to the symphysis in each jaw and the form of the enamel-to-bone junction on the labial aspect of the tooth plate can be used to discriminate species within each genus.

Other characters can be used only for descriptive purposes, although visible differences among tooth plates of the three genera described in this paper are numerous and often distinctive (Figures 3–9). Unfortunately, similar differences are present among the tooth plates of the Recent lungfish, *Neoceratodus forsteri,* from different localities (Figure 2). These depend on such factors as diet, environment, wear, and growth, as well as inherent variation and the presence of developmental aberrations and pathologies. Included in the first two categories, diet and environment, are most of the characteristics of the occlusal surface, such as height of the crest, shape of the inter-ridge furrow, and extension of both to the mediolingual face. The same applies to erosion of the mediolingual aspect to the tooth plate, which is affected strongly by the pH of the environment (Kemp, 1991b). Inherent variation affects the shape of the inter-ridge clefts, and this depends on the number of ridges (also variable), the shape of the adult tooth plate (elongate or oval), and the posterior end of the tooth plate (a heel, a single last ridge, or a double last ridge). Shape of the tooth plate can also vary with size: small *N. forsteri* tooth plates are triangular, whereas larger ones are elongate or oval. Smaller tooth plates also retain cusps on the occlusal surface, and larger ones may have no cusps at all, even on the unworn labial extremities of the tooth plate.

The value of many characters of tooth plates and jaw bones is negated because they are the same over a wide range of dipnoan tooth plates. Overall shapes of jaw bones in neoceratodonts are similar when these are preserved, as are many details of jaw bone structure. All dipnoans have clearly marked incremental lines in the enamel retained on the labial, lingual, and medial faces of the tooth plate. In the genera considered in this paper, symphyses between the paired upper or lower jaw bones are all easily separable. Other characters are of reduced value in Australian material because they are not always preserved, such as characters of the ridge tips and distal extremities of the jaw bones and of the ascending pterygopalatine process.

Grooves in the upper and lower symphysis are strongly marked, but suffer from inherent variability and are affected by growth. Exact position and cross-sectional shape of the pterygopalatine process varies depending on environment, age, and diet in *Neoceratodus forsteri* (Figures 1, 2). The prearticular sulcus, normally double with a small anterior sulcus in large specimens of *N. forsteri,* is single in very young jaws but still a useful character in large specimens.

Developmental aberrations are common in lungfish tooth plates and should not be used for taxonomic assessments in any form (Kemp, 1991b, 1996). Ceratodont and neoceratodont tooth plates are prone to cusp and enamel abnormalities, divided or intercalated ridges, and pattern loss, particularly among the posterior ridges. Specimens of some species often show a marked

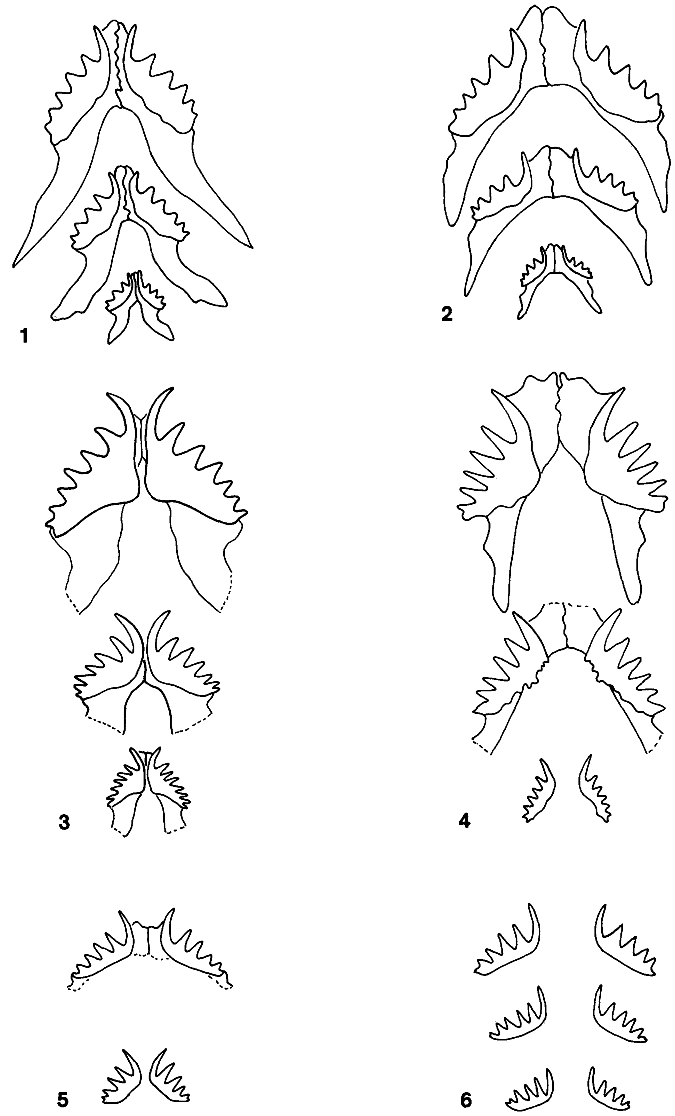

FIGURE *4*—Reconstructions of *Neoceratodus* tooth plates showing occlusal patterns. *1, 2, N. forsteri.* Large based on QM I26016, medium based on QM I26017, small based on QM I25999. *1,* upper tooth plates with attached pterygopalatine bones from the Brisbane River, South East Queensland; *2,* matching lower tooth plates and prearticulars. *3, 4, N. eyrensis. 3,* large upper based on HMV 3380 (holotype), medium based on MV 160312, small based on QM F18846; *4,* large lower based on QM F 14980, medium based on QM F18845, small based on QM F18847. *5, 6, N. nargun. 5,* large upper based on MV 186401, medium upper based on MV P186036, small upper based on QM F14994; *6,* large lower based on MV P157247 (holotype), medium lower based on QM F18627, small lower on QM F18827. Scale line = 2 cm.

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FIGURE *3*—Fossil *Neoceratodus* species in occlusal view. *1–5, N. forsteri. 1,* FV 0355, upper tooth plate and bone, Chinchilla, Queensland; *2,* FV 0616, lower tooth plate and bone, Chinchilla, Queensland; *3,* QM F10239, cast of large lower tooth plate fragment, Lightning Ridge, New South Wales; *4,* QM F10237, cast of small upper tooth plate, Lightning Ridge, New South Wales; *5,* QM F10238 cast of large upper tooth plate Lightning Ridge. *6–10, N. eyrensis. 6,* HMV 3880, holotype, Lower Cooper Creek, South Australia; *7,* QM F18845, lower tooth plate, unnamed locality, Riversleigh, north Queensland; *8,* QM F14980, large lower tooth plate, Bob's Boulders, Riversleigh, North Queensland; *9,* QM F18846, small upper tooth plate with attached bone, unnamed locality, Riversleigh, North Queensland; *10,* MV P160312, upper tooth plate, Lake Kanunka, South Australia. *11–15, N. nargun. 11,* MV P182182, large lower tooth plate and bone, Cape Otway, Victoria; *12,* QM F14994, small upper tooth plate, Main Site, Riversleigh, North Queensland; *13,* QM F18827, a lower tooth plate from Riversleigh, North Queensland; *14,* MV P157247, holotype, lower tooth plate, Cape Otway, Victoria; *15,* MV P186036, upper tooth plate, Eagle's Nest Rock, Victoria. Scale line = 2 cm.

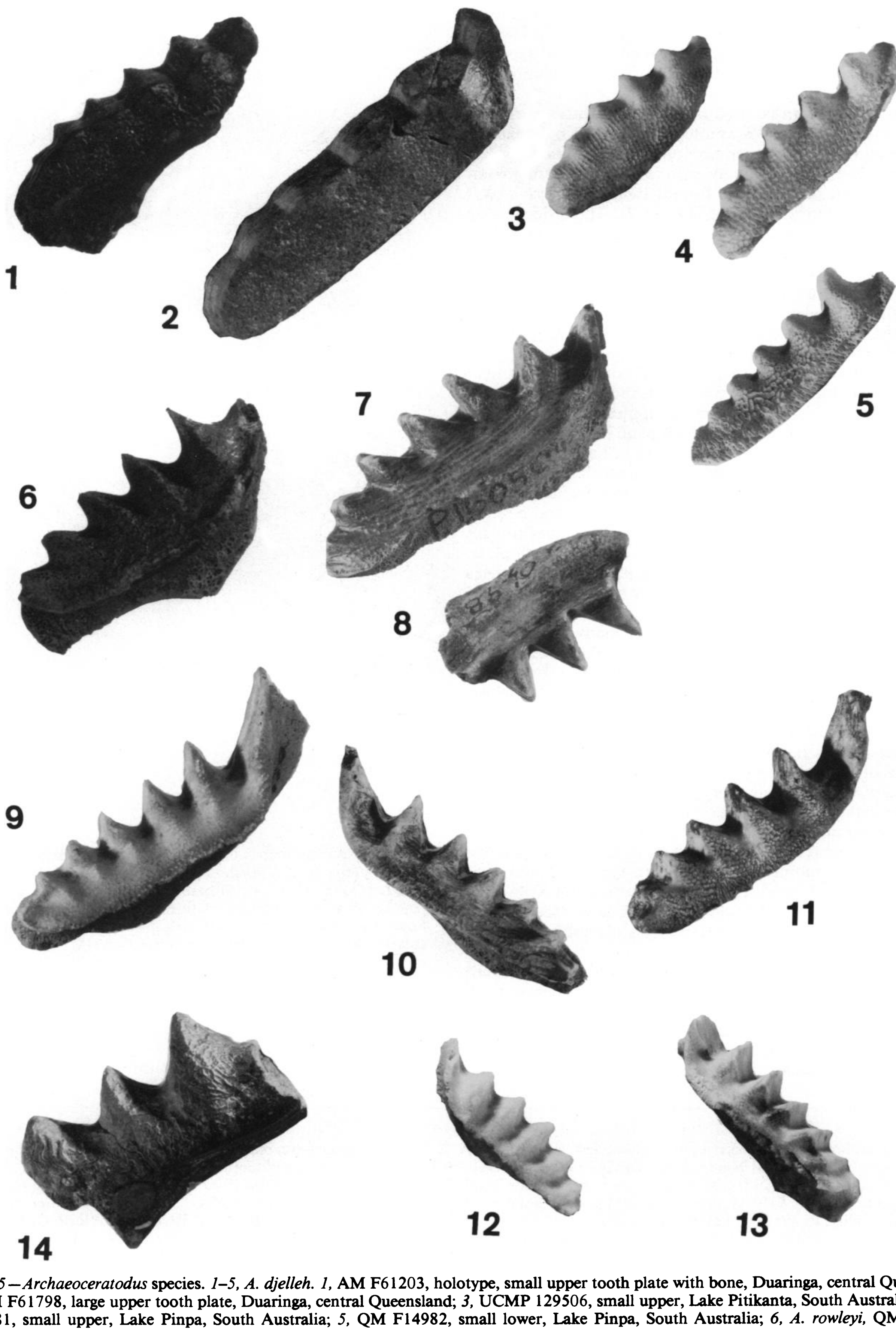

FIGURE 5—*Archaeoceratodus* species. *1–5, A. djelleh. 1,* AM F61203, holotype, small upper tooth plate with bone, Duaringa, central Queensland; *2,* AM F61798, large upper tooth plate, Duaringa, central Queensland; *3,* UCMP 129506, small upper, Lake Pitikanta, South Australia; *4,* QM F14981, small upper, Lake Pinpa, South Australia; *5,* QM F14982, small lower, Lake Pinpa, South Australia; *6, A. rowleyi,* QM F14983,

twist in the posterior ridges, and others are affected by short ridge anomaly (Kemp, 1991b, 1996). Pathologies such as generalized bone and tooth disease may affect taxonomic determinations (Kemp, 1991b, 1995a).

Biometry.—Biometrical analysis of Australian neoceratodonts, on the basis of angles between the ridges and ratios of the length and breadth of the tooth plates, is questionable because biometry depends on a good statistical sample (Kemp, 1977; Lund, 1970, 1973). In Australian material, measurements are often incomplete owing to the fragmentary nature of many specimens. In addition, numbers of specimens in some Australian species may be too low for adequate statistical treatment. Other problems arise when angles and length-to-breadth ratios are similar in a range of different species. Angles between the ridges are variable and often fall within the same range in tooth plates that are patently different (Kemp and Molnar, 1981). It can be difficult to make an accurate measurement of angles between the ridges because the angle of growth is not the same as the angle of wear, and because wear may obliterate the angle of growth in older material. Measurements of length and breadth are included in this paper for descriptive purposes only, and angles have not been used.

Reconstruction of occlusal profiles.—Drawings of occlusal profiles provide a useful method for the rapid identification of species (Figures 4, 7, 10). Outlines of upper and lower tooth plates of each species are drawn with the occlusal surface level. The lower plates are angled steeply when the jaws are in normal articulation, and drawing an outline of the occlusal profile, to match the upper jaws, makes the lower jaws appear wider than they are in the intact animal. Three size classes, small, medium, and large, are used wherever possible. Pterygopalatine and prearticular bones are included when these are preserved. More than one specimen was used in some cases.

SYSTEMATIC PALEONTOLOGY

Order Dipnoi Müller, 1845
Family Neoceratodontidae Miles, 1977

Amended diagnosis of family (additional to Martin 1982a).—Dipnoans with one lung; simplified skull roof with XK and I bones retained; ascending pterygopalatine process articulates with descending process of JLM bone and exposed on lateral aspect; adults with pterygopalatine, prearticular, and vomerine tooth plates.

Remarks.—Martin (1982a) gave a diagnosis of the family Neoceratodontidae proposed by Miles (1977), but additions and changes are required because some of the characters he used are affected by growth, wear, or inherent variation.

Genus Neoceratodus de Castelnau, 1876a

Type species.—*Neoceratodus forsteri* (Krefft, 1870).

Amended diagnosis.—Pulp cavity wide; mantle dentine extensive; ridges originate from an anterior or modified position; upper tooth plates close but not contiguous, lower tooth plates separated widely; upper symphysis sutured loosely, half-oval or elliptic in shape; lower symphysis sutured loosely and linear in shape; pterygopalatine process present; prearticular sulcus double, anterior being shallow; punctations simple; petrodentine (sensu Lison, 1941) absent. Diagnostic generic characters are listed in Table 1.

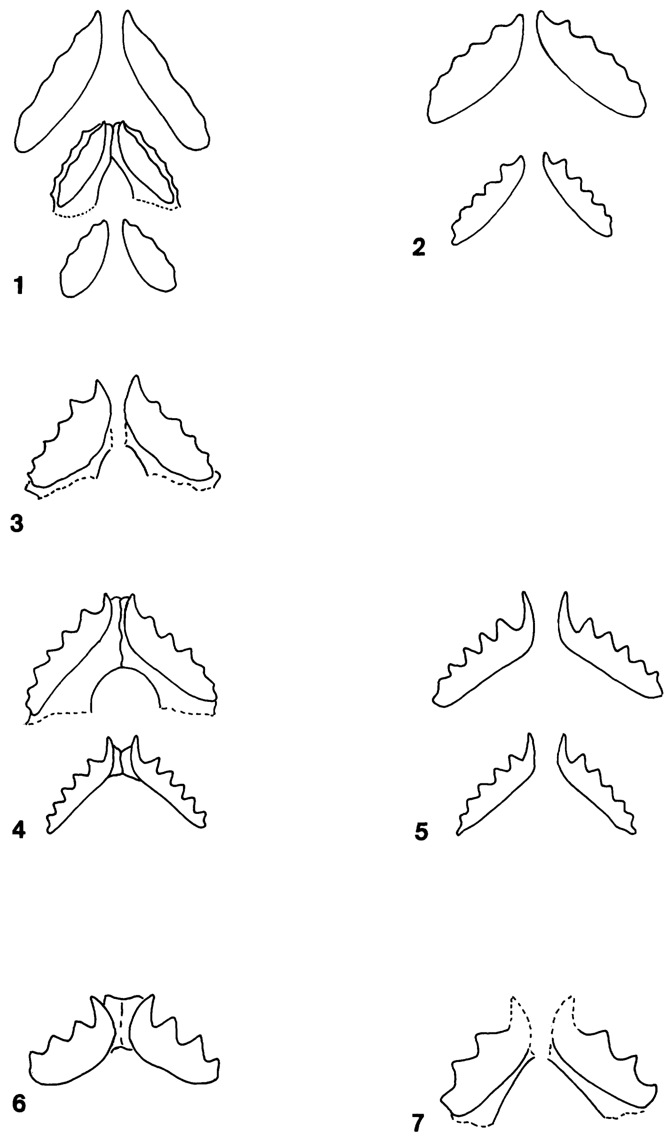

Figure 6—Reconstructions of *Archaeoceratodus* tooth plates showing occlusal patterns. *1, 2, A. djelleh. 1,* large upper based on AM F61798, medium upper based on AM F61203, holotype, small upper based on UCMP 129506; *2,* large lower based on RV 7231, small lower based on QM 14982. *3, A. rowleyi.* upper based on QM F14983. *4, 5, A. theganus. 4,* large upper based on MV P160504 and AMNH 11373, small on QM F12317; *5,* large lower based on MV P160498 and SAM P23470, small based on F12207. *6, 7, A. avus. 6,* upper based on MMF 24788; *7,* lower based on MV P10057. Scale line = 2 cm.

Distribution of genus.—Cretaceous deposits of Australia (Kemp, 1983; Kemp and Molnar, 1981) and possibly South America (Pascual and Bondesio, 1976). Most species occur in

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holotype, from Rundle, central Queensland. *7–13, A. theganus. 7,* MV 160504, holotype, upper tooth plate, Lake Pinpa, South Australia; *8,* MV 160498, matching lower of MV 160504; *9,* SAM 23470, large lower, Lake Kanunka, South Australia; *10,* MV P194526, large lower, Namba Formation, South Australia; *11,* QM F11026, large lower, Frome Downs, South Australia; *12,* QM F12314, medium upper, Lake Kanunka, South Australia; *13,* QM F12207, medium lower, Lake Kanunka, South Australia. *14, A. avus,* MV P10057, holotype, Cape Paterson, Victoria. Scale line = 2cm.

Australian Tertiary deposits, particularly the mid-Tertiary of the central and northern parts of the continent. One species, *Neoceratodus forsteri,* survives in southeast Queensland (Krefft, 1870).

NEOCERATODUS FORSTERI (Krefft 1870)
Tables 2, 3; Figures 1, 2, 3.1–3.5, 4.1, 4.2

Ceratodus forsteri KREFFT, 1870, p. 221–224, pl. 1–3; MEYER, 1875, p. 368; DE CASTELNAU, 1876b, p. 342; DE VIS, 1884, p. 42–43.
Ceratodus miolepis (Krefft, 1870). GUNTHER, 1871, p. 516.
Neoceratodus blanchardi (Krefft, 1870). DE CASTELNAU, 1876a, p.133.
Epiceratodus forsteri (Krefft, 1870). TELLER, 1891, p. 1–38; WHITE, 1926, p. 139; HILLS, 1934, p. 159.
Neoceratodus forsteri (Krefft, 1870). BERTIN, 1940, p. 246.
A complete synonymy list is given in Schultze (1992).

Amended diagnosis.—Punctations simple and without pattern; procumbent mediolingual keel absent; medial edge curved slightly in upper tooth plate and straight in lower; ridge 1 of upper tooth plate slender and falcate, ridge 1 of lower slender and acuminate; posterior ridges short, slender, and acute, crest of ridge 1 slightly curved in upper tooth plate and straight in lower; ridge 1 of upper plate curves evenly into and away from symphysis; ridge 1 of lower tooth plate angles into symphysis anteriorly; enamel-to-bone junction on labial face of tooth plates rises sharply between each ridge.

Holotype.—The specimen described by Krefft (1870) has been mislaid (Whitley, 1929), but the photograph published by Krefft is preserved in the archives of the Australian Museum, Sydney. The photograph of the holotype was not used in this paper.

Type locality.—Burnett River, southeast Queensland, by inference from Krefft (1870), map reference 25° 44′ S, 151° 00′ E.

Other material.—An extensive series of Recent specimens in the collection of the Queensland Museum (numbers I 25995–I 26022) was used for the diagnosis and description. Fossil material consists of QM F10237, F10238, and F10239, all from Lightning Ridge, 29.5° S, 148° E, New South Wales, as well as FV O355 and FV O616, Chinchilla, 28° 48′ S, 150° 41′ E, southeast Queensland. The Lightning Ridge deposit is Cretaceous, Griman Creek Formation, Middle Albian on the basis of palynology (Dettman et al., 1992). The Chinchilla deposit is Pliocene (Chinchilla Local Fauna, Rich et al., 1991), Chinchilla Sands, Early to Middle Pliocene.

Other Recent localities.—The Australian lungfish is now confined to southeast Queensland. The lungfish of the Mary River system, described originally as a separate species, *Ceratodus miolepis* (Gunther, 1871), does not in fact differ from *Neoceratodus forsteri* in significant morphological characters and is not regarded as distinct (Meyer, 1875). Specimens from the Mary River population were used to transplant lungfish to a number of new localities in southeast Queensland, including Enoggera Reservoir (Kemp, 1987). The Enoggera population has remained isolated, but the morphological differences noted in this population compared with the lungfish from other localities can be explained as age-related changes (Kemp, 1991a, 1991b). Adults of similar age from the Mary and Brisbane River systems do not differ from each other in osteological and dental characters. The Brisbane River population, regarded originally as having been introduced, may in fact be a natural population (Kemp, 1987).

Description.—For the purposes of description and comparison with fossil material, the tooth plates of *Neoceratodus forsteri* are categorized into arbitrary size classes. Tooth plates from the Brisbane and Mary Rivers range in size from minute (up to 4.0 mm long) through small (Figure 2. 2), medium (Figure 2. 3) to large (25.1–35.0 mm long, Figures 1, 2. 4). Small and medium size classes, 4. 1–15. 0 mm and 15. 1–25. 0 mm long, respectively, are well represented in this locality. All Enoggera tooth plates are large. Fossil tooth plates from Chinchilla belong in the large size class. Other fossils are medium (Tables 2, 3).

Medium and large *Neoceratodus forsteri* tooth plates vary in shape and can be described best as elongate oval or elongate (Figures 1, 2, 3.1, 3.2). Loss of enamel and dentine on the

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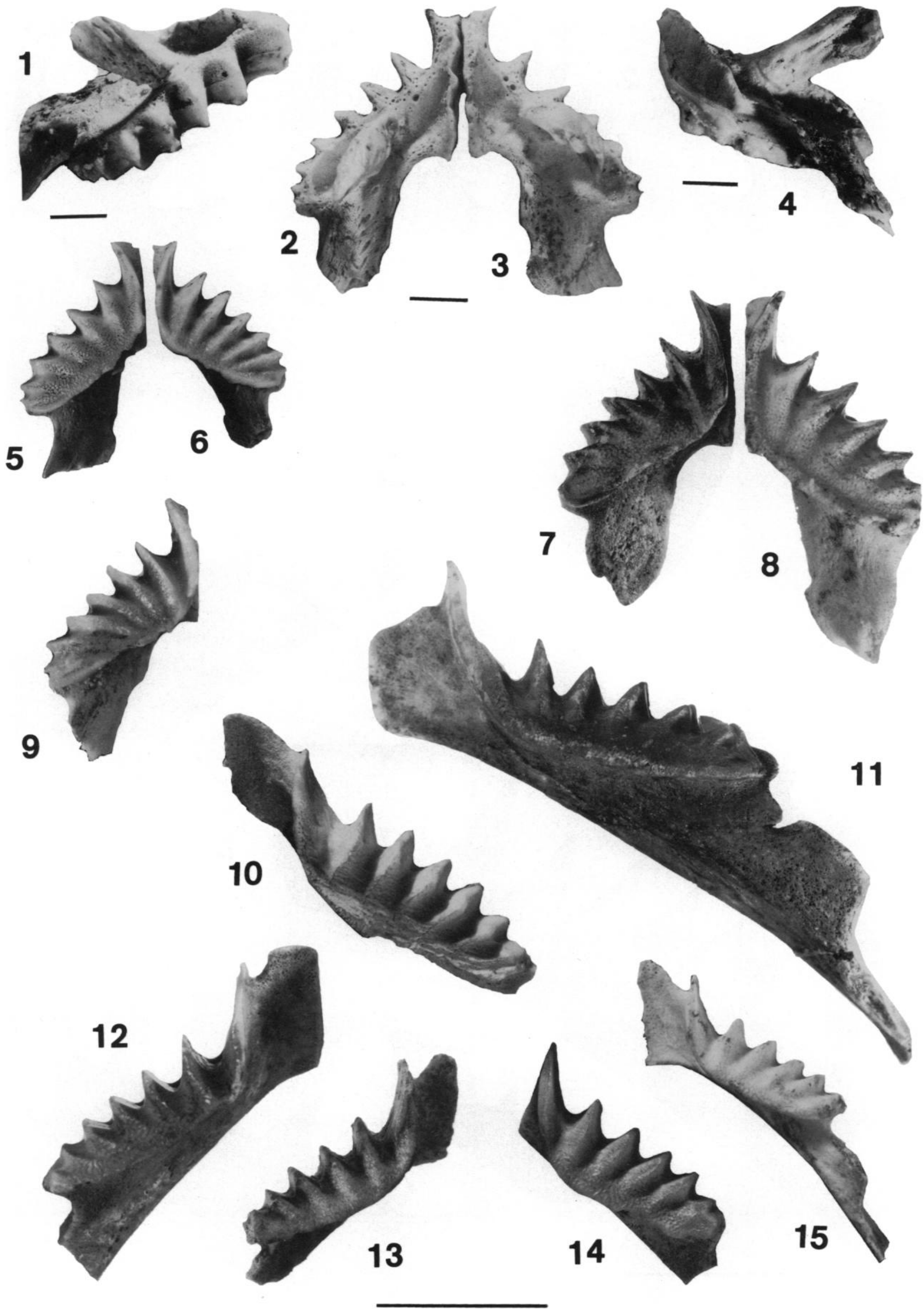
FIGURE 7—*Mioceratodus anemosyrus* from central and northern Australian localities. *1–9,* upper jaws. *1,* QM F15005, holotype, jaw in labial view (Melodie's Maze, Riversleigh, north Queensland); *2,* QM F15006, bone in abocclusal view (unnamed locality, Riversleigh, north Queensland); *3,* QM F15005, holotype, bone in abocclusal view; *4,* QM F15005, holotype, jaw in mediolingual view; *5,* QM F15006, toothplate in occlusal view; *6,* QM F15005, toothplate in occlusal view; *7,* NTM P8695–83, upper tooth plate with bone, in occlusal view (Bullock Creek, Northern Territory); *8,* NTM P87112–1, upper tooth plate with bone in occlusal view (Bullock Creek, Northern Territory); *9,* QM F14995, small upper tooth plate with bone in occlusal view (unnamed locality, Riversleigh, North Queensland). *10–15,* lower jaws. *10,* AMNH 11345, small lower tooth plate with bone in occlusal view (Lake Pinpa, South Australia); *11,* AMNH 11399, lower tooth plate with prearticular in occlusal view (Lake Pinpa, South Australia); *12,* QM F12336, small lower tooth plate with attached prearticular in occlusal view (Leaf Locality, South Australia); *13,* NTM P8694–4, small lower tooth plate in occlusal view (Bullock Creek, Northern Territory); *14,* QM F18623, small lower tooth plate in occlusal view (Group Site, Riversleigh, North Queensland); *15,* NTM P87112–10, small lower tooth plate with bone (Bullock Creek, Northern Territory). Scale lines, 7.1–7.4 = 5 mm; 7.5–7.15 = 2 cm.

FIGURE 8—*Mioceratodus gregoryi* from central and northern Australia. *1–5,* Upper jaws in occlusal view. *1,* QM F11024, large upper tooth plate and bone from Lake Frome, South Australia; *2,* QM M15010, small upper tooth plate, Lake Pinpa, South Australia; *3,* AMNH 11368, small upper tooth plate, Lake Pinpa, South Australia; *4,* HMV 3891, holotype, medium upper tooth plate from Coopers Creek, South Australia; *5,* AMNH 1675, large upper tooth plate frtom Lake Pinpa, South Australia. *6–9,* lower jaws in occlusal view. *6,* NTM P8694–8, small lower tooth plate and attached prearticular (Bullock Creek, Northern Territory); *7,* AMNH 11384, large lower tooth plate with attached prearticular, Ericmas Quarry, South Australia; *8,* AMNH 11320, small lower tooth plate from Lake Pinpa, South Australia; *9,* AMNH 11330, large lower tooth plates from Lake Pinpa, South Australia. Scale line = 2 cm.

FIGURE 9—*Mioceratodus* from Central Australia. *1, 2,* lower jaws of *M. poastrus* in occlusal view. *1,* AMNH 11322, holotype, lower tooth plate with prearticular, from Lake Pinpa, South Australia; *2,* HMV 3887, small lower tooth plate and partial prearticular from Lower Cooper Creek, South Australia. *3–5,* upper jaws of *M. poastrus* in occlusal view. *3,* RV 22332, a large upper tooth plate and partial attached bone, from Stirton Quarry, Lake Kanunka, South Australia; *4,* UCMP 56990, small upper tooth plate from Lake Kanunka, South Australia; *5,* QM F15012, a medium upper tooth plate with partial bone, Lake Ngapakaldi, South Australia. *6–8,* upper jaws of *M. diaphorus* in occlusal view. *6,* QM F11023, holotype, large upper tooth plate and partial bone, from Frome Downs, South Australia; *7,* AMNH 11347, small upper tooth plate and attached bone, Lake Pinpa, South Australia; *8,* NTM P894–4, small upper tooth plate from Bullock Creek, Northern Territory. *9–12,* Lower jaws of *M. diaphorus* in occlusal view. *9,* NTM P87108–9, small lower tooth plate with prearticular, Bullock Creek, Northern Territory; *10,* UCMP 129509, a small lower tooth plate, locality unknown, South Australia; *11,* AMNH 11324, large lower tooth plate with prearticular, Lake Pinpa, South Australia; *12,* NTM 8695–81, small lower tooth plate with prearticular, Bullock Creek, Northern Territory. Scale line = 2 cm.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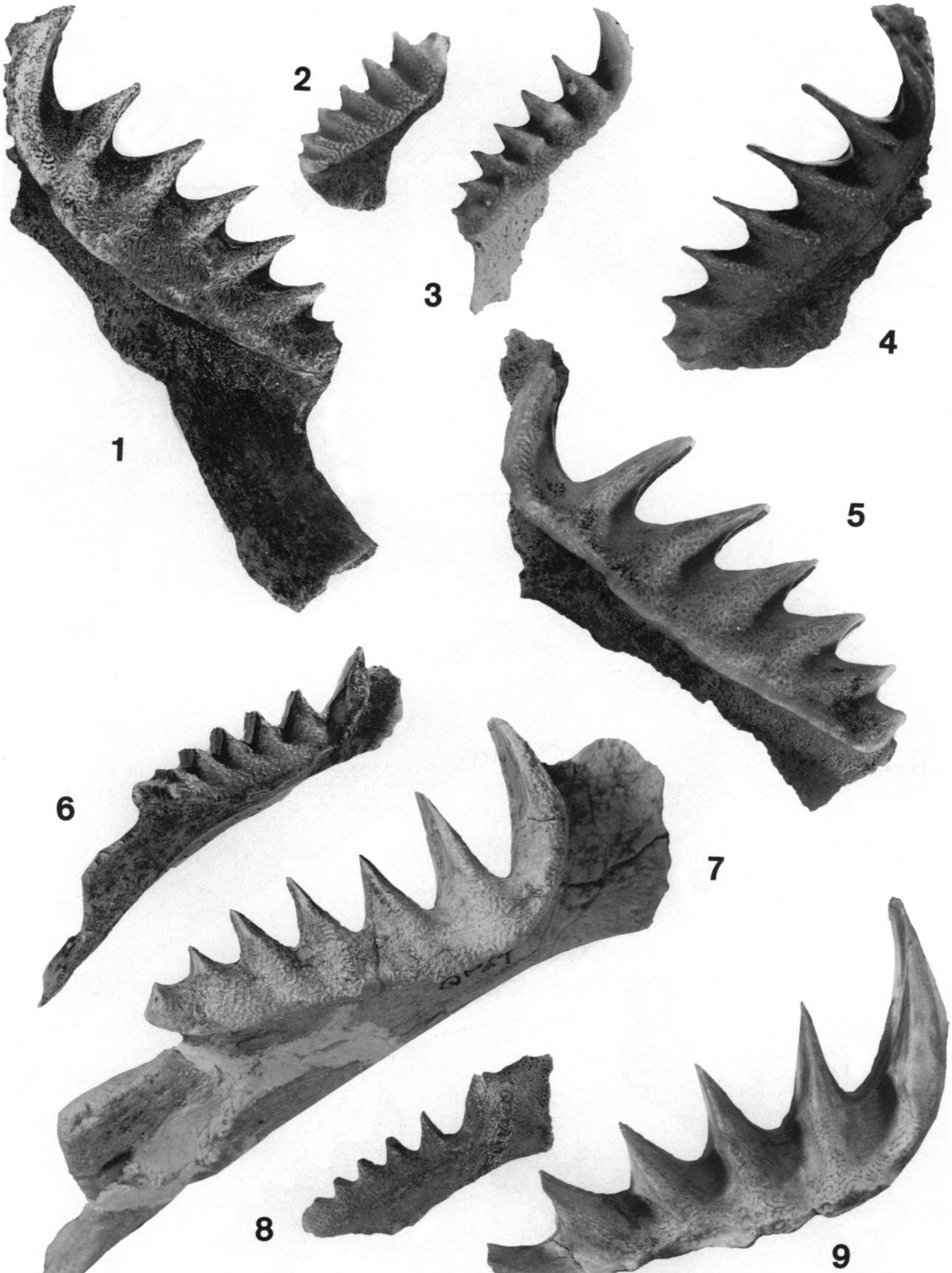
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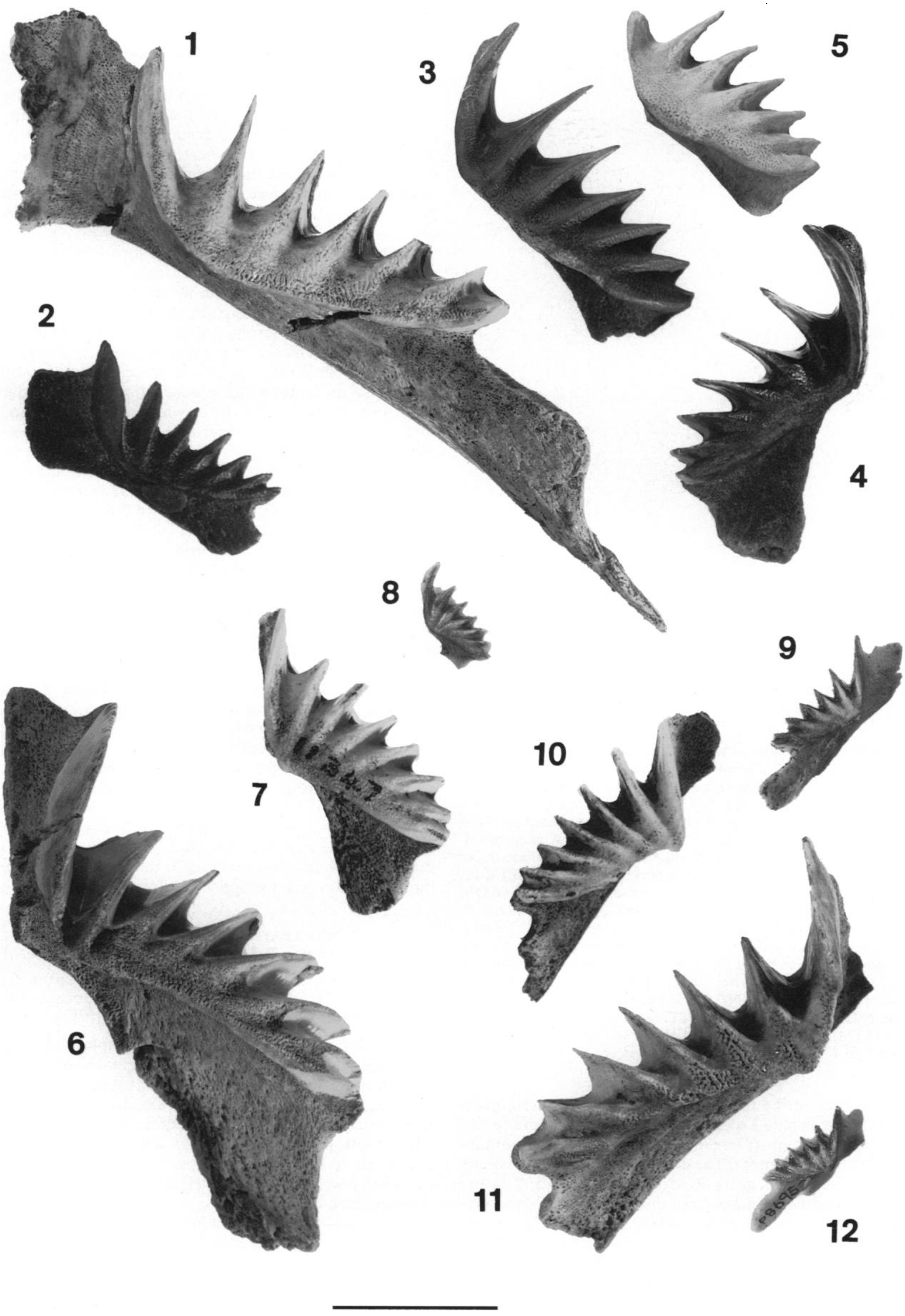
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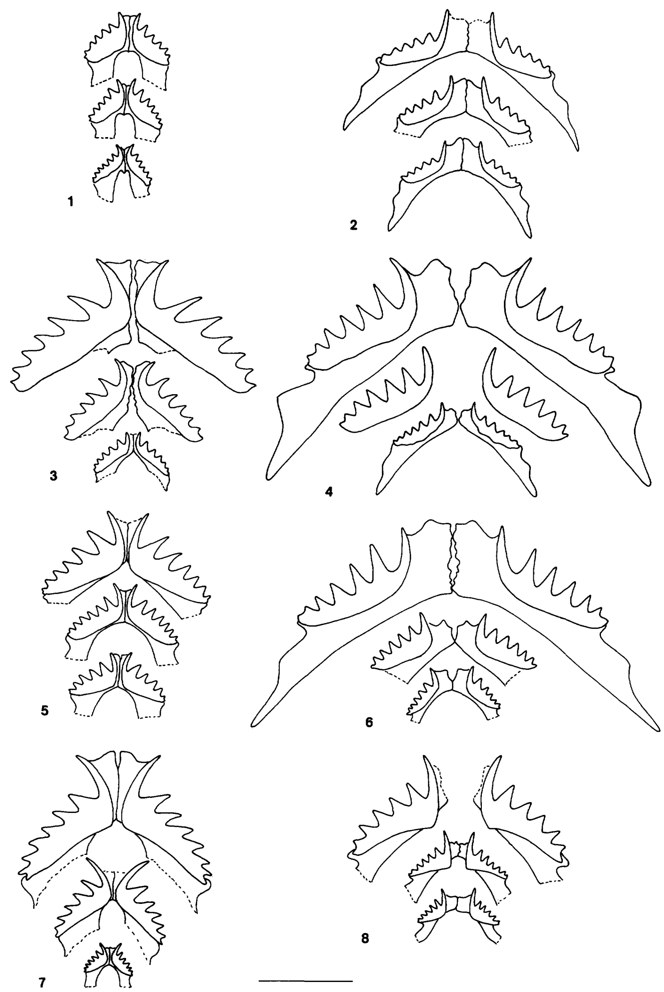

FIGURE *10*—Reconstructions of *Mioceratodus* toothplates, showing occlusal patterns. *1, 2, M. anemosyrus. 1,* large upper based on NTM 8695–83 and P87112–1, medium upper based on QM 15005 (holotype) and 15006, small upper based on QM 14995 and QM F20946; *2,* large lower based on AMNH 11399, medium lower based on NTM P8694–4, small lower based on NTM P87112–10. *3, 4, M. gregoryi. 3,* large upper based on QM F11024 and AMNH 1675, medium upper based on HMV 3891 (holotype), small upper based on QM F15010; *4,* large lower based on AMNH 11384, medium lower based on QM F12333, small lower based on NTM 8634–3. *5, 6, M. poastrus. 5,* large upper based on RV 7240, medium upper based on QM 150011, small upper based on UCMP 56990; *6,* large lower based on AMNH 11327, medium lower based on HMV 3893, small lower based on HMV 3887. *7, 8, M. diaphorus. 7,* large upper based on QM F11023, medium upper based on AMNH 11336 and QM F12320, small upper based on NTM P894–4 and NTM P87113–9; *8,* large lower based on AMNH 11324, medium lower based on UCMP 129509, small lower based on QM F16374. Scale line = 2 cm.

mediolingual face of the tooth plate, a destructive premortem process, is absent in small specimens. Some loss of dentine and enamel is present in most larger tooth plates, but the amount depends on the environment. The destructive process is extreme in tooth plates from Enoggera Reservoir (Figure 2.5, 2.7) but usually moderate in specimens from the Brisbane or Mary Rivers (Figure 2.6, 2.8) and in fossils (Figure 3.1–3.5). The mediolingual junction is roughly curved because the original inner angle of small tooth plates has been removed (Figure 2.1–2.4). Cusps on the labial margin of each ridge are sparse, indistinct, and compressed in line with the long axis of the ridge in most specimens. In some cases, they are vestigial or absent in large specimens. Clefts between the ridges are wide and have straight sides. In relation to the occlusal surface, they may be deep, moderate, or shallow. The labial profile of the unworn ridges of large tooth plates is upright or steep. Tooth plates of both jaws have a single last ridge or a heel of dentine at the back of the tooth plate. The crests of the posterior ridges are straight and may be parallel or radiating, and are rounded or faceted depending on diet. In specimens from Enoggera Reservoir, the crests are parallel and the furrows incised across the tooth plate to the mediolingual face. In Brisbane River fish, the crests meet in a point mediolingually, and the furrows are shallow and do not reach the mediolingual face.

Grooves in the symphysis, which forms the suture with the opposing jaw, are more numerous, more pronounced, and deeper in the pterygopalatine than in the prearticular. They do not make an inseparable fusion, but connective tissue fibres between the bone result in a strong union, particularly in the upper jaw (Kemp, 1979). The ascending pterygopalatine process, which is involved in anchoring the jaw to the calvarium, varies in position and in detailed shape according to diet, and therefore tooth use, in the locality from which it came (Kemp, 1991a). In Enoggera fish, it is slender and circular at the base and positioned above ridge 3 (Figure 2.7). In the Brisbane and Mary River fish, it is more robust, oval in section, and has a more anterior position, from the middle of the base of ridge 2 to the middle of the base of ridge 3 (Figure 2.8). The angle between the process and tooth base is also variable when specimens from these two sources are compared (Figure 2.7, 2.8). In the two upper tooth plates from Lightning Ridge, QM F10237 and F10238, and in the upper tooth plates from Chinchilla, it is circular in section and positioned from the middle of the base of ridge 2 to the middle of the space between ridges 2 and 3 (Kemp and Molnar, 1981).

The distal extremity of the pterygopalatine process that articulates with the calvarium is thin and fluted. The surface is flattened labially for contact with the corresponding socket on the JLM bone, and the distal tip of the process fits into a groove on the ABC bone (Kemp, 1992a). This part of the process is rarely preserved in fossils and is not present in the Lightning Ridge or Chinchilla material. Other fossil specimens are lower tooth plates.

Ridges vary in number from 5–7 in both jaws in tooth plates over 7 mm in size. Smaller tooth plates have 3 or 4 ridges in the lower jaw and 4 or 5 ridges in the upper. Six ridges are the most common in both upper and lower plates.

NEOCERATODUS EYRENSIS (White, 1925)
Tables 2, 3; Figures 3.6–3.10, 4.3, 4.4

Epiceratodus eyrensis (in part) WHITE, 1925, p.139, pl. 6, fig.1.
Neoceratodus eyrensis (White, 1925). KEMP AND MOLNAR, 1981, p. 211.
A complete synonymy list is given in Schultze (1992).

Amended diagnosis.—Punctations simple and without pattern; mediolingual keel procumbent; medial edge strongly curved in both tooth plates; ridge 1 of upper tooth plate long, slender, and falcate, ridge 1 of lower long, slender, and acuminate; posterior ridges, long, slender, and acute; crest of ridge 1 curved in upper tooth plate and straight in lower; ridge 1 curves in and out evenly to symphysis in upper jaw and angles out anteriorly in lower jaw; labially, enamel-to-bone junction rises slightly between each ridge.

Holotype.—HMV 3880, a large, dark red-brown upper tooth plate (Figure 3. 6), collected by Gregory (1909) in central Australia.

Type locality and horizon.—Lower Cooper Creek, 28° 30′ S, 138° 20′ E, South Australia (Malkuni fauna), correlative to the Katipiri Sands, Pliocene (Rich et al., 1991; Stirton et al., 1961).

TABLE 1—Generic characters for Australian neoceratodonts based on tooth plates.

	Neoceratodus	*Mioceratodus*	*Archaeoceratodus*	*Ceratodus*
Pulp cavity	wide	wide	wide	wide
Mantle dentine	extensive	extensive	extensive	limited
Origin of ridges	anterior*	anterior*	anterior*	medial
Position, upper tooth plates	separate	separate	separate	close/contiguous
Position, lower tooth plates	separate	separate	separate	separate
Shape, upper symphysis	half oval	oval	linear	oblong
Shape, lower symphysis	linear	linear	linear	linear
Pterygopalatine process	present	present	present	present
Prearticular sulcus	double	double	confluent	single
Petrodentine *sensu strictu*	absent	present	present	absent

* Anterior unless mediolingual region modified by wear or destruction of dental tissue.

Other material.—*Neoceratodus eyrensis* is not a common species but is represented in the major mid-Tertiary and Quaternary formations of Australia. QM F14980 (Riversleigh, north Queensland, 19° 00′ S, 138° 40′ E), is a large lower jaw tooth plate with attached bone. QM F18845 and F18847 (Riversleigh, north Queensland) are well-preserved lower tooth plates similar to QM F14980. Upper tooth plates with attached bone are represented by QM F18846 (Riversleigh, north Queensland). MV P160312 (Lake Pinpa, central Australia, 31° 08′ S, 140° 13′ E) is an upper tooth plate with some attached bone. Riversleigh deposits are Middle Miocene (Megirian, 1992), and Lake Pinpa is Namba Formation, Late Oligocene to Middle Miocene in age (Rich et al., 1991).

Description.—*Neoceratodus eyrensis* was of moderate to large size. The smallest tooth plates are 16–17 mm long and the largest 36–37 mm long (Tables 2, 3). Tooth plates are set close together (Figures 4.3, 4.4), and have a strong, procumbent mediolingual keel that increases with tooth-plate size. Ridges vary in number, with 7 or 8 in the upper jaw and 6 or 7 in the lower.

Cusps at the labial extremities of the ridges are numerous, distinct, and compressed across the long axis of the ridge. The shape of both the upper and lower tooth plates is triangular with rounded margins, and the mediolingual junction is curved. Removal of dentine and enamel on the mediolingual face is absent except in QM F18845 (Figure 3.7), which has extensive eroded carious lesions in this region, and in QM F14980, also affected by severe erosion and caries (Figure 3.8). Clefts between the ridges are wide, moderate or deep, and have straight sides. The labial profile of the unworn ridges is a low slope and the posterior end of the tooth plate is a single or double ridge in both jaws. Crests of the posterior ridges are radiating, curved in the upper jaw and straight in the lower. Wear on the crests is usually faceted, and the furrows are rounded. Grooves in both symphyses are few and shallow, angled in the upper and upright in the lower. The fusion between the paired bones appears to have been weak. The pterygopalatine process is circular in section at the base and positioned above ridge 3.

The upper tooth plates are close but not contiguous in a natural position (Figure 4.3). The absence of a wear facet in most specimens shows that they did not come into contact with each other. The holotype has chips and fractures on the medial face of the keel (White, 1925), but this is incidental post-mortem damage. It is not a wear facet resulting from abrasion against the keel of the matching tooth plate.

Remarks.—In the original description of *Neoceratodus eyrensis* (White, 1925), the specimens show considerable variation, particularly when the holotype (HMV 3880), an upper tooth plate with a pronounced procumbent keel, is compared with lower plates assigned to the species. The lower tooth plates lack a keel and are narrower and more elongate. The form of upper and lower tooth plates could be expected to be similar by analogy with the Recent species, *N. forsteri,* and the lower tooth plates of White (1925) are not comparable to the holotype. The Riversleigh specimen, QM F14980, is the first lower jaw to match the holotype of *N. eyrensis.* The lower jaws described by White closely resemble a new upper jaw from the Leaf Locality, Lake Ngapakaldi, South Australia, and a new species is described below to accommodate them. Subsequent finds of upper and lower specimens of *N. eyrensis* have confirmed this decision.

NEOCERATODUS NARGUN (Kemp, 1983)
Tables 2, 3; Figures 3.11–3.15, 4.5, 4.6

Ceratodus nargun KEMP, 1983, p. 23, fig. 1.
Neoceratodus nargun (Kemp 1983). KEMP, 1991a, p. 476, pl. 3E.
Schultze (1992) gave a complete synonymy list but places the species in *Ceratodus*? without explanation.

Amended diagnosis.—punctations simple and without pattern; procumbent mediolingual keel absent; medial edge of both lower and upper plates slightly curved; crest of ridge 1 curved in upper plate and straight in lower; ridge 1 of upper jaw curves into and away from symphysis evenly and ridge 1 of lower jaw angles in to symphysis anteriorly; enamel-to-bone junction on labial face straight.

Holotype.—An incomplete prearticular with attached tooth plate, MV P157247 (Figure 3.14).

Type locality and horizon.—Shore platform, Point Lewis, Cape Otway, 38° 51′ S, 143° 34′ E, Victoria, Otway Group, Early Cretaceous (Gleadow and Duddy, 1981). The deposit is Late Aptian–Early Albian on the basis of invertebrate fossils (Wagstaff and Mason, 1989).

Other material.—*Neoceratodus nargun* is represented by three other Cretaceous specimens, MV P182182, a large nearly complete lower tooth plate (Cape Otway, Victoria, 38° 51′ S, 143° 34′ E), MV P186036, a small upper tooth plate with some bone still attached (Eagle's Nest Rock, 38° 51′ S, 143° 34′ E, Victoria), and MV P186401, a large upper tooth plate with pterygopalatine bone (Punchbowl, 38° 51′ S, 143° 34′ E, Victoria). There are several specimens of a younger age, including QM F14994, (Riversleigh, 19° 00′ S, 138° 40′ E, north Queensland), a small upper jaw plate without attached bone, and some lower plates, UCMP 56992 (Lake Kanunka, 28° 23′ S, 138° 18′ E, South Australia), and QM F18629 and QM F18227 (Riversleigh, north Queensland). Lake Kanunka is Etadunna Formation, Late Oligocene–Middle Miocene, and Riversleigh is Middle Miocene (Megirian, 1992). The Cape Otway site is Otway Group, Late Albian–Early Albian on the basis of invertebrate fossils (Wagstaff and Mason, 1989), and Punchbowl and Eagle's Nest Rock localities are Strezlecki Formation, Valangian–Aptian on the basis of invertebrate fossils (Wagstaff and Mason, 1989).

Description.—*Neoceratodus nargun* is of small to moderate size (Tables 2, 3). MV P182182 and MV P186401 are the largest tooth plates, both 32 mm long, and the others are all less than 25 mm in length. Tooth plates are elongate, narrow, and high

crowned with five, six, or seven long, thin ridges (Figure 4.5, 4.6.). Removal of enamel and dentine from the mediolingual face of the tooth plates is absent. Cusps on the holotype and on MV P182182 are numerous, distinct, and compressed in line with the long axis of the ridge. MV P186401 has no cusps. On MV P186036, cusps are sparse and indistinct. The smallest upper plate, QM F14994 (Figure 3.12), has the last ridge divided into two at the labial extremity, a common developmental abnormality among dipnoans with tooth plates based on radiating ridges of fused cusps (Kemp, 1991b).

The mediolingual face is curved sharply even in the largest specimens. Clefts between the ridges are wide and deep and have straight sides. The labial profiles of the unworn parts of the ridges are upright or steep, and upper and lower tooth plates may end in a double or single last ridge. Ridge crests are straight and radiating. Grooves are absent from the lower jaw symphysis in MV P182182 and are few, shallow, and upright in the upper symphysis of MV P186036 and MV P186401. The pterygopalatine process rises from the base of ridge 2. Crests are faceted or slightly rounded and separated by deep, rounded furrows.

Although the species was first described as *Ceratodus nargun* (Kemp, 1983), new material has shown that its closest affinities lie with species of the genus *Neoceratodus.* MV P186401 has a complete ascending pterygopalatine process that resembles the corresponding process on the upper jaw of *N. forsteri* and is quite unlike that of *Mioceratodus anemosyrus* (Kemp, 1992a). The shapes of the tooth plates of *N. nargun* conform closely with the shapes of *N. forsteri* and *N. eyrensis* tooth plates (Figure 4) and do not resemble any species of dipnoan currently regarded as a member of the genus *Ceratodus* (Kemp, 1993a, 1994; Schultze, 1992).

Genus ARCHAEOCERATODUS new genus

Type species.—*Archaeoceratodus djelleh* (Kemp, 1982a).

Diagnosis.—pulp cavity wide; mantle dentine limited; origin of ridges modified from an anterior pattern; upper and lower symphyses linear in shape and loosely sutured; upper tooth plates close or contiguous in midline, lower widely separated; ascending pterygopalatine process present; prearticular sulcus confluent; punctations complex; petrodentine (sensu Lison, 1941) present (Table 1).

Etymology.—The prefix to the generic name is from the Greek noun *arche,* meaning a beginning.

Distribution of genus.—Species referable to *Archaeoceratodus* are found in Triassic and Cretaceous deposits in southeastern Australia and in mid-Tertiary localities in northern, eastern, and central Australia.

ARCHAEOCERATODUS DJELLEH (Kemp, 1982a) new combination
Tables 2, 3; Figures 5.1–5.5, 6.1, 6.2

Neoceratodus djelleh KEMP, 1982a, p. 151, fig. 1; KEMP, 1982b, p. 138, Table 2; KEMP, 1991a, p. 481, fig. 4F.
A complete synonymy list is given in Schultze (1992).

Amended diagnosis.—punctations complex with a pattern of knobs, short lines, or polygons; procumbent mediolingual keel absent; medial edge of tooth plate sharply curved in upper and slightly in lower; ridge 1 in upper jaw robust and falcate or acute; ridge 1 in lower jaw robust and acute; posterior ridges robust and short or barely delineated; enamel-to-bone junction on labial aspect of both upper and lower tooth plates rises sharply between each ridge; basal sulcus of pterygopalatine bone shallow.

Holotype.—A nearly complete left upper tooth plate, AM F61203 (Figure 5.1).

Type locality and horizon.—Bore DD10, depth 75 m, central area of the Duaringa Basin, 23° 51′ S, 149° 17′ E, Queensland, Tertiary (Traves, 1960). A more precise stratigraphic determination of the deposit is not possible because pollen in the surrounding matrix is sparse (Kemp, 1982a).

Other material.—AM F61798, a large upper tooth plate that resembles the holotype, from Duaringa, 23° 51′ S, 149° 17′ E, in bore CDD3. Additional specimens are a small upper tooth plate, UCMP 129506, from Lake Pitikanta, 28° 21′ S, 138° 18′ E, South Australia, and two specimens from Lake Pinpa, 31° 08′ S, 140° 13′E, South Australia, QM F14981, a small upper, and QM F14982, a small lower. Lake Pitikanta is Etadunna Formation and Lake Pinpa is Namba Formation. Both are Late Oligocene–Middle Miocene (Rich et al., 1991).

Description.—*Archaeoceratodus djelleh* is a rare species, although it is represented in most major mid-Tertiary localities except those at Bullock Creek, in the Northern Territory, and at Riversleigh, in Queensland (Kemp, 1991a). The tooth plates are elongate and similar in size to those of the Recent *Neoceratodus forsteri* (Tables 2, 3). There are six or seven ridges, of variable length, in both upper and lower plates. The ridges are often so short as to be almost absent. There is considerable destruction of dentine and enamel on the mediolingual face of the tooth plates, and reparative enamel may be formed over the roughened surface in some specimens. Cusps on the labial extremities of the ridges are absent, but incremental lines are present in the enamel in this area. The mediolingual junction is curved, with no trace of an inner angle. Clefts between the ridges, where present, are wide, shallow and curved. Labial profiles of the ridges are upright, usually lack cusps, and both upper and lower tooth plates end in a heel. The crests of the ridges from ridge two to the last are straight and parallel.

Because the tooth plates of *Archaeoceratodus djelleh* have true petrodentine that forms complex punctations, and because details of the tooth plates and jaw bones do not match those of species of *Neoceratodus* (Figures 4, 6.1, 6.2), *A. djelleh* has been made the type of a new genus.

ARCHAEOCERATODUS ROWLEYI new species
Table 2; Figures 5.6, 6.3

Neoceratodus species 2 KEMP, 1991a, p. 478, pl. 4B.

Diagnosis.—Punctations complex and arranged in knobs, short lines, and polygons; medial edge of upper tooth plate a wide curve; no buttress or slope on ridge 1 of upper jaw; enamel-to-bone junction of labial face of tooth plate straight; basal sulcus on pterygopalatine bone deep; ridge bases square; base of upper tooth plate curves dorsally.

Holotype.—QM F14983 (Figure 5.6), a right upper tooth plate with some bone attached.

Etymology.—The species is named after Mr. B. Rowley of Rockhampton, Queensland, who donated the specimen to the Queensland Museum.

Type locality and horizon.—CQ slot cut, Shale Oil Site, Rundle, 20° 32′ S, 148° 38′ E, central Queensland, Rundle Formation, Eocene (Henstridge and Missen, 1982).

Other material.—QM F14984, a fragment of an upper tooth plate consisting of ridges 2 and 3 with traces of bone attached, from the same locality as the holotype.

Description.—*Archaeoceratodus rowleyi,* one of only four species of dipnoan represented in Eocene deposits of Australia (Kemp, 1991a), is known only from the upper dentition and attached jaw bone. The holotype is elongate and of moderate size (Table 2). There are seven ridges with sparse, indistinct cusps on the upright labial margin of each (Figure 5.6). The enamel on the unworn surfaces of the tooth plate carries discrete

TABLE 2—Sizes of upper tooth plates in millimeters.

	Minute	Small	Medium	Large
Neoceratodus forsteri (Recent)				
Length	2.0 ± 1.0	8.9 ± 1.5	19.7 ± 2.8	28.5 ± 2.8
Breadth	0.3 ± 0.2	2.0 ± 0.6	6.1 ± 0.8	7.5 ± 1.3
Number	17	12	15	24
Neoceratodus eyrensis				
Length	–	17.5 ± 1.3	26.1	36.0
Breadth	–	5.6 ± 0.6	7.7 ± 1.5	11.2
Number	–	3	2	1
Neoceratodus nargun				
Length	–	13.3	23.4 ± 2.7	34.5
Breadth	–	2.5	4.1 ± 0.7	10.0
Number	–	1	2	2
Archaeoceratodus avus				
Length	–	–	34.4	–
Breadth	–	–	8.3	–
Number	–	–	1	–
Archaeoceratodus djelleh				
Length	–	23.1 ± 1.9	–	5.6
Breadth	–	5.7 ± 1.2	–	8.2
Number	–	7	–	1
Archaeoceratodus rowleyi				
Length	–	–	25.4	–
Breadth	–	–	8.0	–
Number	–	–	1	–
Archaeoceratodus theganus				
Length	–	24.2 ± 0.2	29.2 ± 3.0	–
Breadth	–	5.0 ± 0.8	6.2 ± 0.9	–
Number	–	2	6	–
Mioceratodus anemosyrus				
Length	8.6 ± 0.7	20.8 ± 1.9	26.3 ± 1.2	42.9 ± 2.0
Breadth	2.6 ± 0.5	5.4 ± 0.7	6.9 ± 0.4	10.3 ± 0.5
Number	3	17	2	2
Mioceratodus diaphorus				
Length	11.3 ± 2.1	18.9 ± 3.0	28.3 ± 2.8	43.8 ± 9.1
Breadth	2.9 ± 0.9	4.0 ± 0.5	4.2 ± 0.6	5.1 ± 1.0
Number	4	10	5	2
Mioceratodus gregoryi				
Length	–	19.8 ± 1.8	32.6 ± 6.0	53.4 ± 3.8
Breadth	–	4.2 ± 0.2	5.7 ± 1.0	12.1 ± 1.5
Number	–	3	3	8
Mioceratodus poastrus				
Length	–	22.8 ± 1.8	29.2 ± 1.0	41.2 ± 2.8
Breadth	–	4.7 ± 0.5	6.7 ± 0.4	8.5 ± 1.1
Number	–	3	3	3

incremental lines. The tooth plate ends in a double last ridge, and the crests of ridges 2 to the last are straight and radiating. Ridge crests are faceted slightly but have occlusal spurs on both specimens, and the furrows between the ridges are wide, rounded, and deep. The crests do not extend to the mediolingual face. The occlusal surface is worn smooth, and destruction of dentine and enamel on the mediolingual face is absent in both specimens.

ARCHAEOCERATODUS THEGANUS new species

Tables 2, 3; Figures 5.7–5.13; 6. 4, 6.5

Neoceratodus sp. 3 KEMP, 1991a, p. 444, 445, 449, pl. 2E, F, 3B.
Neoceratodus sp. 5 KEMP, 1991b, p. 480–482, pl. 6A.

Diagnosis.—Punctation pattern complex and arranged as knobs and short lines; procumbent mediolingual keel absent; medial edge of tooth plate a wide curve in upper jaw and nearly straight in lower; no buttress or slope on ridge 1 of either jaw; enamel-to-bone junction irregularly wavy on labial aspect of tooth plates; basal sulcus on pterygopalatine bone distinct; base of upper tooth plate curves dorsally.

TABLE 3—Sizes of lower tooth plates in millimeters.

	Minute	Small	Medium	Large
Neoceratodus forsteri (Recent)				
Length	1.8 ± 0.6	8.4 ± 1.2	19.3 ± 2.6	28.0 ± 2.6
Breadth	0.3 ± 0.1	1.8 ± 0.4	5.0 ± 0.7	6.0 ± 1.2
Number	22	12	15	23
Neoceratodus eyrensis				
Length	–	16.0	27.8	35.9
Breadth	–	4.0	7.9	8.4
Number	–	1	1	1
Neoceratodus nargun				
Length	–	14.0	20.3 ± 1.0	32.0
Breadth	–	2.9	4.2 ± 0.7	9.7
Number	–	1	2	1
Archaeoceratodus avus				
Length	–	–	–	–
Breadth	–	–	7.2	–
Number	–	–	1	–
Archaeoceratodus djelleh				
Length	–	24.1 ± 0.8	–	–
Breadth	–	5.0 ± 0.7	–	–
Number	–	3	–	–
Archaeoceratodus theganus				
Length	–	–	27.9 ± 1.6	–
Breadth	–	–	5.1 ± 0.6	–
Number	–	–	5	–
Mioceratodus anemosyrus				
Length	–	21.1 ± 2.2	28.2	–
Breadth	–	4.3 ± 0.7	6.4	–
Number	–	13	1	–
Mioceratodus diaphorus				
Length	11.5 ± 2.4	20.0 ± 2.7	27.9 ± 0.5	43.1 ± 1.5
Breadth	2.3 ± 0.6	3.4 ± 0.6	4.3 ± 0.1	6.1 ± 1.3
Number	14	20	2	2
Mioceratodus gregoryi				
Length	–	21.4 ± 0.6	–	56.1 ± 4.8
Breadth	–	4.2 ± 0.2	–	9.6 ± 1.5
Number	–	4	–	7
Mioceratodus poastrus				
Length	–	18.5	30.9 ± 4.0	49.1 ± 5.6
Breadth	–	3.6	5.2 ± 0.9	8.2 ± 1.6
Number	–	1	4	5

Holotype.—MV P160504 (Figure 5.7), an upper tooth plate with some bone attached, and MV P160498 (Figure 5.8), a matching lower tooth plate fragment from the same individual.

Etymology.—The specific name, *theganus,* is derived from the Greek *thegane,* a whetstone, in recognition of the peculiar attrition found on the surface of many specimens (Kemp, 1991a, 1991b).

Type locality and horizon.—Lake Pinpa, 31° 08′ S, 140° 13′E, South Australia, Namba Formation, Late Oligocene to Middle Miocene (Rich et al., 1991).

Other material.—SAM P23470, QM F12207, and QM F12314 from Lake Kanunka, 28° 23′ S, 138° 18′ E, South Australia, Etadunna Formation, Late Oligocene to Middle Miocene, and QM F11026, MV P194526, and MV P160499 from the type locality.

Description.—*Archaeoceratodus theganus* occurs in most major mid-Tertiary localities of central Australia, although it is never common. It has been recorded from the northern Australian mid-Tertiary deposits at Bullock Creek and at Riversleigh and is found in Pliocene sands at Lake Palankarinna,

South Australia. *Archaeoceratodus theganus* has exceptionally long, low-crowned, narrow tooth plates of small to moderate size with seven or eight, short, widely spaced ridges in both jaws. The mediolingual aspect of the tooth plate sometimes shows destruction of dental tissues, and reparative enamel covers the damaged area in a few specimens. Cusps on the steep labial face of each ridge are sparse, indistinct, and in line with incremental lines in the enamel. There is no inner angle because the mediolingual junction of the tooth plate is curved. Both upper and lower tooth plates may end in a single or double last ridge, and the crests of ridges 2 to the last are straight and radiating.

ARCHAEOCERATODUS AVUS (Woodward, 1906) new combination
Tables 2, 3; Figures 5.14, 6.6, 6.7

Ceratodus avus WOODWARD, 1906, p. 2–3, pl. 1, fig. 1; KEMP, 1982b, p. 134; KEMP, 1991a, p.470, 472, 473, pl.3F.
Ceratodus laticeps (Woodward, 1906). WADE, 1931, p.123.
Sagenodus laticeps (Woodward, 1906). WOODWARD, 1908, p. 6–8, pl. 11, figs. 1–4.
Neoceratodus avus (Woodward, 1906). SCHULTZE 1992, p. 309.
A full synonymy list is given in Schultze, 1992.

Amended diagnosis.—Punctations coarse and complex, arranged in polygons; procumbent mediolingual keel absent; medial edge of upper tooth plate a wide curve; enamel-to-bone junction straight between ridges on labial face of tooth plate; ridge bases rounded.

Holotype.—MV P10057 (Figure 5.14), an incomplete left lower tooth plate with some prearticular bone attached.

Type locality and horizon.—Cape Paterson, Victoria (Woodward, 1906), originally described as Lower Jurassic, but now regarded as Strzelecki Group, Early Cretaceous (Wagstaff and Mason, 1989).

Referred material.—An incomplete and damaged specimen, MMF 24788, and an isolated scale, MMF 13460, were described by Woodward (1908) as *Sagenodus laticeps* because the material was thought to have come from a Permian deposit, the Hawkesbury Sandstone at St. Peters in New South Wales, and because *Sagenodus* was regarded then as the characteristic Permian species of lungfish. Subsequent work (Nashar, 1967; Wade, 1931) showed that these rocks belong in the Triassic Ashfield Shale. Wade (1931) placed the species in the genus *Ceratodus.* The material is badly preserved and consists of a macerated head and part of the body with some scales. Little is recognizable in the head region except for the anterior part of the distinctively patterned, fan-shaped parasphenoid, fragments of the shoulder girdle, and the anterior half of the pterygopalatine bones that have been sheared transversely below the teeth. Thus, nothing shows of the occlusal punctation pattern of the teeth, but in shape, the bone base of the upper tooth plates closely resembles the lower tooth base of *Archaeoceratodus avus.* The bases of the upper tooth plates are in a natural position and are close together along the midline. Microscopic structure of this region includes bony trabeculae with little dentine and a layer of thick enamel with growth lines that covers the labial extremities of the ridge bases. The base of the tooth plate is deep in MV P10057, and the parts that are left in the upper bone are comparable in depth. Sufficient characters are present to place this specimen in the same species as MV P10057.

Description.—This species is one of several Australian dipnoan taxa that apparently existed with little evolutionary change in tooth plate structure for a long time. Material of this species is unfortunately fragmentary. The tooth plates are of moderate size, elongate with four short robust ridges in both jaws. Cusps are absent from the upright labial profile of the ridges of the lower jaw, but incremental lines are evident in the enamel. Absence of cusps in MV 10057 is probably incidental because specimens without cusps are known in the Recent *Neoceratodus forsteri,* which usually has cusped ridges.

Archaeoceratodus avus shares several important characters with *A. djelleh* and none with *Neoceratodus forsteri.* In both *A. avus* and *A. djelleh,* punctations are complex, with polygons formed from petrodentine (sensu Lison, 1941) and enclosing punctations that develop from interdenteonal and circumpulpar dentine as in *N. forsteri* (Kemp, 1992b). Both also have elongate tooth plates with robust short ridges (Figures 5.14, 6.6, 6.7). There is no inner angle, and the mediolingual aspect is curved. In addition, *A. avus* has little in common with species of *Ceratodus* from other parts of the world, particularly with the type species, *Ceratodus latissimus,* a Triassic species from Aust Cliff in England (Agassiz, 1838).

Although this species has been placed recently in the genus *Neoceratodus* by Schultze (1992), without explanation, this determination is incorrect.

Genus MIOCERATODUS Kemp, 1992a

Type species.—*Mioceratodus anemosyrus* Kemp, 1992a.

Diagnosis.—(on tooth plates) pulp cavity wide; mantle dentine extensive; ridges originate from anterior or modified anterior position; upper tooth plates close but not contiguous, lower widely separated; upper symphysis elliptic or orbicular, lower linear; pterygopalatine process present; prearticular sulcus double or confluent; punctations complex; petrodentine (*sensu* Lison, 1941) present (Table 1).

This genus has been described previously on skull bones and tooth plates (Kemp, 1992a). Diagnosis on tooth plates is given to facilitate comparison with species in which no skull material is preserved.

Distribution of genus.—Species referable to the genus *Mioceratodus* occur in Eocene, Late Oligocene–Middle Miocene and Pliocene–Pleistocene deposits of eastern, central, and northern Australia (Kemp, 1992a).

MIOCERATODUS ANEMOSYRUS Kemp, 1992a
Tables 2, 3; Figures 7, 10.1, 10.2

Mioceratodus anemosyrus KEMP, 1992a, pp. 285–286 figs. 4–6.

Diagnosis.—(on tooth plates) punctations complex and arranged in knobs, short lines, and polygons; procumbent mediolingual keel absent, medial edge of tooth plates a wide curve; ridge 1 of upper slender and falcate, of lower slender and acute or falcate; posterior ridges of both tooth plates acute; first ridge curves in and out evenly to symphysis in upper plate; first ridge curves into symphysis in lower; enamel-to-bone junction rises between each ridge.

Holotype.—QM F15005, an upper tooth plate with attached pterygopalatine bone and complete ascending process (Figure 7.1).

Type locality and horizon.—Melodie's Maze, at Riversleigh, 19° 00′ S, 138° 31′ E, north Queensland; Carl Creek Limestones, Middle Miocene (Megirian, 1992).

Other material.—NTM P8695–83, NTM P8694–4, NTM P87112–10, and NTM P87112–1 (Bullock Creek, 17° 47′ S, 131° 31′ E, Northern Territory), QM F14995 and QM F18623 (Riversleigh, 19° 00′ S, 138° 31′ E, north Queensland); AMNH 11345 and AMNH 11399 (Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia) ; QM F12336 (Leaf Locality, 28° 17′ S, 138° 17′ E, South Australia). Bullock Creek is Camfield Beds, Middle Miocene (Megirian, 1992), as is the Riversleigh locality. Lake Pinpa is Namba Formation, Late Oligocene–Middle Miocene, and the Leaf Locality is Wipijiri Formation, also Late Oligocene–Middle Miocene (Rich et al., 1991).

Description.—A detailed diagnosis and description of skull structure and associated characters of the jaw bones in *Mioceratodus anemosyrus* is given in Kemp (1992a). Tooth plates are described here for comparison with species known only from the dentition.

Tooth plates of *Mioceratodus anemosyrus* are usually small, but a single large specimen has been collected from the Namba Formation at Lake Pinpa, South Australia. Both upper and lower tooth plates are elongate with rounded mediolingual contours. The tooth plates have six or seven straight or slightly curved ridges that are often arranged in a fan shape, particularly in the upper jaw. Destruction of dentine and enamel on the mediolingual face is slight. Cusps, if present, are sparse, indistinct, and compressed in line with the long axis of the ridge. Clefts between the ridges are wide, curved, and shallow. The labial profile of the ridges is upright or steep, and both upper and lower plates may end in a heel or a single last ridge. The wear pattern on the ridge crests is usually faceted, and furrows are rounded.

Those characters of the jaw bones that are inherently variable in *Neoceratodus forsteri* show little variation in this species. The upper symphysis is oval with shallow upright grooves. In the linear lower symphysis, grooves are few in number and also shallow and upright. The pterygopalatine process rises from the base of the third ridge, the sulcus below the pterygopalatine bone is distinctive, and the prearticular sulcus is divided with a small anterior portion.

Polished thin sections of *Mioceratodus anemosyrus* tooth plates show that the clear hard dentine on the occlusal surface is petrodentine sensu Lison (1941). It is hypermineralised, containing only small amounts of fine collagen fibres and, unlike the interdenteonal dentine, is not transected by denteons surrounded by circumpulpar dentine (Kemp, 1992b).

MIOCERATODUS GREGORYI new combination
Tables 2, 3; Figures 8, 10.3, 10.4

Epiceratodus gregoryi WHITE, 1925, p. 141, pl.7, fig. 1.
Epiceratodus denticulatus (White, 1925). HILLS, 1934, p.157–159, fig. 1.
Neoceratodus gregoryi (White, 1925). KEMP AND MOLNAR, 1981, p. 211, fig. 8. KEMP, 1982b, p. 134, figs. 5 B, 6 D, 6 E.
Mioceratodus gregoryi (White, 1925). KEMP, 1992a, p. 285.
Schultze (1992) provided a full synonymy list.

Diagnosis.—Punctations complex and coarse and arranged as knobs, short lines, and interdigitating lines; mediolingual keel absent; medial edge of upper tooth plate sharply curved; medial edge of lower widely curved; enamel-to-bone junction on labial face rises slightly between each ridge.

Holotype.—HMV 3891, collected by Gregory (1909); a light-brown upper tooth with some bone attached (Figure 8.4).

Type locality and horizon.—Lower Cooper Creek, 28° 30′ S, 138° 20′ E, South Australia. Malkuni fauna, correlative to the Katipiri Sands, Pliocene (Stirton et al., 1961).

Other material.—Upper tooth plates AMNH 1675, AMNH 11325, and AMNH 11368 (Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia) and QM F11024 (Frome Downs, 30° 23′ S, 139° 56′ E, South Australia), AMNH 11331 (Lake Kanunka, 28° 23′ S, 138° 18′ E, South Australia), QM 15010 (Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia). Lower tooth plates are NTM P 8694–8 (Bullock Creek, 17° 47′ S, 131° 31′ E, Northern Territory), AMNH 11320, AMNH 11330, (Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia), and AMNH 11384 (Ericmas Quarry, 31° 12′ S, 140° 14′ E), South Australia. Lake Kanunka and Frome Downs are Etadunna Formation, Late Oligocene–Middle Miocene. Ericmas Quarry and Lake Pinpa are Namba Formation, Late Oligocene–Middle Miocene (Rich et al., 1991). Bullock Creek is Camfield Beds, Middle Miocene (Megirian, 1992).

Referred material.—*Epiceratodus denticulatus* (QM F2347) from Redbank Plains, 27° 40′ S, 152° 45′ E, near Brisbane, Queensland, was described by Hills (1934) on the basis of a macerated specimen with impressions of both upper and lower tooth plates. These correspond closely with tooth plates of *Mioceratodus gregoryi* juveniles (Kemp, 1991a). Skull bones also correspond with those of *M. gregoryi*. *E. denticulatus* is synonymized with *M. gregoryi*. The Redbank Plains deposit is in the Redbank Plains Formation, Eocene (Kemp, 1991a). This material was identified as *Neoceratodus* sp. by Schultze (1992), but no reasons were given.

Impressions of the tails of lungfish, also from Redbank Plains, have been referred to *Epiceratodus denticulatus* (Hills, 1934), though they are not associated with identifiable skeletal or dental remains. Recently acquired material from Redbank Plains consists of broken but recognizable tooth plate and skeletal fragments (QM F14986) and additional impressions of skull bones. These specimens are referred to *Mioceratodus gregoryi*.

The fossil described as a scale of *Epiceratodus* by Hills (1943) is an impression of a fragment of turtle carapace.

Description.—Tooth plates of *Mioceratodus gregoryi* attained a large size, many being well over 35 mm in length, and small specimens are rare (Tables 2, 3). They display some variability. Both upper and lower tooth plates are elongate with 6 or 7 ridges, or occasionally 8. Erosion of the mediolingual face may be absent, slight, moderate, or severe. Cusps are sometimes absent. If present, they are sparse, indistinct, and compressed in line with the long axis of the ridge. The mediolingual junction is a rough curve, and the last ridge of the tooth plate makes an angle greater than 45° to the lingual face. Clefts between the ridges are wide and curved, deep anteriorly, and become progressively shallower posteriorly. The labial profile of the ridges is upright or steep, and upper or lower plates may end in a heel or a single last ridge. The wear pattern on the ridge crests is faceted and furrows are rounded. Wear is often extreme in this species, particularly in large specimens.

Those characters that are inherently variable in other species show little variation in *Mioceratodus gregoryi*. Crests of ridges 2 to the last are curved and parallel or subparallel in both jaws. The upper symphysis has an unusual orbicular shape with many deep upright grooves. The pterygopalatine process rises from the base of ridge 3 and slightly anterior to it. The smallest juveniles referred to this species resemble the large specimens in the criteria used for specific diagnosis. However, the crests of the ridges tend to be radiating rather than subparallel, and they are straight.

Remarks.—*Mioceratodus gregoryi* differs in many significant details from species of *Neoceratodus*, particularly in the punctation pattern of the occlusal surface, the shape of the ridges of the tooth plate, the form of the upper symphysis, and in shapes of the skull bones (Kemp, 1991a, 1992a). Skull bones, tooth plates and jaw bones are closer to those of *M. anemosyrus* than to those of *N. forsteri*.

Martin (1982b) has used superficial similarities in the illustrations of *Mioceratodus gregoryi* and related species (Kemp, 1982a; Kemp and Molnar, 1981) to *Ceratodus africanus* (Haug, 1904) to include the latter in the genus *Neoceratodus*. While there are certain comparable points between *M. gregoryi* and *C. africanus*, such as strongly indented parallel ridges, these similarities are dependent on growth and wear and are unreliable as generic indicators. *Ceratodus africanus* and related species, *C. tuberculatus* and *C. pectinatus* (Tabaste, 1963), should not be included with *N. forsteri* because they do not resemble any species of the genus *Neoceratodus*. For the same reason, they do not belong in the genus *Mioceratodus*.

MIOCERATODUS POASTRUS new species
Tables 2, 3; Figures 9.1–9.5, 10.5–10.6

Epiceratodus eyrensis (in part) WHITE, 1925, p. 139, pl. 6, fig. 7.9, pl. 8, fig. 4.
Neoceratodus species 1 KEMP, 1991a, p. 478–483, pl. 4 A; KEMP, 1991b, p. 447, 450.

Diagnosis.—punctation pattern delicate and complex, arranged in knobs and lines; medial edge sharply curved in upper jaw and widely curved in lower; enamel-to-bone junction straight on the labial face of both jaws; lower symphysis extends anteriorly beyond tip of ridge 1; basal sulcus on pterygopalatine shallow; ridge bases sloping.

Holotype.—AMNH 11322, a large well-preserved lower tooth plate with complete bone attached (Figure 9.1).

Etymology.—The specific name *poastrus,* from the Greek *poastrion,* a sickle, refers to the smooth curves characteristic of the tooth plates.

Type locality and horizon.—Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia; Namba Formation, Late Oligocene–Middle Miocene (Rich et al., 1991).

Other material.—UCMP 56990 , an upper tooth plate with bone attached, from Lake Kanunka, 28° 23′ S, 138° 18′ E, South Australia, Etadunna Formation, Late Oligocene to Middle Miocene (Rich et al., 1991), shares the important characters of the holotype. Additional upper jaws are QM F15012 (Lake Ngapakaldi, 28° 17′ S, 138° 17′ E, South Australia) and RV 22332 (Stirton Quarry, 28 ° 23′ S, 138 ° 18′ E, South Australia), both Etadunna Formation, Late Oligocene to Middle Miocene (Rich et al., 1991). HMV 3887 (Coopers Creek, South Australia) is a lower jaw from the original material collected by Gregory (1909).

Description.—*Mioceratodus poastrus* is a common species, found in most central and northern Australian mid-Tertiary and Pliocene deposits, as well as the Eocene locality at Rundle in Queensland (Kemp, 1991a). The tooth plates are usually small, but can attain a large size. Both upper and lower tooth plates are elongate, with seven or eight long slender ridges with curving outlines. Removal of dentine and enamel from the mediolingual face is absent. Cusps on the sloping ridge extremities are sparse and indistinct and usually associated with incremental lines in the enamel. Upper and lower tooth plates may end in a single or double last ridge, and ridge crests are radiating, slightly curved in the upper jaw and straight in the lower. Grooves in the upper symphysis are absent. The pterygopalatine process arises from the base of ridge 3 and slightly anterior to it.

Specimens belonging to this species were originally included with *Neoceratodus* (*Epiceratodus*) *eyrensis* (White, 1925). These are all lower jaw tooth plates, but they do not match the holotype of *N. eyrensis,* an upper tooth plate. New material from Australian collections has produced upper tooth plates that match White's lower jaw specimens (White, 1925: plate 6, figure 7.9 and plate 8, figure 4), as well as lower tooth plates that match the holotype of *N. eyrensis.*

MIOCERATODUS DIAPHORUS new species
Tables 2, 3; Figures 9.6–9.12, 10.7, 10.8

Neoceratodus eyrensis KEMP AND MOLNAR, 1981, p. 215, pl. 1, figs. 9,10; KEMP, 1982b, p. 134, fig. 6 B, table 2.
Neoceratodus species 4 KEMP, 1991a, p. 480–482, pl. 6B, 6C; KEMP, 1991b, p.444, 448, 454, pls. 2B–D, 4E, 5A.

Diagnosis.—Punctation pattern complex, arranged in coarse knobs; mediolingual keel large and procumbent; medial edge of ridge 1 a wide curve in upper jaw and straight in lower; inner angle acute; enamel-to-bone junction irregularly wavy on labial face of both tooth plates; basal sulcus on upper jaw bone deep.

Holotype.—QM F11023 (Figure 9.6) a large nearly complete upper tooth plate with bone attached, included originally with *Neoceratodus eyrensis* (Kemp and Molnar, 1981). It differs from the latter species in many significant characters, and new specimens that match QM F11023 have since been collected.

Etymology.—The specific name, *diaphorus,* is derived from the Greek *diaphoris* meaning different because this species has many unusual characteristics, related mainly to a high proportion of developmental abnormalities (Kemp, 1991a).

Type locality and horizon.—Frome Downs, 30 ° 23′ S, 139 ° 56′ E, South Australia; Etadunna Formation, Late Oligocene–Middle Miocene.

Other material.—AMNH 11347 (Figure 9.7), a small upper tooth plate from another site at Lake Pinpa, 31° 08′ S, 140° 13′ E, South Australia, shares the diagnostic specific characters with QM F11023; and NTM P894–4 from Bullock Creek, 17° 47′ S, 131° 31′ E, Northern Territory (Figure 9.8). Lower tooth plates used are AMNH 11324 (Figure 9.11) (Lake Pinpa, South Australia), UCMP 129509 (Figure 9.10) (locality unknown, South Australia), and NTM P8695–81 (Figure 9.12), Bullock Creek, Northern Territory. Lake Pinpa is Namba Formation, Late Oligocene–Middle Miocene (Rich et al., 1991). Bullock Creek is Camfield Beds, Middle Miocene (Megirian, 1992).

Description.—Although never as common as other species of this genus, *Mioceratodus diaphorus* is represented in most of the Late Oligocene–Middle Miocene localities in central and northern Australia and occurs in several Pliocene deposits. It attained a large size (Tables 2, 3), but most specimens are small. Tooth plates of this species are strongly triangular and high crowned with long, slender, deeply indented ridges, seven or eight in number in both jaws. Destruction of dental tissues on the mediolingual face is common and may reach pathological proportions (Kemp, 1991b), but the damaged surface is never covered in reparative enamel. Cusps are numerous, distinct, and compressed across the long axis of the ridge. The labial profile of the unworn ridge extremities is sloping and nearly horizontal in the more posterior ridges. Both upper and lower tooth plates may end in a single or double last ridge. The crests of ridges 2 to the last are radiating, straight in the lower and straight or curved in the upper.

DISCUSSION

The Recent lungfish was first described as *Ceratodus forsteri* by Krefft (1870), who noted the similarity of the dentition of the fossil tooth plates described by Agassiz (1838) to the tooth plates in the newly discovered living fish. When Teller (1891) described *Ceratodus* (*Tellerodus*) *sturii,* a Triassic fossil lungfish consisting of a partial skull associated with ceratodont tooth plates that differ in important ways from those of *Neoceratodus forsteri,* morphological reasons for separating the living lungfish from its fossil relatives became apparent. Teller retained the name *Ceratodus* for the fossil material and proposed the name *Epiceratodus* for the living species. However, de Castelnau (1876a) had already described a specimen of the Australian lungfish as a new species, *N. blanchardi.* This species proved to be identical with *N. forsteri* (de Castlenau, 1876b), but the name *Neoceratodus* takes precedence over *Epiceratodus* if the living lungfish is to be separated from the fossil forms on anatomical grounds (Bertin, 1940).

Description of the Recent Australian lungfish was followed by the discovery of several Mesozoic and Cenozoic fossil dipnoans, placed either in *Ceratodus* or *Neoceratodus* except for one, *Gosfordia truncata,* which has many unique characters (Ritchie, 1981; Woodward, 1890). New studies of Australian Mesozoic and Cenozoic fossil lungfish have suggested that this taxonomy is too simple (Kemp, 1992a, 1993a, 1993b, 1994, 1995b). Unfortunately, separation of species known only from tooth plates is made more difficult because many criteria are

variable within one species and can be hard to define precisely, such as the shape of the posterior end of the tooth plate and the number of ridges present. However, Australian Mesozoic and Cenozoic dipnoans can be divided into several genera on the basis of morphological criteria based on tooth plate and jaw characters if these are chosen with care. These are *Archaeoceratodus,* a genus with elongate narrow tooth plates and short robust ridges, *Mioceratodus,* having long tooth plates and slender curving ridges, and *Neoceratodus,* with elongate oval tooth plates and short ridges. Australian deposits include a few isolated species of *Metaceratodus* (Chapman, 1914; Kemp, 1997; Schultze, 1992) and a single representative of *Ceratodus* (Kemp, 1993a).

Biometry, based on angles between ridges or on ratios of length and breadth of the tooth plate, is not useful to separate Australian species. As with other characters that depend on measurements, angles are not valid taxonomic characters unless derived from a large statistical sample. Angles between the ridges also change as the tooth plate grows (Kemp, 1977), particularly early in development. Technical difficulties cause problems too because angles measured along the wear crest of the ridge differ from angles measured on the growing labial extremity of the ridge (Kemp, 1977; Kemp and Molnar, 1981). In the Australian material, angles are similar in visually different tooth plates, and equivalent objections apply to ratios of length to breadth.

Developmental abnormalities, like intercalated or divided ridges and short ridge anomaly, have been used in a taxonomic sense, but these can be misleading, although they are common among dipnoans (Kemp, 1991b, 1996). Taxonomic characters for Australian dipnoans have to be based on the known normal morphology of the species concerned.

Incremental lines in the enamel have been regarded as a good character for taxonomic purposes in lungfish (Zidek, 1975), but clearly marked incremental lines in the enamel surrounding the dipnoan tooth plate are universal, as are incremental lines within the dentines. Cusps, or denticles, at the labial extremities of the ridges are equally invalid as taxonomic determinants. All lungfish with tooth plates based on radiating ridges have cusped or denticulated tooth plates at some stage in the life cycle, and the structures are part of the continuing growth process in all (Kemp, 1977, 1979, 1995c; Lund, 1970, 1973). Most adult lungfish have cusps or traces of cusps on the labial extremities of the ridges associated with the incremental lines in the enamel.

Species of *Archaeoceratodus* and *Mioceratodus* have complex occlusal surfaces including petrodentine (sensu Lison, 1941) as well as interdenteonal and circumpulpar dentine (Kemp, 1991a, 1992a, 1992b; Lund et al., 1992). This results in variable degrees of wear on the tooth surface because petrodentine is harder than interdenteonal dentine and wears more slowly. *Neoceratodus* species lack petrodentine sensu strictu, and wear on the occlusal surface is smoother. The term petrodentine, initially used to describe a specific hard tissue in *Protopterus* (Lison, 1941), and found in *Sagenodus, Gnathorhiza, Mioceratodus,* and *Archaeoceratodus* (Kemp, 1992b; Lund et al., 1992), was not used at first to describe most of the hard tissue found in lungfish tooth plates (Denison, 1974). Extension of this term (Smith, 1984) to include the dentines in most dipnoan tooth plates is without justification (Kemp, 1991b, 1992b, 1996; Lund et al., 1992) and the name should be restored to its original usage (Lison, 1941).

Martin (1982b) has used a character analysis to separate Australian, European, and African dipnoans using seven tooth plate characters and two bone characters. Use of these characters to separate even a limited number of genera does not work because only one of the characters stands up to critical analysis. This character, a bar of bone across the sulcus on the ventral surface of the prearticular bone ("Ruge's Ridge," Martin, 1982b, p. 54), applies only to the lower jaw. The smallest size class of *Neoceratodus forsteri* differs in this character from the condition in the largest, but it is otherwise consistent, and with slight modifications, can be useful also for other genera, if the prearticular bone is preserved. To avoid confusion with names of parts of the tooth plate, the character is redefined in this paper as a single or divided prearticular sulcus, with the anterior portion small or vestigial. In *Archaeoceratodus,* the two sulci are confluent. Five other characters are not useful. One of these, the position of the pterygopalatine process, shows variability within a single species, *N. forsteri,* depending on diet and environmental factors (Kemp, 1991a). The other four characters are unreliable because they change with growth or with growth and wear. These are two characters of the "inner angle" and two wear features of the occlusal surface, crests parallel or radiating, flat or furrowed. It cannot be determined with certainty if a fossil tooth plate came from an adult and fully formed fish, and characters of the ridge crests vary considerably among large ("adult") specimens of *N. forsteri.* Another character, the position of the right upper or lower tooth plates in relation to the left upper or lower tooth plates does not vary across a range of different genera and is not useful unless it is qualified. Most species have upper tooth plates separated by a narrow space and lower tooth plates separated by a wide space, although a few are contiguous. Number of ridges is unhelpful for most Mesozoic and Cenozoic tooth plates. One of the categories, less than seven ridges, accounts for nearly all of the species considered, and several, including *N. forsteri,* belong in two categories, less than seven and seven to twelve ridges. Of the two remaining characters, the "length of ridge 1 in relation to the length of the lingual face," (Martin, 1982b, p. 54) is potentially useful, but the length of ridge 1 is hard to measure because its starting point can be difficult to determine in tooth plates with damaged mediolingual regions. Ridge 1 is often broken in Australian specimens. A further character, "first valley (cleft between ridge 1 and 2) as long as the following or longer," (Martin, 1982b, p. 54) is of no value because it is always longer than the more posterior clefts.

Generic characters used in this paper for the separation of Australian Mesozoic and Cenozoic dipnoans relate to both jaw bones and tooth plates. Upper characters are contiguity or separation of the tooth plates, the shape of the upper symphysis, and the presence of a pterygopalatine process. Lower characters are contiguity or separation of the tooth plates, the shape of the lower symphysis, and the form of the prearticular sulcus or sulci. Characters relating to both jaws are the size of the pulp cavity, the amount of mantle dentine visible on the occlusal surface, the origin of the ridges, and the presence of petrodentine. Specific characters are more numerous. They include the form of the enamel-to-bone junction on the medial face of the tooth plate, presence or absence of a procumbent mediolingual keel, length and shape of the ridges, and the relationship of the medial face of the tooth plate to the symphysis in each jaw. Detailed comparison of a large number of potential discriminating characters indicates that useful generic and specific features are limited and open to argument, and visual comparison of specimens, with comparison of occlusal profiles of described species may be required for a final decision. The characters chosen for taxonomic determination in these groups of dipnoans can be applied to other genera and species of dipnoans from Australia and from other continents (Kemp, 1992a, 1993a, 1993b, 1995b, 1996, 1997).

Several Australian species have apparently survived with little change in skeletal and dental stuctures over long periods of geological time. The Recent Australian lungfish, *Neoceratodus forsteri,* is found in the Early Cretaceous of Lightning Ridge, New South Wales, and in Pliocene deposits at Chinchilla in Queensland, as well as rivers and lakes in southeast Queensland.

Neoceratodus nargun is found in Early Cretaceous deposits in Victoria, and in Middle Miocene rocks in Queensland. *Archaeoceratodus avus* is known from Triassic and Cretaceous deposits in New South Wales. *Ceratodus diutinus* has been recorded from the Early Cretaceous of New South Wales and Queensland (Kemp, 1993a) and from the Late Oligocene–Middle Miocene of Lake Pinpa in South Australia. There seems to be little point in describing morphologically identical specimens as new taxa only because they appear to come from deposits of different ages, particularly in a group as bradytelic as the dipnoans. Leaders in evolutionary thought indicate that there are many examples of Recent teleostome fish also known as fossils that have changed little through geological time (Carroll, 1988; Williams, 1992). Giving the fossil specimens separate generic and specific names is not justified if the only difference is in their age.

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