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LATE TRIASSIC TRAVERSODONT CYNODONTS FROM NOVA SCOTIA AND SOUTHERN AFRICA

by

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ABSTRACT

The first gomphodont cynodont from North America is described from the Upper Triassic Wolfville Formation, Fundy Group, Newark Supergroup, of Burntcoat, Minas Basin, Nova Scotia, Canada. Known material consists of a large mandible, edentulous but for two incisors, a probably associated canine, and two small dentaries; an isolated multicusped tooth may belong to this species. This gomphodont closely resembles the large traversodont *Scalenodontoides macrodontes* from the lower Elliot Formation (= Red Beds) of Lesotho; it is provisionally placed in this genus but is a distinct species, ?*Scalenodontoides plemmyridon* sp. nov. It differs from *S. macrodontes* primarily in its more massive symphyseal region and much larger mental foramen from which a prominent groove extends posterodorsally. The large, posteriorly-located mental foramen is believed to be a well-developed oral vestibule and cheek. The isolated tooth, provisionally interpreted as a traversodont lower postcanine, is anteroposteriorly compressed, with a high anterior blade formed by three transversely-aligned cusps and a short heel; it does not resemble postcanines of *S. macrodontes* and so reference to ?*S. plemmyridon* is questionable. *Scalenodontoides* is the sister genus of *Exaeretodon* from the Late Triassic of Argentina, Brazil, and India; they are allied on the basis of: upper incisors reduced from 4 to 3, all incisors greatly enlarged, and internarial bar incomplete. These resemblances to tritylodontids are convergent. *Scalenodontoides* and *Exaeretodon* share with *Gomphodontosuchus* the enlargement of the anterolabial cusp of the lower postcanines and posterior inclination of the anterolingual cusp. The Wolfville and basal Elliot faunas are considered to be Late Carnian or Carno-Norian in age. Faunas containing *Exaeretodon* are older Carnian, though the Santa Maria Formation of Brazil may be Late Ladinian.

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INTRODUCTION

During the Triassic there occurred an extensive radiation of herbivorous cynodont therapsids which largely replaced the dicynodonts as the principal terrestrial herbivores of the Permo-Triassic. These cynodonts are characterized by having postcanine teeth which are transversely expanded and possess precise crown-to-crown occlusion comparable to that later developed by mammals. Their radiation had two phases : (1) a late Early Triassic to approximately mid-Late Triassic radiation of "gomphodonts" (the families Diademodontidae, Trirachodontidae, and Traversodontidae; Romer

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1967), and (2) a latest Triassic to Late Jurassic radiation of the family Tritylodontidae (Olsen and Galton 1977). This assemblage of gomphodonts plus tritylodonts constitutes the superfamily Tritylodontoidea (Hopson and Kitching 1972; Hopson and Barghusen, in press).

Gomphodont cynodonts are abundantly known from southern Africa, Tanzania, Argentina, and Brazil, and a few taxa have been described from Russia, China and India. To date, however, none has been described from North America.

Beginning in the late 1950's, field parties from Princeton University, McGill University, and the Nova Scotia Museum of Science have been collecting vertebrate fossils from the Upper Triassic Wolfville Formation at Burntcoat on the southern shore of Minas Basin, an arm of the Bay of Fundy, in Nova Scotia, Canada. Between 1963 and 1970, a number of specimens were collected which were tentatively identified as cynodonts. The best of these specimens, a large incomplete dentary from which all teeth but two incisors had been lost prior to burial, was identified by Dr. Donald Baird of Princeton University as a probable gomphodont. This specimen has been mentioned in print by Romer (1967, 1975) and Crompton (1972). Crompton states: 'A large lower jaw of what may prove to be a traversodontid cynodont was discovered in the Upper Triassic Wolfville Formation of the Newark Group in Nova Scotia by Dr. R.L. Carroll and Dr. D. Baird (Romer, 1967); unfortunately no postcanine teeth were preserved *in situ*, but the size of the jaw and the structure of the symphysis showed close similarity to *Scalenodontoides macrodontes* from southern Africa" (Crompton 1972:60). Several additional specimens from the Wolfville Formation probably pertain to the same cynodont species; these include a small but well-preserved partial dentary lacking teeth, another small dentary split longitudinally so that the empty alveoli are exposed, and an isolated canine (which is probably from the large jaw). In addition, a complete multicusped tooth is questionably referred to the cynodont.

A description of the Wolfville fossil localities at Burntcoat is given by Carroll *et al.* (1972). The fossils occur in conglomerate foreset deposits and sandstones, and the bones are dissociated, broken, and more or less water-worn. In addition to the cynodont, the fauna contains stereospondyl amphibians, procolophonids, trilophosaurids, various thecodonts and saurischians, an ornithischian, rhynchosaurs, and a dicynodont. Preliminary reports on the fauna have been published by Baird and Take (1959) and Baird (1963). The most recent summary of the fauna is by Baird and Olsen (1983).

Dr. Baird suggested that I describe the Burntcoat cynodont inasmuch as I have been engaged in a long-term study of the gomphodont cynodonts. For this study I have directly compared the Burntcoat material with the type jaws of *Scalenodontoides macrodontes* Crompton and Ellenberger 1957, which are housed in the Institut de Paléontologie, Paris, and with an undescribed partial snout of *S. macrodontes* in the South African Museum, Cape Town. I have also made comparisons with other gomphodont material from Africa and South America.

This study corroborates Crompton's (1972) suggestion of a close relationship between the Burntcoat gomphodont and *S. macrodontes*. The Nova Scotia cynodont is a new species which, on the basis of the size and preserved morphology of its lower jaw, should probably be placed in the genus *Scalenodontoides*. However, in the absence of undoubtedly associated postcanine teeth (on which the taxonomy of gomphodont cynodonts is primarily based), I am not completely confident about this generic allocation; therefore, I have qualified the generic references as ?*Scalenodontoides*.

In this paper I give revised diagnoses of the genus *Scalenodontoides* and the species *S. macrodontes*, based on restudy of the type specimen and study of new material. The Burntcoat species is named and diagnosed and the available specimens described. Following this is a consideration of the relationship of the new species to *S. macrodontes* and of the genus *Scalenodontoides* to other gomphodonts. I then consider the composition and age of the Wolfville fauna and of the fauna from the basal beds of the Elliot Formation (= Red Beds) from which *S. macrodontes* comes. Finally, the ages of related gomphodont genera are reviewed and the evolutionary history of Middle and Late Triassic gomphodonts is briefly discussed.

The system of classification adopted in this paper is a cladistic one in which only "natural" groups, i.e., groups which are monophyletic in the Hennigian sense, are recognized. As defined by Farris (1974); quoted by Wiley 1981: 76): "A monophyletic group is a group of species that includes an ancestral species (known or hypothesized) and all of its descendents." Such groups are recognized on the basis of synapomorphics – shared derived characters – possessed by their members. Groups which do not contain all of the descendants of the ancestral species are termed "paraphyletic" (see Wiley 1981: 86–92) and are not considered to be natural; an example of a paraphyletic group is the Reptilia, which is equivalent to the monophyletic group Amniota (whose members possess the amnion as a synapomorphy) minus Aves and Mammalia. As is evident from this example, the Synapsida (i.e. the mammal-like reptiles) are also a paraphyletic group, being equivalent to Theropsida minus Mammalia. Hopson and Barghusen (in press) have attempted to make a number of paraphyletic groups, such as Synapsida Therapsida, Theriodontia, and Cynodontia, strictly monophyletic by redefining them to include the mammals.

Within the non-mammalian cynodonts, i.e., the traditional reptilian-grade cynodonts, the gomphodonts plus tritylodontids form a strictly monophyletic group, the Tritylodontoidea. Within this group, however, the family Traversodontidae is not monophyletic. This is because the family Trtylodontidae is believed to be derived from within the family Traversodontidae (Crompton and Ellenberger 1957), which makes the latter group paraphyletic (Hopson and Barghusen, in press). The relationships of traversodontid genera to one another and to the tritylodontids have yet to be worked out so strictly monophyletic groups within the traversodontid/tritylodontid assemblage cannot yet be recognized. This paper is the first of a series in which I hope to determine such natural groups. For the time being, I use the term traversodont to refer to an informal group containing the taxa usually included within the family Traversodontidae.

Institutions mentioned in this paper are abbreviated as follows:—

MCZ — Museum of Comparative Zoology, Harvard University.
NSM — Nova Scotia Museum of Science, Halifax.
PU — Museum of Natural History, Princeton University.
SAM — South African Museum, Cape Town.

SYSTEMATIC PALEONTOLOGY

Genus *SCALENODONTOIDES* Crompton and Ellenberger 1957.

Type Species — Scalenodontoides macrodontes Crompton and Ellenberger 1957.

Diagnosis — A very large traversodont cynodont resembling *Exaeretodon* in possessing three, rather than the typical traversodont four, upper incisors and in having upper and lower incisors greatly enlarged and the internarial bar incomplete; differing from *Exaeretodon* in that the lower incisors and canine are more robust, the snout and lower jaw are relatively more massive, and the symphyseal region is broader, longer and deeper. The lower portion of the symphysis extends ventrally as a chin-like projection, is absent in *Exaeretodon.* The mental foramen on the lateral surface of the dentary is larger and more posterior in position than in other traversodonts. The lower postcanine teeth have the typical traversodont pattern of two transversely-aligned cusps on the anterior half of the crown and a posterior basined heel, but resemble the postcanines of *Exaeretodon* (and probably of *Gomphodontosuchus)* in that the anterolabial cusp is much larger than the anterolingual cusp and occupies approximately three-fifths of the transverse diameter of the crown; in other genera of traversodonts the labial cusp is transversely narrower than the lingual cusp. In crown view, the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct curve, concave lingually, whereas in *Exaeretodon* (and presumably *Gomphodontosuchus*) the ridge is straight.

Scalenodontoides macrodontes Crompton and Ellenberger 1957.

Holotype — Unnumbered specimen in the Institut de Paléontologie, Museum National d' Histoire Naturelle, Paris. Paired dentaries lacking the region behind the postcanines.

Horizon and Locality — Base of the Elliot Formation (= Red Beds), Stormberg 'Group', Karoo Supergroup, Upper Triassic; not upper layers of the Molteno Beds as originally described (see Turner 1972). "Site A" of Crompton and Ellenberger (1957), Morobong Hill, southwestern Lesotho.

Referred Specimen — SAM K336, right half of a large snout, collected at "Site B, approximately 100 yards west of Site A" (Crompton and Ellenberger 1957: 1).

Diagnosis — A species of the genus *Scalenodontoides;* dentary about the same size as that of *?S. plemmyridon* sp. nov. but with a shallower and narrower symphyseal region, a deeper horizontal ramus below the posterior postcanines, and a much smaller mental foramen; lower incisors extend completely across the widest part of the anterior face of the mandible so that the lower canine lies posteromedial rather than posterolateral to I_3 and is separated from I_3 by a diastema (which is absent in *?S. plemmyridon* sp. nov.); incisors possess medial and distal marginal ridges which lack cuspules; the lower canine is oriented vertically or slightly posteriorly, rather than obliquely forward.

Description of Material

The type of *S. macrodontes* is well described by Crompton and Ellenberger, and only a few additional points need be made here. The snout referred to this species is described here.

The mandible of *S. macrodontes* (fig. 1a–c; table 1) closely resembles that of very large individuals of the South American and Indian genus *Exaeretodon* (fig. 2b; tables 1,2), though the latter lacks the ventral chin-like projection of the symphysis. The anterior surface of the symphysis is inclined forward at an angle of approximately 45 to 50 degrees to the vertical in both *S. macrodontes* and the large Burntcoat jaw, and in the largest specimens of *Exaeretodon* (in which I include the type specimen of *Ischignathus sudamericanus* Bonaparte 1963; Hopson, in preparation). The lower borders of the horizontal rami of *S. macrodontes* are increasingly everted behind the level of the canine. This is partly natural, but is undoubtedly exaggerated by dorsoventral compression, as noted by Crompton and Ellenberger. The base of the coronoid process has an out-turned anterior border which continues forward, on to the lateral surface of the horizontal ramus, as a ridgelike swelling. This swelling and the everted lower border of the mandible create between them an elongate depression. A similar depression occurs in *Exaeretodon, Gomphodontosuchus,* and, to a lesser, degree, in other advanced cynodonts, it is usually interpreted as the area of insertion of the masseter muscle (Barghusen 1968).

Further preparation of the lateral surface of the horizontal ramus has exposed a large foramen

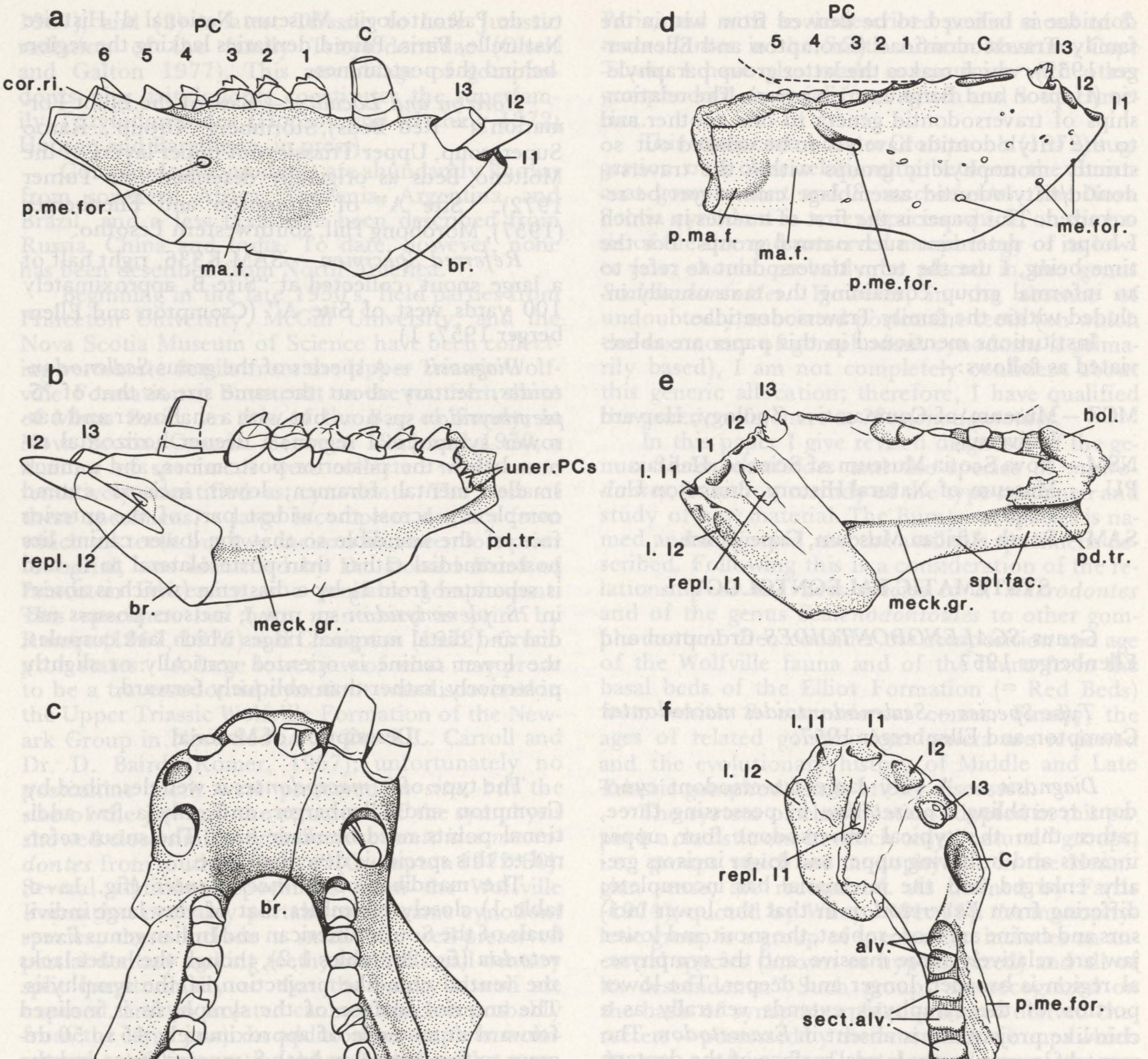

Figure 1. Type dentaries of (a, b, c) *Scalenodontoides macrodontes* (unnumbered specimen, Institut de Paléontologie, Paris) and (d, e, f) ?*Scalenodontoides plemmyridon* sp. nov. (PU 19190) in (a, d) lateral, (b, e) medial, and (c, f) dorsal views. All to same scale. (a–c modified from Crompton and Ellenberger 1957).

Abbreviations:
alv, alveoli; br, break; C, canine; cor. ri., coronoid ridge; hol, hollow for newly-erupted and unerupted postcanines; I, incisor; l. I, left incisor; ma. f., masseteric fossa; meck. gr., meckelian groove; me. f., mental foramina; PC, postcanines; pd. tr., trough for postdentary bones; p. ma. f., posterior masseteric fossa p. me. for., posterior mental foramen; repl. I, replacing incisor; sect. alv., cross-sections through alveoli; spl. fac., facet for splenial bone; uner. PCs, unerupted postcanines.

on the left side (the comparable area on the right is restored in plaster). The foramen lies below the fourth postcanine (PC_4), about midway between the alveolar border and the restored lower edge of the jaw. The bone surface is generally poor so that the precise margins of the foramen are not clear. The foramen lies at the bottom of a depression and is about 6 mm in horizontal diameter. A break across its lower border shows that it opens medially into the mandibular (inferior alveolar) canal which

TABLE 1

LOWER JAW AND TOOTH MEASUREMENTS (in mm) OF THE TYPE SPECIMENS OF *SCALENODONTOIDES MACRODONTES* AND *?S. PLEMMYRIDON* SP. NOV. AND A LARGE SPECIMEN OF *EXAERETODON ARGENTINUS* (MCZ 4486).

		S. macrodontes		*?S. plemmyridon*	*Exaeretodon*
Length from ant. border symphysis to end of PC row		196,5		180,0	212,0
Length from ant. border symphysis to ant. end PC row		80,6		85,7	117,0
Length PC row		129,3		120,0	113,0
Ant-post. length of symphysis		79,2		81,7	66,5
Max. length of symphysis (measured obliquely)		85,9		103,0 ± 5,0	74,3
Depth of mandible at symphysis		80,0		88,0	75,5
Max. width symphyseal region at canine		115,4		146,0 ± 10,0	90,0
Depth mandible at last PC		73,3		———	93,0
Length diastema between I_3 and C		13,0		15,5	69,5
Ant-post. diam. canine alveolus		27,9		28,2	25,5
Incisors:					
I_1	LL (labiolingual)	9,4 (erupting)		———	———
	MD (mesiodistal)	16,1 (erupting)		17,6 ± 2,0*	16,0
I_2	LL	13,8		16,8	13,2
	MD	19,5		19,0 ± 2,0	13,1
I_3	LL	13,8		18,4	10,8
	MD	17,8		18,4 ± 0,5	11,7
Canine:	LL	18,3		18,1*	———
	MD	20,6		28,2	———
Postcanines:		Right	Left		
PC_1	LL	16,9	———	13,1*	———
	MD	17,5	15,9	11,0	———
PC_2	LL	16,9	17,2	13,5	———
	MD	17,7	15,7	11,8	———
PC_3	LL	17,1	17,2	15,8	———
	MD	15,9	17,3	11,9	———
PC_4	LL	16,8	16,7	16,7	———
	MD	16,0	18,1	12,2	———
PC_5	LL	17,1	17,4	18,9	———
	MD	19,3	19,8	11,2	———
PC_6	LL	17,2	17,5	23,6	———
	MD	19,9	22,1	———	———

*All dental measurements on *?S. plemmyridon* are of alveoli

TABLE 2

SNOUT AND UPPER INCISOR AND CANINE MEASUREMENTS (in mm) OF *SCALENODONTOIDES MACRODONTES* (SAM K336) AND A LARGE SPECIMEN OF *EXAERETODON ARGENTINUS* (MCZ 4486)

		S. macrodontes	*Exaeretodon*
Maximum width of snout at canine swellings		167,5± 6,5	146,5
Depth of snout at diastema		84,0	99,7
Width of snout from midline to inner edge of canine		60,0± 0,5	37,0
Incisors:			
I^1	LL (labiolingual)	11,4	12,7
	MD (mesiodistal)	9,8	12,7
I^2	LL	14,6	15,9
	MD	12,5	15,4
I^3	LL	---	10,8
	MD	---	10,8
Canine:	LL	17,8	25,5
	MD	25,4	31,7

lies within the jaw below the roots of the teeth. The foramen appears to open to the outside in a dorsolateral direction, as does the homologous foramen, the mental foramen, in other gomphodont cynodonts. It differs from the comparable foramen in the new species from Nova Scotia in that it lies below, rather than above, the swelling which merges to the rear with the thickened anterior border of the coronoid process; it also appears to lack a posteriorly-directed groove leading from the foramen.

The lower incisors are extremely large, robust teeth in comparison with those of other cynodonts, including *Exaeretodon* (see Table 1) and tritylodontids. They completely occupy the front of the broad mandible, with I_3 extending further laterally than the canine. They are very procumbent, rising only about 30 degrees above the horizontal (taken as the plane of the alveolar margin). The crown of the presumed left canine described by Crompton and Ellenberger is, in fact, the first incisor on the left side. It has nearly the same dimensions as the exposed cross-section of the broken left canine, but it possesses a different pattern of longitudinal ridges (see below). All of the incisors are spatulate, with a crescentic cross-section, symmetrically-placed mesial and distal marginal ridges, and a longitudinal swelling on the lingual surface of the crown. This swelling lies mesial (i.e., toward the symphysis) of the center of the crown. As noted by the original describers, the enamel is much thicker on the labial (anterior) surface than on the lingual (posterior) surface; on the latter surface it is thickest in the center of the crown and thins toward the marginal ridges. There are no serrations on the marginal ridges, although their apparent absence may be attributable to small size and inadequate preservation of the enamel surfaces of the teeth. There is no doubt, however, that marginal cuspules, or megaserrations, as occur in the Nova Scotia cynodont, were entirely lacking.

Unlike the condition in *Exaeretodon* and the Nova Scotia cynodont, the canine is separated from the incisor row by a diastema and is not inclined anteriorly. It is inclined slightly laterally at its base and curves both backward and inward toward its apex. It is ovoid in section, with a very thin, unserrated, longitudinal ridge on its anterointernal and its posteroexternal surface.

The lower postcanines are well described by Crompton and Ellenberger. There are six functional teeth which increase slightly in size from front to back; behind PC$_6$ are two unerupted teeth which appear to be smaller than the last functional tooth. Decrease in size of teeth at the posterior end of the postcanine row is indicative of maturity in tritylodontids (Hopson, unpublished), and it is likely that this specimen represents a full-grown individual. The tooth rows are nearly parallel anteriorly and diverge progressively toward the rear. The anterior teeth are implanted in the jaw vertically, but the posterior teeth are inclined increasingly toward the midline rearward. Such a pattern is also seen in *Exaeretodon* and tritylodontids.

The crown morphology of the lower postcanines is nearly identical to that of *Exaeretodon* (fig. 3), as noted by Crompton (1972). The basic pattern is that seen in all traversodonts, two cusps transversely aligned across the anterior half of the tooth and a basined heel on the posterior half of the tooth. However, in *Scalenodontoides*, *Exaeretodon*,

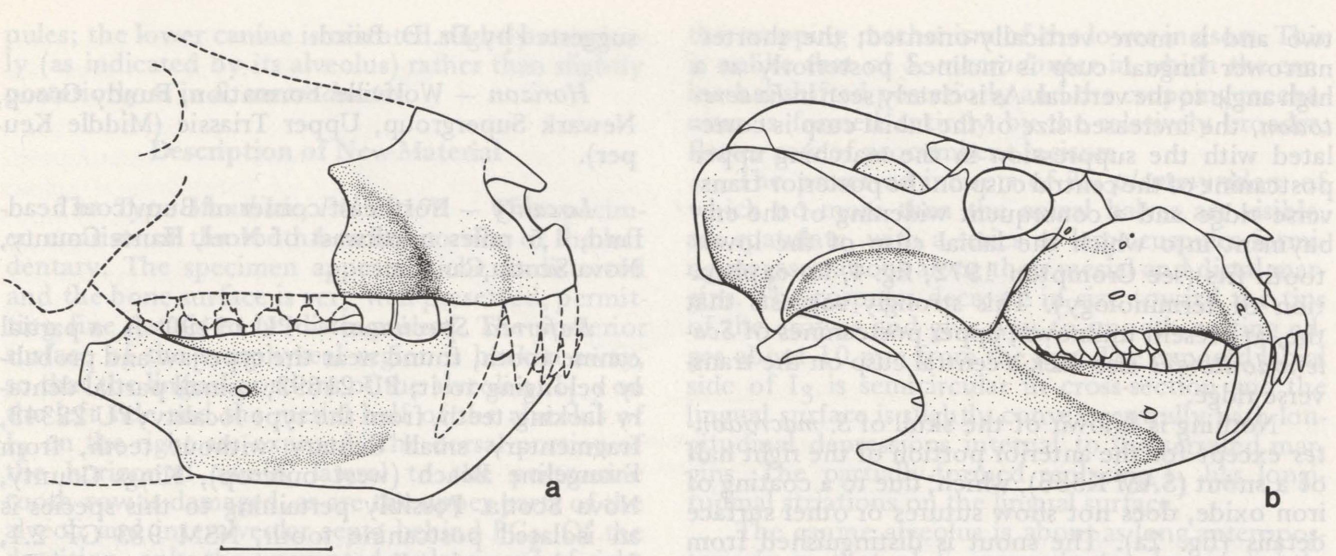

Figure 2. a, *Scalenodontoides macrodontes*, lateral view of snout (SAM K336) and type dentary; b, *Exaeretodon argentinus*, lateral view of skull and lower jaws (modified from Bonaparte 1962, and Chatterjee 1982). Both to same scale.

and, presumably, *Gomphodontosuchus* (in which the lower postcanines are not well-preserved), the transversely-aligned anterior cusps are relatively larger and the posterior basin relatively smaller than in other traversodonts (fig. 3). Also, there is a great disparity in size and shape between the anterior cusps that does not occur in other traversodonts: the labial cusp is much the taller and wider of the

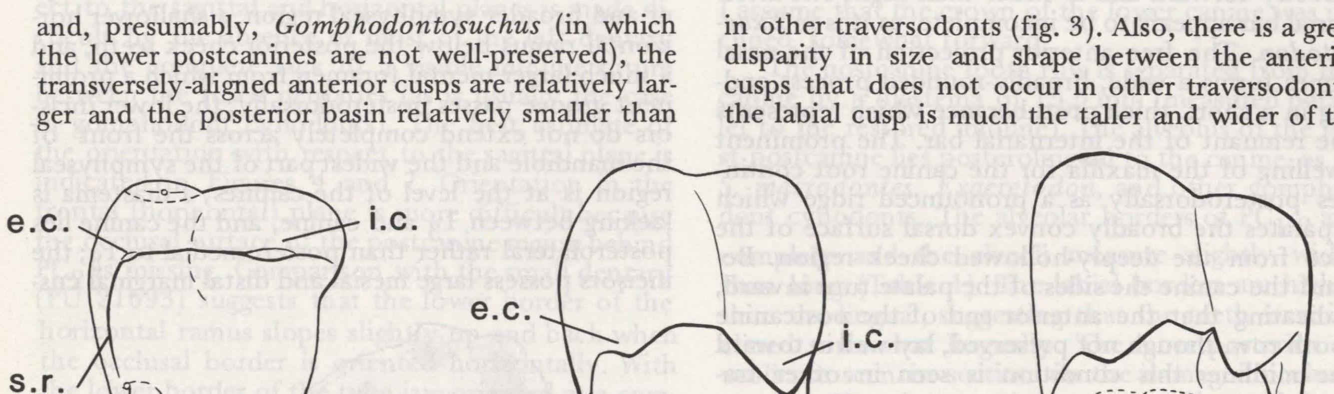

Figure 3. Lower left postcanine teeth of three genera of traversodont cynodonts in crown (top) and lingual (bottom) views; *Scalenodon* (left), representing the primitive traversodont condition, is contrasted with *Scalenodontoides* and *Exaeretodon* (center and right). Not to scale. (*Scalenodon* redrawn from Crompton 1972; others drawn from specimens).

Abbreviations:
b., basin of heel; e.c.,external (labial) cusp;i.c., internal (lingual) cusp; s.r., shearing ridge on external side.

two and is more vertically-oriented; the shorter narrower lingual cusp is inclined posteriorly at a high angle to the vertical. As is clearly seen in *Exaeretodon,* the increased size of the labial cusp is correlated with the suppression in the matching upper postcanine of the central cusp on the posterior transverse ridge and a consequent widening of the embayment into which the labial cusp of the lower tooth fits (see Crompton 1972, fig. 4, for explanation of terminology). This strongly suggests that the, at present unknown, upper postcanines of *Scalenodontoides* also lack a central cusp on the transverse ridge.

Nothing is known of the skull of *S. macrodontes* except for the anterior portion of the right half of a snout (SAM K336), which, due to a coating of iron oxide, does not show sutures or other surface details (fig. 2a). The snout is distinguished from that of other cynodonts, including *Exaeretodon,* by its extraordinary breadth across the canine swellings, the width of the skull at this level being twice its height (see Table 2). The narial opening faces directly forward and is wider than high. The internarial bar appears to be incomplete, as it is in *Exaeretodon.* The free anterior projection of the nasal bones forms a wide, broadly-rounded process ending in a short, thick protuberance which represents the remnant of the internarial bar. The prominent swelling of the maxilla for the canine root continues posterodorsally as a pronounced ridge which separates the broadly convex dorsal surface of the face from the deeply-hollowed cheek region. Behind the canine the sides of the palate turn inward, indicating that the anterior end of the postcanine tooth row, though not preserved, lay well in toward the midline; this condition is seen in other traversodonts.

The upper dentition is represented by the roots of the right first and second incisors, the alveolus of the third incisor, and the root of the canine. The second incisor is larger than the first, as in *Exaeretodon* (see Table 2). The relative size of the third cannot be determined. The lower incisors are all greater in cross-sectional area than is upper I^2.

The upper canine has a greater anteroposterior diameter than the lower; this is a resemblance to *Exaeretodon* and *Gomphodontosuchus,* in which the upper canine is longer and more robust than the lower. Also similar is the absence of a diastema between the canine and I^3, suggesting that the upper canine is becoming incorporated into the cropping mechanism of the incisors in these genera.

?*Scalenodontoides plemmyridon* sp. nov.

Holotype — PU 19190, the horizontal ramus of a right dentary with a small portion of the left dentary adjacent to the symphysis.

The species name means "of the high tides", alluding to the fact that the world's highest tides occur at Burntcoat, Bay of Fundy, Nova Scotia, the type locality of this species. The name was suggested by Dr. D. Baird.

Horizon — Wolfville Formation, Fundy Group, Newark Supergroup, Upper Triassic (Middle Keuper).

Locality — Northeast corner of Burntcoat headland, 1,5 miles northwest of Noel, Hants County, Nova Scotia,Canada.

Referred Specimens — PU 19190–A, a partial canine tooth, found near the type jaw and probably belonging to it; PU 21693, a small partial dentary lacking teeth, from the type locality; PU 22343, fragmentary small dentary without teeth, from Evangeline Beach (west outcrop), Kings County, Nova Scotia. Possibly pertaining to this species is an isolated postcanine tooth, NSM 983 GF 2.1, from the type locality.

Diagnosis — A species provisionally placed in the genus *Scalenodontoides;* dentary about the same size as that of *S. macrodontes* but with a deeper and broader symphyseal region, a shallower horizontal ramus below the posterior cheek teeth, and a much larger mental foramen from which a prominent groove passes posterodorsally; the lower incisors do not extend completely across the front of the mandible and the widest part of the symphyseal region is at the level of the canines; a diastema is lacking between I_3 and canine, and the canine lies posterolateral rather than posteromedial to I_3; the incisors possess large mesial and distal marginal cus-

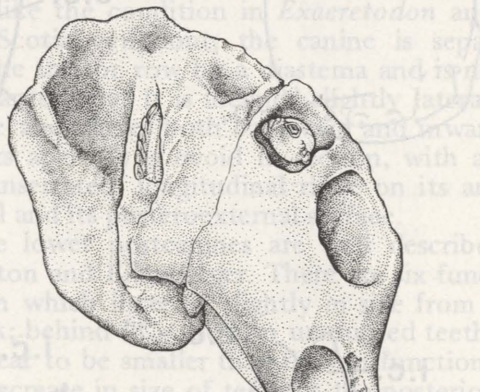

Figure 4. ?*Scalenodontoides plemmyridon* sp. nov., PU 19190 type lower jaw in dorsal view. See Figure 1 for identification of parts.

pules; the lower canine is oriented slightly anteriorly (as indicated by its alveolus) rather than slightly posteriorly as in *S. macrodontes.*

Description of New Material

The Type Mandible, PU 19190 – This specimen consists of the tooth-bearing portion of the left dentary. The specimen appears to be undistorted and the bone surface is very well preserved, permitting fine details to be distinguished. The posterior surface of the symphyseal region is broken away, so that the lingual portions of the alveoli of $I_{1\text{-}2}$ on the left side and the mesial half of the alveolus of I_1 on the right are exposed. The dorsal portion of the horizontal ramus lateral to the postcanine tooth row is damaged, as are the upper parts of the alveoli and interalveolar septa behind PC_2. Of the dentition, only the unerupted replacement of right I_1 and the partially erupted right I_3 are preserved in place. The isolated canine, PU 19190-A, may belong to this specimen.

Correct orientation of the specimen with respect to the sagittal and horizontal planes is made difficult by the absence of most of the left dentary and the complete lack of a visible midline suture between the fused dentaries (as is usually the case in gomphodont cynodonts). The best estimate of the orientation with respect to the sagittal plane is indicated in Figures 4 and 7. Orientation in the frontal (horizontal) plane is more difficult because the occlusal surface of the postcanine region behind PC_2 is missing. Comparison with the small dentary (PU 21693) suggests that the lower border of the horizontal ramus slopes slightly up and back when the occlusal border is oriented horizontally. With the lower border of the type jaw oriented at a comparable angle, the restored alveolar border is presumed to be horizontal (see fig. 1 d-e) and the symphysis slopes forward at a 45 degree angle.

The type jaw of ?*S. plemmyridon* is slightly shorter than the type jaws of *S. macrodontes;* measured from the front of the symphysis to the posterior end of the postcanine row (restored position of PC_6), the jaw of ?*S. plemmyridon* is approximately 180,0 mm long, compared with 196,5 mm for *S. macrodontes.* Examination of the measurements in Table 1 indicates that the region of the jaw anterior to the cheek teeth is relatively longer, wider, and deeper in ?*S. plemmyridon.* Its greatest width is at the level of the posterior half of the canine, whereas in *S. macrodontes* it is between I_3 and the canine.

The incisor row of ?*S. plemmyridon* has a much shorter radius of curvature than that of *S. macrodontes* and the canine lies in the same arc as the incisors, being separated from I_3 by a very short interalveolar septum. In *S. macrodontes* the canine lies posterointernal to I_3 and is separated from it by a relatively long diastema. The canine of ?*S. plemmyridon* appears to have been slightly procumbent (see below); thus like that of *Exaeretodon* (fig. 2b), it appears to have been incorporated into the cropping mechanism of the lower incisors. This is unlike that of *S. macrodontes* in which the canine has shifted posteriorly and the cropping mechanism is formed entirely by the relatively broader, flatter row of procumbent incisors.

The preserved incisors of ?*S. plemmyridon,* of which no more than the apical halves are visible, are spatulate, with a series of large cuspules forming megaserrations along their mesial and distal margins. The cuspules decrease in size toward the tips of the crowns and give way to smooth cutting edges about 10 mm from the tips. The exposed labial side of I_3 is semicircular in cross-section and the lingual surface is slightly convex centrally with longitudinal depressions internal to the serrated margins. The partially-formed replacing I_1 has longitudinal striations on the lingual surface.

The canine alveolus is about as long anteroposteriorly as that of *S. macrodontes,* but is slightly less wide. It is 53,6 mm deep, with straight tapering sides; the bottom of the socket lies below the posterior half of the dorsal opening, so the root would have sloped anterodorsally. For this reason, I assume that the crown of the lower canine was inclined somewhat forward.

The postcanine tooth row is separated from the canine by a diastema of 15,5 mm (measured parallel to the restored midline). The alveolus of the first postcanine lies posterolingual to the canine, as in *S. macrodontes, Exaeretodon,* and other gomphodont cynodonts. The alveolar borders of $PC_{1\text{-}2}$ are complete and the alveoli measure slightly wider than long (Table 1). The labial borders are higher than the lingual, suggesting that the teeth were inclined somewhat lingually. The more posterior alveoli are seen in section on the damaged occlusal margin. They increase in transverse diameter from front to back, but their anteroposterior diameter remains essentially unchanged. There are five postcanine alveoli preserved, plus a large undivided hollow (still containing matrix) at the posterior end of the tooth row. In *S. macrodontes,* the undivided hollow at the back of the postcanine row contains the erupted PC_6 and two more, unerupted, teeth behind it. In ?*S. plemmyridon,* the hollow provides space for a sixth postcanine and at least one unerupted tooth behind it.

The inclination of the lingual side of the horizontal ramus toward the midline indicates that the entire tooth row was inclined lingually (as are the complete alveoli of $PC_{1\text{-}2}$). The tooth row also shows a slight outward curvature toward the rear, as in *S. macrodontes.*

In lateral view (fig. 5), the dentary is dominated by the massive symphyseal region. The lower border of the symphysis is damaged, but enough is preserved to indicate that it descends below the level of the horizontal ramus as a chin-like process, as it does in *S. macrodontes* but not in *Exaeretodon* and other gomphodonts. The front of the symphysis is inclined forward about 45 degrees. The incisor alveoli are inclined forward at about the

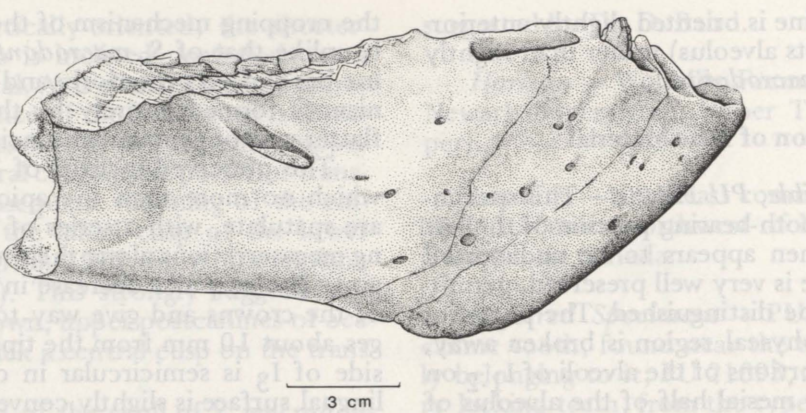

Figure 5 ?*Scalenodontoides plemmyridon* sp. nov., PU 19190, type lower jaw in lateral view. See Figure 1 for identification of parts.

same angle, indicating that the incisors, though procumbent, were not so horizontally-oriented as those of *S. macrodontes* (though the possibility that the inclination of the latter may be exaggerated by postmortem dorsoventral compression cannot be dismissed).

The anterior and lateral surfaces of the dentary, back to the level of PC$_2$, are penetrated by numerous small irregularly-arranged foramina (fig 5,7). The dorsally-located foramina on the front and sides of the incisor and canine regions open in a dorsolateral direction and usually have short dorsally-directed grooves leading from them. The more ventrally-located foramina open directly laterally. The foramina located behind the level of the canine open more toward the rear, with short grooves extending posteriorly from them. These mandibular foramina are homologous with the mental foramina of reptiles (Oelrich 1956, fig. 29) and the anterior and middle mental foramina of mammals (the posterior mental foramen of mammals can be homologized with a larger and more posterior foramen in cynodonts; see below); these openings pass branches of the inferior alveolar ramus of the trigeminal nerve and accompanying vascular twigs to the skin of the anterior part of the lower jaw.

The lateral surface of the horizontal ramus between the canine swelling and the masseteric fossa is slightly convex in its ventral half, but below the diastema and PC$_{1-4}$, the upper half is indented by a large semicircular depression, the limits of which are distinctly marked by changes in the curvature and texture of the surface. (fig. 1d). The ventral border of the depression curves down and back from the region of the diastema, then rises along the ridge marking the forward continuation of the anterior rim of the coronoid process. The surface of the bone within the depression is faintly striated, but is otherwise smooth and lacking in small foramina. Within the posterior part of the depression, however, is an extremely large foramen (see below). The most likely interpretation of the significance of this depression is that it held a ventrolateral extension of the oral vestibule, the part of the oral cavity lying external to the teeth. It was probably bounded laterally by a cheek.

Perhaps the most striking feature of the mandible, and that which is the strongest indication that the specimen pertains to a distinct taxon, is the very prominent foramen and associated groove on the lateral surface of the jaw below PC$_{3-4}$. The foramen opens into the jaw in an anteromedial direction and appears to be a forward continuation of the prominent groove as an intramandibular canal. The foramen is greatly elongated anteroposteriorly, being 20,0 mm in horizontal diameter and 6,5 mm in dorsoventral diameter. The foramen and groove are bounded above by a slight out-turning of the mandibular surface and below by the coronoid ridge. The groove is shallowest posterodorsally (its posterior end is missing) and deepens as it curves anteroventrally. At about 20,0 mm from its posterior end, its inner wall turns sharply medially to form the posterior border of the foramen. The foramen opens in a ventromedial direction into the deep intramandibular canal, the floor of which lies well below the lower rim of the foramen on the outer surface of the jaw. The dorsal margin of the external groove continues forward as a roof to the foramen and, further forward, merges into the roof of the intramandibular canal.

As the intramandibular canal has been only partially cleared of matrix, its true dimensions cannot be determined. Anterior to the lateral foramen, the canal has a minimum transverse diameter of 10,0 mm and a minimum vertical diameter of 8,0 mm. At the level of the foramen, neither the floor nor the medial wall of the canal has been cleared of matrix; the minimum transverse diameter is 12,0 mm and the minimum dorsoventral diameter is 13,0 mm. Although the canal has not been traced posterior to the foramen, it undoubtedly continues back to exit from the jaw at the mandibular (inferior alveolar) foramen below the posterior-most cheek teeth; the foramen is not preserved in this specimen.

This large foramen in the lateral surface of the mandible is interpreted as a greatly enlarged posterior mental foramen. In many mammals, such as the dog (Miller *et al.* 1964, fig. 10–5), there are several mental foramina in the dentary which transmit sensory branches of the mandibular alveolar nerve and vascular twigs to the skin of the incisor and canine region of the lower jaw. In the dog, the most posterior of these foramina lies below the third premolar. In a primitive gomphodont such as *Trirachodon,* the dentary below the incisors and canine is perforated by numerous small foramina, comparable to those described above in ?*S. plemmyridon;* these are comparable to the far fewer, and larger, anterior and middle mental foramina of the dog. Below PC_2 or PC_3 in *Trirachodon* is a larger foramen which is comparable to the posterior mental foramen of the dog. In *Trirachodon* and most other cynodonts, the posterior mental foramen opens in a dorsal direction. In *Exaeretodon* the foramen opens posterodorsally and is associated with a short posterodorsally-directed groove (fig. 2b); it is also larger than in more primitive cynodonts. In *S. macrodontes,* the foramen is somewhat larger still and lies further back in the jaw, between PC_3 and PC_4. Thus, *Trirachodon, Exaeretodon,* and *S. macrodontes* form a morphological series bridging the gap between the primitive gomphodont condition of the posterior mental foramen and the extremely specialized condition in ?*S. plemmyridon.*

The functional significance of the enlarged and posteriorly-located posterior mental foramen of ?*S. plemmyridon* is probably related to the development of a cheek lateral to the postcanine teeth. As suggested above, a large oral vestibule was probably developed lateral to the postcanine teeth; almost certainly this space was bounded laterally by a cheek. I suggest, therefore, that the large posterior mental foramen indicates the presence of an extensive flexible cheek and oral vestibule which required a greater degree of innervation and vascularization than occurred in more primitive gomphodonts. In all other gomphodonts, with the exception of the more primitive genus, *Diademodon,* the tooth rows are set in from the outer border of the snout and mandible suggesting that they too had an oral vestibule and, consequently, a cheek. In none, however, is there an indication of the enlargement of the posterior mental foramen seen in *Exaeretodon* and, especially, *Scalenodontoides.*

In all Triassic cynodonts, the anterior border of the coronoid process lies lateral to the posteriormost postcanine teeth. It continues forward on the outer surface of the horizontal ramus as a rounded ridge which forms the anterodorsal margin of the masseteric fossa. In the type mandible of ?*S. plemmyridon,* the preserved portion of the anterior ridge of the coronoid process merges completely into the convexly-rounded surface of the jaw below PC_3. Extrapolation of the preserved portion of the ridge posterodorsally indicates that the anterior border of the coronoid process lay lateral to PC_5, as it does in *S. macrodontes.*

The masseteric fossa, which is the insertion area of the masseter and zygomaticomandibularis muscles of mammals and, presumably, cynodonts (Barghusen 1968), consists of two distinct portions in the type mandible. Anteriorly, below the coronoid ridge, it is a very shallow depression which merges imperceptibly into the convexly-rounded area anterior to the posterior mental foramen. The ventral margin of the fossa consists of a faint angulation which sets the fossa off from the convex lower border of the jaw (fig. 1d, 5). At the level of PC_5, the posterior part of the masseteric fossa deepens to form a separate depression. This deeper part has distinct lower and anterior borders but is open dorsally onto the lateral face of the coronoid process (fig. 1d, 5). Although the anterior, more shallow, part of the masseteric fossa is only faintly indicated, support for its interpretation as an area of muscle insertion is provided by the small jaw, PU 21693, in which the extremely prominent anterior border of the masseteric fossa encloses the entire area below the coronoid ridge (fig. 9). The difference in morphology between the two specimens is provisionally interpreted as due to ontogenetic variation.

The medial surface of the type dentary of ?*S. plemmyridon* (fig. 1e, 6) is essentially identical to that of the type of *S. macrodontes* (fig. 1b). The anteroposteriorly-elongate symphysis of the latter bears a deep depression on its lower third which is overlain by a transverse shelf; the shelf continues

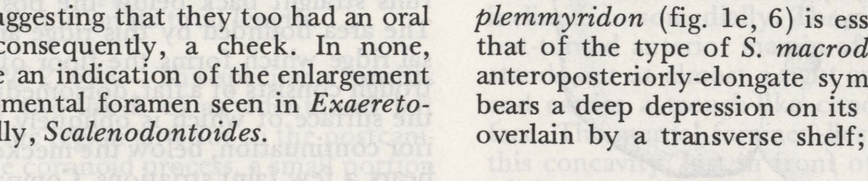

Figure 6. ?*Scalenodontoides plemmyridon* sp. nov., PU 19190, type lower jaw in medial view. See Figure 1 for identification of parts.

posterolaterally as a slight ridge. In the Burntcoat jaw, the lower part of the sympheal region is missing, but the lateral continuation of the overhanging shelf is preserved. Passing back from the forwardly-inclined incisor region to the postcanine region, the lingual surface of the dentary becomes progressively more vertical until the alveolar border overhangs the portion below it. This medial overhang of the inner surface of the postcanine region increases progressively from PC$_1$ to the rear of the tooth row. The alveolus of PC$_5$ and the crypt for the more posterior teeth lie within a medial swelling which forms a wide shelf overhanging the trough for the postdentary bones.

The lower third of the medial surface of the mandible is extremely well preserved and shows several grooves, depressions and contact facets. The ridge which overhangs the symphyseal depression extends back along the inside of the jaw to merge into the roof of the postdentary trough. It forms the superior border of the narrow, shallow meckelian groove which is about 4,0 mm high along its entire length (fig. 1e, 6). Anteriorly, below the diastema, the groove is partially subdivided by a low ridge into dorsal and ventral grooves. Posteriorly, the meckelian groove is less deeply incised and increases slightly in height as it merges into the wide postdentary trough. At the posterior end of the preserved portion of the jaw, beneath the overhanging crypt for the developing teeth, the postdentary trough is about 20,0 mm in height.

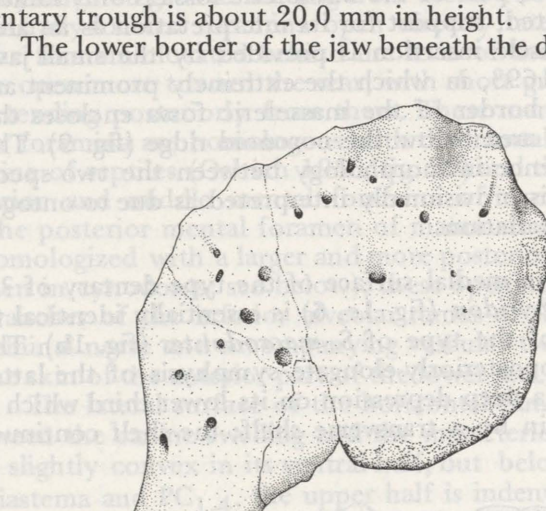

Figure 7. ?*Scalenodontoides plemmyridon* sp. nov. PU 19190, type lower jaw in ventral view.

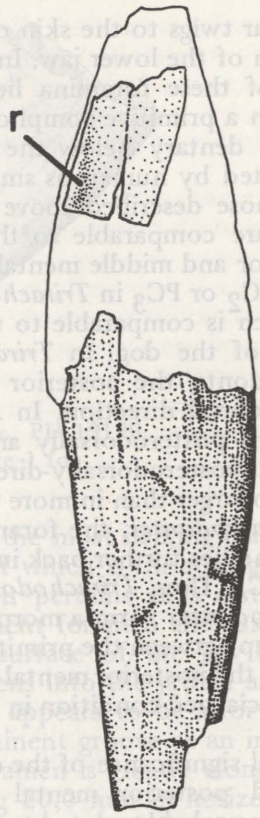

Figure 8. Partial canine tooth, PU 19190–A, attributed to the type specimen of ?*Scalendontoides plemmyridon* sp. nov. Abbreviation: r, ridge on fragment of enamel.

The lower border of the jaw beneath the diastema and PC$_{1-2}$ forms a relatively sharp ventromedially-inclined ridge. This ridge continues posteriorly as a distinct angulation which extends obliquely upward on to the inner surface of the jaw and then runs straight back below the postdentary trough. The area bounded by this ridge and the more dorsal ridge which forms the floor of the postdentary trough consists of a flat, dorsomedially-facing facet, the surface of which is obliquely striated. Its anterior continuation, below the meckelian groove, also bears a few faint striations Comparison with other cynodonts indicates that the entire striated surface was overlain in life by the splenial bone (fig. 1e, 6). In *Cynognathus,* for example (see Kermack *et al.* 1973, fig. 10 and 25), the posterior part of the splenial forms a slender process extending along the ventral border of the postdentary trough to end just above the angle of the dentary. The type jaw of ?*S. plemmyridon* is missing the region of the angular process, but the splenial facet extends to the broken edge. The splenial in this specimen presumably also covered the meckelian groove and, as in other cynodonts, overlapped a portion of the dentary above the groove; however, there is no evidence on the surface above the groove for such a contact.

In dorsal and ventral views of the type mandible (fig. 4,7), the strongly developed coronoid ridge obscures the fact that the posteroventral border of the jaw turns outward beyond the vertical level of the posterior postcanine alveoli. In *S. macrodontes,* the posteroventral part of the jaw is very strongly everted but as noted by Crompton and Ellenberger, this is due in part to dorsoventral compression of the specimen.

Isolated Canine, PU 19190–A – This specimen consists of most of the root of a large canine, with a portion of the crown preserved as a natural mold containing a small (13x18 mm) piece of enamel (fig. 8). From its size, and the fact that it was found near the type mandible, this canine probably belongs to the type. The mesiodistal and labiolingual diameters of the alveolus in the mandible are 28,2 and 18,1 mm respectively, and the comparable measurements on the upper end of the canine root are 24,5 and 16,4 mm, indicating a close correspondence in cross-sectional dimensions. Additional morphological features suggest that the canine is from a right dentary. When viewed perpendicular to its greatest diameter, one side of the root is slightly convex and the other side is straight; the mesial (anterior) and distal (posterior) walls of the canine alveolus show comparable curvatures, indicating that the more curved portion of the tooth is the mesial side. Furthermore, the labial side of the alveolus has a flatter curvature than the lingual side, as do the inferred labial and lingual sides of the root. Finally, the posterior edge of the enamel fragment on the inferred labial surface of the crown shows the remnant of a longitudinal ridge separated from the rounded lateral surface of the crown by a slight longitudinal depression (fig. 8); such a ridge also occurs on the posterolabial part of the canine of *S. macrodontes* (fig. 1a). On this interpretation, Figure 8 is the lateral view of a right lower canine.

The tip of the root is missing; the preserved part is 61,6 mm long. The canine alveolus in the type jaw is 53,6 mm deep, but some matrix remains to provide information on its total length.

Small Dentary, PU 21693 – This specimen consists of the posterior two-thirds of an edentulous left dentary lacking the region anterior to the postcanine tooth row, the coronoid process, a small portion of the angle, and the lingual walls of the postcanine alveoli (fig. 9). The specimen provides additional information about the morphology of the dentary of ?*S. plemmyridon,* to which it is assigned on the basis of the uniquely large size and posterior location of the mental foramen and its association with a posterodorsally-directed groove. Because of the very small size of the dentary (Table 3; restored length about 75 mm), this specimen is considered to be a juvenile individual.

The total number of postcanine teeth cannot be determined due to the loss of the anterior part of the specimen. Alveoli for four teeth and an enlarged posterior crypt for at least two more are preserved. The jaw differs from the type in: (1) the relatively more rounded outline of the mental foramen and less deeply-incised groove leading from the foramen; (2) the greatly out-turned coronoid ridge and extremely prominent anterior and ventral margins of the masseteric fossa. In addition, the masseteric fossa is not subdivided into two portions as in the type.

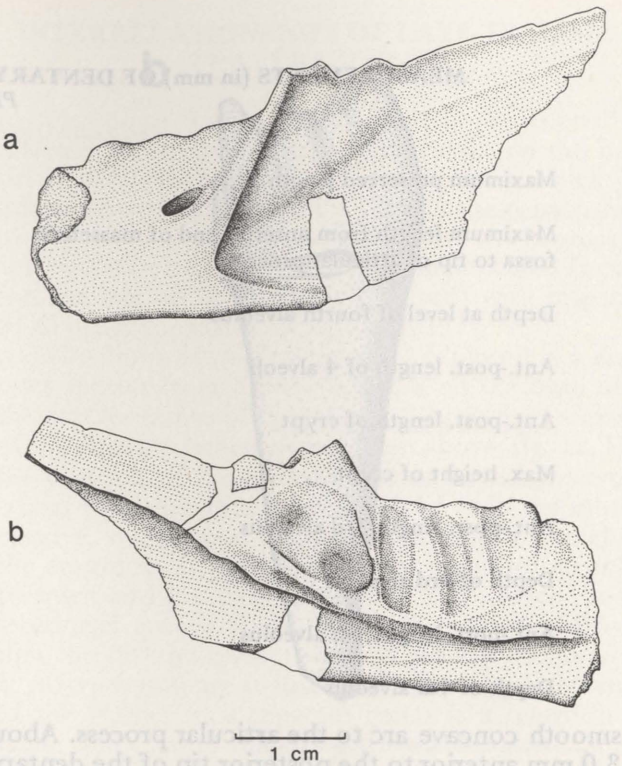

Figure 9. Small left dentary, PU 21693, attributed to ?*Scalenodontoides plemmyridon* sp. nov. a, lateral view; b, medial view.

The lateral surface of the tooth-bearing portion of the dentary is smoothly-rounded in transverse section, with the alveolar and ventral borders lying well medial to the outermost point on the ramus. The upper half of the ramus does not show a well-defined hollow as in the type jaw, but this region is inclined dorsomedially. The ridge which forms the out-turned anterior margin of the coronoid process stands out at almost a right angle to the horizontal and carries a trough-like concavity on its anterior face. The mental foramen lies in the lower part of this concavity, just in front of the expanding base of the coronoid ridge where the latter merges into the surface of the jaw. The mental foramen is about 1,2 mm in diameter and enters the mandible in an anteroventral direction. A short groove passes posterodorsally from the foramen into the trough between the body of the jaw and the coronoid process.

The masseteric fossa and more posterior part of the dentary form an essentially flat surface which is set in medially from the convexly-rounded tooth-bearing portion of the jaw. The anterodorsal margin of the masseteric fossa is formed by the out-turned coronoid ridge. The shelf which forms the ventral margin of the fossa narrows posteriorly and merges into the surface of the fossa a short distance (about 10,0 mm) in front of the angle.

Posterior to the angle, the lower border of the jaw is a thin ridge which curves up and back in a

TABLE 3

MEASUREMENTS (in mm) OF DENTARY (PU 21693) REFERRED TO ?*SCALENODONTOIDES PLEMMYRIDON*

Maximum preserved length	56,7
Maximum length from anterior end of masseteric fossa to tip of articular process	41,6
Depth at level of fourth alveolus	17,2
Ant.-post. length of 4 alveoli	20,0
Ant.-post. length of crypt	10,4
Max. height of crypt	10,5
Ant.-post. length 3rd alveolus	4,1
Depth of 3rd alveolus	9,6
Ant.-post. length 4th alveolus	4,2
Depth of 4th alveolus	9,0

smooth concave arc to the articular process. About 3,0 mm anterior to the posterior tip of the dentary, the curvature becomes convex. The posterior tip of the dentary is slightly damaged; it probably came to a distinct point, as in other cynodonts, to form the articular process. The base of the coronoid process is preserved as a thin lamina extending back to the tip of the articular process. Its anterior edge is turned outward to form the coronoid ridge.

The lateral surface of the masseteric fossa is essentially flat. A slight angulation of the surface extends obliquely up and back to a point just below the tip of the articular process; this angulation is an external reflection of the trough on the medial surface of the dentary which housed the postdentary rod. The upper half of the masseteric fossa, just behind the coronoid ridge, bears a low swelling which reflects the outer wall of the crypt for developing teeth on the lingual side of the jaw.

The tooth-bearing portion of this small jaw is similar in appearance to that of the type, except that the inner walls of the postcanine alveoli are missing so that the cross-sectional shape of the roots cannot be determined. The alveoli of four postcanines are preserved, plus a large crypt behind the last alveolus; the crypt lies internal to the coronoid process and has about the same anteroposterior diameter as two alveoli. In life, this crypt probably contained two partially-developed teeth. The meckelian groove is narrow below the first two alveoli but widens posteriorly and, below the crypt, merges into the postdentary trough. Behind the crypt, a prominent ridge passes obliquely up and back to terminate at the tip of the articular process; this ridge overhangs the trough for the post-dentary bones. The lower border of the trough extends back and slightly downward to terminate just above the angle. Below the crypt, in the roof of the trough, is a small foramen which passes forward into the body of the dentary; this is the mandibular foramen by which the mandibular alveolar nerve and associated blood vessels entered the jaw.

Fragmentary Small Dentary, PU 22343 – This is a portion of the horizontal ramus of a dentary split longitudinally to expose the alveoli of six postcanine teeth. The specimen is 27, 0 mm long and 13,2 mm in greatest height. As preserved, the alveolar border is slightly concave and the lower border is deepest at the posterior end and curves up and forward in a gentle arc. The alveoli increase in forward inclination from back to front, the most anterior being inclined at an angle some 30 degrees greater than the rearmost; the latter, depending on the orientation of the specimen, is inclined forward up to ten degrees.

If this specimen pertains to ?*S. plemmyridon*, which is likely, it indicates that the roots of the cheek teeth increase in forward inclination in an anterior direction. This inclination cannot be determined in the other small dentary (PU 21693) because it is missing the anterior alveoli, or in the type dentary because the alveoli are preserved only in cross section. Progressively forward inclination of the anterior cheek teeth in the lower jaw is characteristic of tritylodontids, but does not appear to occur in traversodonts. However, the present specimen, if indeed it pertains to ?*S. plemmyridon*, represents a very young individual, and so may have been in the process of rapid replacement of its cheek teeth. This could mean that anterior cheek teeth were being shed in rapid succession as new posterior teeth were erupting and moving forward into occlusal position.

Isolated Tooth Possibly Pertaining to ?S. plemmyridon, NSM 983GF2.1. – A complete multicusped tooth with an elongate tapering root, from the type locality of ?*S. plemmyridon*, may pertain to this species and so is described here (fig. 10; table 4). This assignment is extremely tentative because the tooth, though interpretable on a traversodont mo-

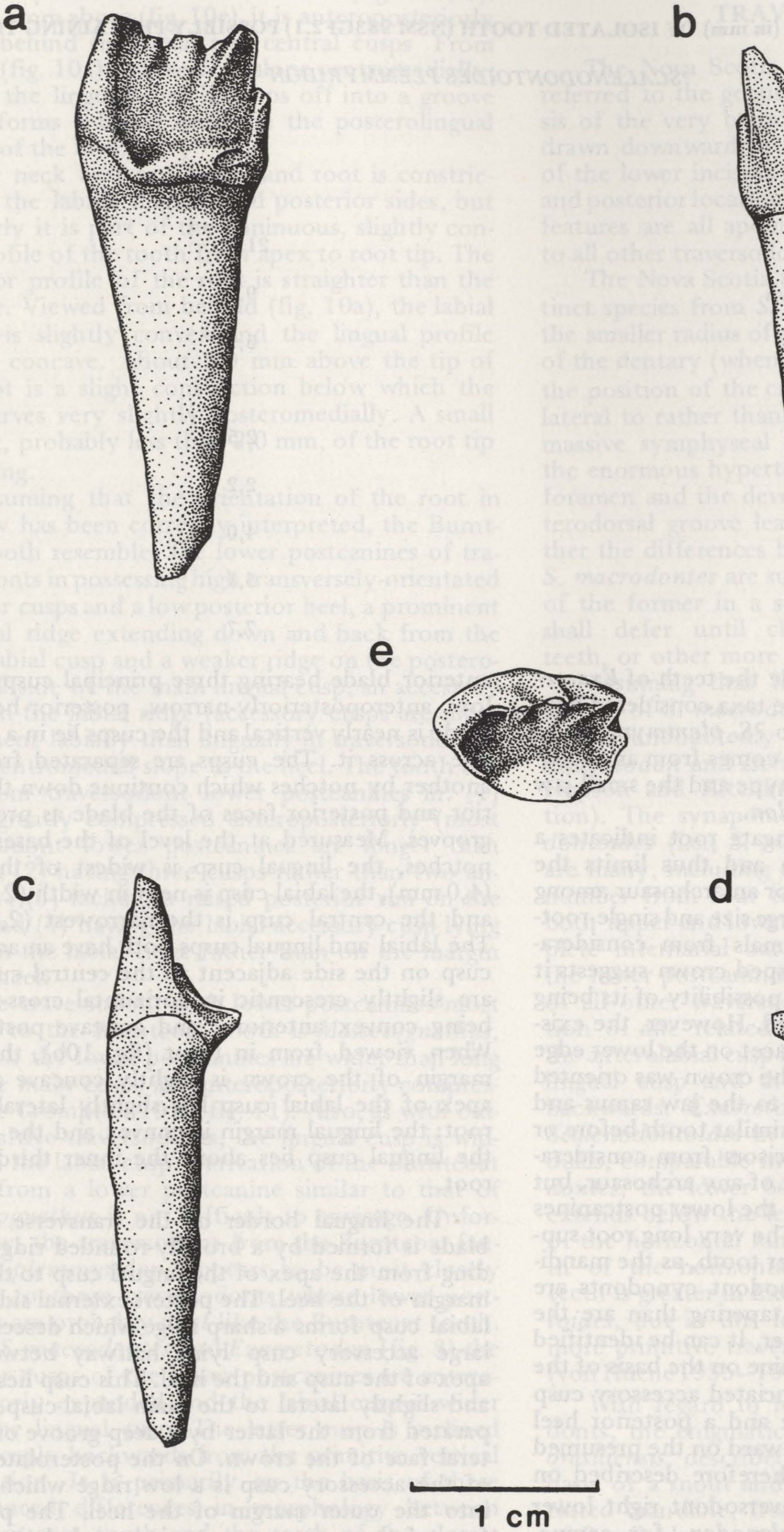

Figure 10. Isolated tooth, NSM 983GF2.1, possibly pertaining to ?*Scalenodontoides plemmyridon* sp. nov., or to another traversodont cynodont; views tentatively identified as a, posterior; b, anterior; c, medial; d, lateral; e, dorsal.

TABLE 4

MEASUREMENTS (in mm) OF ISOLATED TOOTH (NSM 983GF2.1) POSSIBLY PERTAINING TO

?*SCALENODONTOIDES PLEMMYRIDON*

Maximum height	30,0
Height of crown	8,8
Height of root	21,2
Transverse diameter of crown	9,9
Ant-post. diameter of crown	6,9
Transverse diameter of:	
Labial cusp	2,5
Central cusp	2,2
Lingual cusp	4,0
Ant-post. diameter of root	5,1
Transverse diameter of root	7,7

del, does not closely resemble the teeth of *Exaeretodon* or *S. macrodontes,* the taxa considered here to be most closely related to ?*S. plemmyridon.* If it is a gomphodont tooth, it comes from an individual between the size of the type and the small jaw (PU 21893) of ?*S. plemmyridon.*

The presence of an elongate root indicates a thecodont-type implantation and thus limits the tooth to that of a synapsid or an archosaur among Late Triassic tetrapods (its large size and single-rooted condition exclude mammals from consideration). The complex, multicusped crown suggests it is a postcanine, although the possibility of its being an incisor cannot be excluded. However, the existence of a probable contact facet on the lower edge of the crown indicates that the crown was oriented with its long axis transverse to the jaw ramus and that it was in contact with a similar tooth before or behind it; this eliminates incisors from consideration. The tooth is unlike that of any archosaur, but it does bear a resemblance to the lower postcanines of traversodont cynodonts. The very long root supports the idea that it is a lower tooth, as the mandibular postcanines of gomphodont cynodonts are longer and more smoothly tapering than are the maxillary postcanines. Further, it can be identified as a right mandibular postcanine on the basis of the presence of a ridge and associated accessory cusp on the presumed labial side and a posterior heel which slopes obliquely downward on the presumed lingual side. The tooth is therefore described on the basis of its being a traversodont right lower postcanine (see fig. 3, *Scalenodon,* for comparison), but it cannot be overemphasized that this identification is extremely tentative.

Interpreted as a right lower postcanine, the crown is divisible into a tall, transversely-widened, anterior blade bearing three principal cusps, and a low, anteroposteriorly-narrow, posterior heel. The blade is nearly vertical and the cusps lie in a straight line across it. The cusps are separated from one another by notches which continue down the anterior and posterior faces of the blade as prominent grooves. Measured at the level of the bases of the notches, the lingual cusp is widest of the three (4,0 mm), the labial cusp is next in width (2,5 mm), and the central cusp is the narrowest (2,2 mm). The labial and lingual cusps both have an accessory cusp on the side adjacent to the central cusp, and are slightly crescentic in horizontal cross-section, being convex anteriorly and concave posteriorly. When viewed from in front (fig. 10b), the labial margin of the crown is slightly concave and the apex of the labial cusp lies slightly lateral to the root; the lingual margin is convex and the apex of the lingual cusp lies above the inner third of the root.

The lingual border of the transverse anterior blade is formed by a broadly-rounded ridge extending from the apex of the lingual cusp to the inner margin of the heel. The posteroexternal side of the labial cusp forms a sharp ridge which descends to a large accessory cusp lying halfway between the apex of the cusp and the heel. This cusp lies behind and slightly lateral to the main labial cusp. It is separated from the latter by a deep groove on the lateral face of the crown. On the posterolateral side of the accessory cusp is a low ridge which merges into the outer margin of the heel. The posterior face of the accessory cusp is rounded; its medial face is slightly concave and forms with the concave posterior face of the main labial cusp a slight basin above the heel.

The heel is a horizontal shelf which extends beyond the posterior face of the root (fig. 10c, d). Viewed from above (fig. 10e), it is anteroposteriorly widest behind the labial and central cusps From behind (fig. 10a), it is seen to slope ventromedially; behind the lingual cusp it drops off into a groove which forms a broad notch in the posterolingual margin of the heel.

The neck between crown and root is constricted on the labial, lingual, and posterior sides, but anteriorly it is part of the coninuous, slightly convex, profile of the tooth from apex to root tip. The posterior profile of the root is straighter than the anterior. Viewed from behind (fig. 10a), the labial profile is slightly convex and the lingual profile slightly concave. About 5,0 mm above the tip of the root is a slight constriction below which the root curves very slightly posteromedially. A small amount, probably less than 2,0 mm, of the root tip is missing.

Assuming that the orientation of the root in the jaw has been correctly interpreted, the Burntcoat tooth resembles the lower postcanines of traversodonts in possessing high transversely-orientated anterior cusps and a low posterior heel, a prominent external ridge extending down and back from the main labial cusp and a weaker ridge on the postero-internal side of the main lingual cusp, an accessory cusp on the labial ridge (accessory cusps are more prominent labially than lingually in traversodonts), and a ventromedial slope to the heel. The tooth differs from traversodont lower postcanines in: (1) being greatly compressed anteroposteriorly (most traversodont lower postcanines are longer than broad); (2) having three cusps rather than two anteriorly; (3) lacking a raised posterior rim on the heel; and (4) having the labial accessory cusp lying high on the labial ridge rather than on the margin of the heel.

The traversodont with lower postcanines most similar to the Burntcoat tooth is *Massetognathus*, in which the lower postcanines are wider than long and the main cusps are anteroposteriorly compressed (see Crompton 1972, fig. 11). Also, as with older primitive traversodonts, the lingual cusp is wider than the labial cusp. Derivation of the Burntcoat tooth from a lower postcanine similar to that of *Massetognathus* is not difficult to envisage. Unfortunately, the traversodont from the Burntcoat fauna, ?*S. plemmyridon*, appears to be most closely related to those traversodonts whose lower postcanines are probably *least* like the Burntcoat tooth.

In *S. macrodontes* and *Exaeretodon* (fig. 3) the anterior cusps of the lower postcanines are anteroposteriorly expanded and the labial cusp is wider than the lingual cusp. The latter cusp is inclined very steeply backwards from the primitive vertical orientation. It is primarily on the basis of these pronounced differences in morphology between the Burntcoat tooth and the teeth of the closest relatives of ?*S. plemmyridon* that I am hesitant to attribute the Burntcoat tooth to the latter taxon, even though a case can be made for considering it to be from a traversodont cynodont.

INTERRELATIONSHIPS OF LATE TRIASSIC TRAVERSODONTS

The Nova Scotia traversodont is provisionally referred to the genus *Scalenodontoides* on the basis of the very broad symphyseal region which is drawn downward to form a "chin", the robustness of the lower incisors and canine, and the large size and posterior location of the mental foramen. These features are all apomorphic (derived) with respect to all other traversodont cynodonts.

The Nova Scotia traversodont is placed in a distinct species from *S. macrodontes* on the basis of: the smaller radius of curvature of the incisor region of the dentary (when viewed from above; fig. 1c, f): the position of the canine closer to I_3 and posterolateral to rather than posteromedial to it; the more massive symphyseal region; and, most strikingly, the enormous hypertrophy of the posterior mental foramen and the development of a prominent posterodorsal groove leading from the foramen. Whether the differences between ?*S. plemmyridon* and *S. macrodontes* are sufficient to warrant placement of the former in a separate genus is a question I shall defer until clearly-attributable postcanine teeth, or other more complete remains , are found.

Assuming that ?*S. plemmyridon* is the sister species of *S. macrodontes*, the sister genus of these two is undoubtedly *Exaeretodon* (including *Proexaeretodon* and *Ischignathus* as junior synonyms; Hopson and Kitching 1972; Hopson, in preparation). The synapomorphies which unite *Scalenodontoides* (i.e., *S. macrodontes*) and *Exaeretodon* are many, including the reduction of upper incisor number from four to three, great enlargement of both upper and lower incisors and loss of the complete internarial bar (fig. 2). The morphology of the lower postcanines is greatly modified from that of all other traversodonts (fig. 3), with the exception of the related *Gomphodontosuchus*, in that the anterolabial cusp is much larger than the anterolingual cusp and the latter is inclined obliquely backwards. *Exaeretodon* is more primitive than *Scalenodontoides* in that even in the largest individuals, comparable in size to the type of *S. macrodontes*, the lower border of the symphysis hardly extends below the level of the more posterior part of the horizontal ramus. (fig. 2; Table 1). The depth of the horizontal ramus below the posterior teeth is greater in *Exaeretodon* than in *Scalenodontoides*, but in this feature *Exaeretodon* resembles more primitive traversodonts, such as *Traversodon* (von Huene 1935–1942) and *Luangwa* (Kemp 1980).

With regard to relationships to other traversodonts, the enigmatic species *Gomphodontosuchus brasiliensis*, described by von Huene (1928) on the basis of a snout and the anterior part of the associated mandible, from the Santa Maria Formation of Brazil, shows a number of synapomorphies with *Scalenodontoides* and *Exaeretodon*. Primary among these are the morphology of the postcanine teeth (Crompton 1972; Hopson, manuscript). In addition, all three are unique among traversodonts in that the lower jaw is unusually deep and the masseteric fossa extends far forward (at least to beneath PC_3, whereas in other traversodonts it lies behind the level of PC_5), and the upper canine is relatively larger and more anteriorly inclined. As in *Exaeretodon*, the lower canine of *Gomphodontosuchus* is relatively short and slightly procumbent. As discussed elsewhere (Hopson, manuscript), a number of the peculiarities of *Gomphodontosuchus* which were noted by Romer (1967: 22) — the "short face, short tooth row, and massive jaws" — are features shared with very young juvenile individuals of *Exaeretodon*. Therefore, I have suggested that the type, and only described specimen, of *G. brasiliensis* represents a juvenile individual and that the adult was more like the adults of other advanced traversodonts in skull proportions and postcanine tooth number. *Gomphodontosuchus* is distinct from, and more primitive than, *Exaeretodon* and *Scalenodontoides* in that all of its incisors are small and the number of upper incisors is four. The internarial bar of the type specimen is damaged, but enough is preserved to suggest that it was complete in the undamaged skull.

At the present time, the phylogenetic relationships of more primitive traversodonts are not well understood and I shall not attempt to discuss the wider affinities of the clade containing *Gomphodontosuchus, Exaeretodon,* and *Scalenodontoides.*

AGE OF THE LATE TRIASSIC TRAVERSODONTS

Composition and Age of the Burntcoat Fauna of Nova Scotia

The material described here as ?*Scalenodontoides plemmyridon* is part of a small fauna from the lower Wolfville Formation of which it is the first member to be described. The vertebrates from this fauna consist of the following taxa (Carroll *et al.* 1972 ; Baird and Olsen, 1983):

Amphibia	— Stereospondyli	: *Metoposaurus (Buettneria) bakeri*
Reptilia	— Procolophonia	: *Leptopleuron* sp., and three undescribed genera
	— ?Trilophosauria	: a probable trilophosaurid
	— Rhynchocephalia	: a rhynchosaur similar to *Paradapedon*
	— Thecodontia	: aetosaurids related to *Stagonolepis, Aetosaurus,* and *Stegomus;* rauisuchids (earlier described as carnosaurs)
	— Saurischia	: small and medium-sized theropods; plateosaurid prosauropods, cf. *Anchisaurus, Ammosaurus*
	— Ornithischia	: small primitive ornithischian
	— Therapsida	: ?*Scalenodontoides plemmyridon;* a dicynodont

Concerning the age of the lower Wolfville fauna from Burntcoat, Dr. Donald Baird has provided the following summary of the evidence for a late Carnian or Carno-Norian (middle to upper Middle Keuper) age:

The reddish-brown sandstones exposed along the shore of the Minas Basin near Burntcoat, Hants County, Nova Scotia, are part of the Wolfville Formation of the Fundy Group, a component of the Newark Supergroup. A comprehensive analysis of the Burntcoat site — its sedimentology, fauna, and ecology — has been presented by Carroll *et al.* (1972, p. 22—30). In that publication the age of the fauna was stated provisionally as "approximately middle Keuper (Norian)"; however, subsequent finds of vertebrates, plus the results of palynological analysis, now indicate a slightly earlier date. As the new evidence has not been published elsewhere, it is summarized here.

1. A footprint faunule from the upper Wolfville (51 feet (c.15m) below the overlying Blomidon Formation) at Paddy's Island Cove, Kings County, correlates with that of the Passaic Lower Brunswick) Formation at Milford, New Jersey (Baird 1957; Olsen, McCune and Thomson 1982). A palynoflora from Milford has been dated by Cornet and Traverse (1975; 27) as early Norian — upper Middle Keuper); this locality falls in Newark Basin faunal zone 1 of Olsen and Galton (1977) which they correlate with the Middle Keuper of Germany. Although the stratigraphic interval between them cannot be measured, the Burntcoat faunal zone lies appreciably lower in the Wolfville Formation than that of Paddy's Island Cove, and is thus probably pre-Norian in age.

2. One-half mile (c. km) east of Burntcoat the faunal zone recurs at Noel Head where a well-preserved skull roof (PU 21742) of the labyrinthodont amphibian *Metoposaurus (Buettneria) bakeri* (Case) has been found. *M. bakeri* belongs to the same species-group as the type species, *M. diagnosticus* (Meyer), characterized by exclusion of the lacrimal from the orbit. *M. diagnosticus* (= *M. heimi* Kuhn) occurs in the Schilfsandstein and Blasensandstein (Middle Keuper) of Germany; *M. bakeri* was described from the Dockum Group of Scurry County, Texas. Palynoflorules from the Dockum correlate with those of the uppermost Gipskeuper and Schilfsandstein and indicate a late Carnian age (Dunay and Fisher 1979).

3. A skull and partial skeleton (NSM F–420) from Noel Head are assigned to the procolophonid reptile *Leptopleuron*, which is otherwise known only from the Lossiemouth Beds of Elgin, Scotland. The armored pseudosuchian reptile from Elgin, *Stagonolepis*, is closely related to *Aetosaurus* from the upper middle Stubensandstein (upper Middle Keuper) of Germany and to *Stegomus* from the New Haven Arkose of Connecticut and the Passaic Formation of New Jersey. *Stegomus* belongs to faunal zone 1 of Olsen and Galton (1977). (Aetosaurid remains also occur at Burntcoat but are generically indeterminate.) This roundabout correlation is less secure, of course, than that based on *Metoposaurus bakeri*.

Taken together, these lines of evidence indicate a middle to upper Middle Keuper age for the Burntcoat fauna. Correlation of the continental German stages with those of the Alpine marine Triassic is less straightforward than the literature would imply, but the Lower Keuper can be considered Ladinian and the Upper Keuper equivalent to Rhaetic, leaving the Middle Keuper as Carnian-plus-Norian. The vertebrate and palynological evidence, in conjunction, suggest a late Carnian or Carno-Norian age for the Burntcoat fauna.

Composition and Age of the Basal Elliot Fauna

Crompton and Ellenberger (1957: 1) state that specimens of *Scalenodontoides macrodontes* come from two sites on Morobong Hill in southwestern Lesotho which "occur well below the typical Red Bed facies indicating that they occur in the uppermost layers of the Molteno Beds." Charig *et al.* (1965: 200, footnote) later gave the name "Passage Beds" to " the beds which are lithologically transitional between the typical Molteno below and the typical Reds Beds above." Turner (1972) has since shown that the Morobong Hill localities lie in the lower part of the Red Beds, i.e., of the Elliot Formation of modern lithostratigraphic nomenclature. At the same stratigraphic level are abundant remains of large dinosaurs, presumably melanorosaurid prosauropods which, according to Charig *et al.* (1965) are restricted to the lower Red Beds, including the "Passage Beds". These authors further state that the melanorosaurids are associated with "large amphibians, large anomodonts and large herbivorous cynodonts (i.e., *Scalenodontoides macrodontes*)" (Charig *et al.* 1965: 210–211). The presence of large amphibians, presumably capitosaurids, in the basal beds of the Elliot Formation was documented in 1978 by Dr. J.W. Kitching and myself (Hopson 1980). I am not aware of anomodont remains from the lower Elliot, but a trackway from Morobong, described by Ellenberger (1972: 32) as *Pentasauropus morobongensis,* was probably made by a large dicynodont (D. Baird, personal communication; Olsen and Galton, this volume).

In 1978, I collected the fragmentary lower jaw of a rauisuchid thecodontian from dark purple beds near the base of the Elliot Formation on the farm Foutanie in the Fouriesburg District of the northeastern Orange Free State. Charig *et al.* (1965: 207) note that the lower Red Beds contain teeth of large size which are "very compressed labiolingually, with sharp crenulate anterior and posterior margins." They suggest that these teeth are those of melanodosaurid prosauropods; more likely, however, they are rauisuchid teeth.

The fauna of the basal beds ("Passage Beds") of the lower Elliot Formation contains the following taxa:

Amphibia–Stereospondyli : probable capitosaurids

Reptilia

Thecodontia : unidentified rauisuchid

Saurischia : melanorosaurid prosauropods

Therapsida–Cynodontia: *Scalenodontoides macrodontes*

?Anomodontia : probable large dicynodont

According to the range chart for amphibians and terrestrial vertebrates of the Late Triassic and Early Jurassic published by Olsen and Galton (1977, fig. 4), this faunal assemblage would be middle Late Triassic in age. Olsen *et al.* (1982, fig. 17) indicate a Carnian age for the Molteno Formation and a Norian plus Rhaetian age for the lower Elliot Formation. Because the assemblage discussed here lies just above the Molteno–Elliot contact, in the so-called Passage Beds, its age can best be considered latest Carnian or early Norian. Within the possible limits of resolution, the basal Elliot fauna, containing *S. macrodontes*, and the Burntcoat fauna, containing ?*S. plemmyridon*, can be considered contemporaneous.

The Age of *Exaeretodon*

Exaeretodon, the sister genus of *Scalenodontoides*, is known from three named species: *E. argentinus* (= *E. frenguellii, Proexaeretodon vincei, Ischignathus sudamericanus,* among other synonyms; see Hopson and Kitching 1972) from the Ischigualasto Formation of Argentina (Bonaparte 1962); *E. major* from the Santa Maria Formation of Brazil (Barberena 1974); and *E. statisticae* from the Maleri Formation of India (Chatterjee 1982). The Ischigualasto Formation is probably Carnian in age (Bonaparte 1966) and the Santa Maria Formation is probably somewhat older, either early Carnian or late Ladinian (Barberena 1974). Chatterjee (1978) considers the Maleri Formation to be probably late Carnian to early Norian. However, Olsen (personal communication) has informed me that the microfauna of the Maleri Formation is very similar to that of the Molteno Formation, suggesting a Carnian age for the Maleri. The time range of *Exaeretodon* would thus be Carnian, with the Santa Maria species possibly being latest Ladinian. The Ischigualasto and Maleri species are probably very similar in age. All appear to be older than *Scalenodontoides.*

EVOLUTION OF MIDDLE AND LATE TRIASSIC TRAVERSODONTS

The traversodont genera *Gomphodontosuchus, Exaeretodon,* and *Scalenodontoides* form a distinct clade within the traversodont/tritylodontid assemblage. Possibly related to this clade is *Scalenodon charigi* (Crompton 1972) of the Middle Triassic Manda Formation of Tanzania. *S. charigi* is known only from a maxilla containing two teeth and the alveoli of seven others; it was first described by Crompton (1955) as cf. *Gomphodontosuchus brasiliensis.* As noted by Crompton (1972: 56), *S. charigi* resembles *Exaeretodon* in that the upper postcanines are set obliquely in the jaw and the central cusp on the posterior transverse ridge appears to be absent (though damage to the crowns renders this not completely certain). *S. charigi* is quite distinct from *S. angustifrons,* the type species of the genus *Scalenodon,* and merits placement in a new genus.

Middle Triassic traversodonts are most diverse in the Manda Formation, from which four species of *Scalenodon* have been named (Crompton 1955, 1972); these species show a wide range of morphological variation and probably all merit separation at the generic level. An additional east African genus, *Luangwa* (Brink 1963; Kemp 1980), has been described from the Ntawere Formation of Zambia. In South America the Chañares Formation of Argentina has yielded in great abundance of traversodonts which can all be accommodated in the genus *Massetognathus* (Romer 1967, 1972). The Santa Maria Formation of Brazil, possibly late Middle or early Late Triassic in age, contains a diverse traversodont fauna : *Massetognathus, Exaeretodon, Gomphodontosuchus,* and *Traversodon* (Barberena 1974).

Faunas of definite Late Triassic age contain either *Exaeretodon* or *Scalenodontoides.* Tritylodontids appear to be of Jurassic age (Olsen and Galton 1977), with the exception of a possible tritylodontid, known only from postcranial fragments, from the Los Colorados Formation of Argentina which is of probable Norian age (Olsen and Galton, this volume).

I am at present reviewing the taxonomy and interrelationships of the traversodonts, and present here a preliminary overview of the evolution of the Middle and Late Triassic members of the group. The most primitive traversodont of the Middle Triassic is *Scalenodon angustifrons;* it is easily derived from an Early Triassic ancestor such as *Andescynodon* from the Las Cabras Formation of Argentina (Bonaparte 1967). Very similar to *S. angustifrons,* but somewhat more derived in postcanine morphology, are *Traversodon* of the Santa Maria and *Luangwa* of the Ntawere Formation; possibly *Scalenodon attridgei* (Crompton 1972) from the Manda Formation should be grouped here. Diverging markedly from this more primitive complex are *Massetognathus, Scalenodon hirschoni* of the Manda Formation, and the clade containing *Gomphodontosuchus, Exaeretodon,* and *Scalenodontoides* (and probably *Scalenodon charigi).* Each of these three groups shows marked changes from the primitive complex in postcanine tooth morphology and in the morphology of the skull and lower jaw. Tritylodontids appear to be most closely allied either to *Massetognathus* (Crompton 1972) or *Scalenodon hirschoni* (Hopson, in preparation). Resemblances of tritylodontids to *Exaeretodon* are, I believe, convergent.

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