Chapter 14
The Traversodontid Cynodont *Mandagomphodon hirschsoni* from the Middle Triassic of the Ruhuhu Valley, Tanzania

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Abstract *Mandagomphodon hirschsoni* (gen. nov., comb. nov.) is one of three species of traversodontid cynodont placed in *Scalenodon* [type species *S. angustifrons* (Parrington, 1946)] by Crompton ([1972]). It is based on a partial skull and lower jaws from the Middle Triassic of the Ruhuhu Valley, southwestern Tanzania. The upper postcanine teeth were used to diagnose species of *Scalenodon*, but newer traversodontid material indicates that the three species represent distinct genera. Material of "*S.*" *hirschsoni*, except for the postcanines, has not been described. It is unusual among traversodontids in having only three upper incisors, which are enlarged and procumbent. Three enlarged, procumbent anterior lower teeth are interpreted as two incisors and a canine. Analysis of postcanine wear facets indicates that the power stroke of the lower teeth was entirely in a posterior direction, including a slightly downward and backward grinding movement at the end of the stroke.

Keywords Africa • Dental function • Gomphodontia • Manda beds • Therapsida • Theriodontia

Introduction

Cynodonts are a clade of synapsids that includes Mammalia as its most derived subgroup. The non-mammalian component of the Cynodontia comprises a series of taxa mainly of Late Permian and Triassic age that includes, in addition to the persistently carnivorous ancestral lineage of mammals, several specialized subgroups of which one became highly modified for an herbivorous diet. This plant-eating clade of cynodonts, the Gomphodontia, is characterized by the transverse expansion of the postcanine teeth, which develop a precise crown-to-crown occlusion. Of the three families of Triassic gomphodonts, two—the Gomphognathidae (=Diademodontidae) and Trirachodontidae—show limited taxonomic and morphological diversity and are restricted to the Early and Middle Triassic, primarily of south and east Africa [though *Diademodon* has recently been described from the Early to Middle Triassic of Argentina (Martinelli et al. [2009])]. The supposed trirachodontids *Sinognathus* and *Beishanodon* (Gao et al. [2010]) from China are more likely to be probainognathians close to *Aleodon brachyrhamphus* (Hopson in preparation). In contrast, the third family, the Traversodontidae, is taxonomically and morphologically much more diverse and occupies a much wider geographic range, including North and South America, Europe, Africa, Madagascar, and India.

Sues and Hopson ([2010]) have recently summarized the history of traversodontid discovery and description. The family Traversodontidae was established by Huene ([1936]) for *Gomphodontosuchus* and *Traversodon* from the Middle or Late Triassic of Brazil. Crompton ([1955]) named the genus *Scalenodon*, based on *Trirachodon angustifrons* Parrington, [1946], from the Middle Triassic Manda Beds of Tanzania. Though not placing *Scalenodon* in the family Traversodontidae, Crompton noted that the mandibular postcanines of *S. angustifrons* are "remarkably similar" to those of *Traversodon*. Since then, approximately 20 new species of traversodontid have been described, indicating a wide range

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of dental morphologies evolving from an ancestral pattern similar to that of *S. angustifrons*. An even more primitive (more like that of *Diademodon*) postcanine tooth pattern occurs in the South American traversodontids *Pascualgnathus* (Bonaparte 1966) and *Andescynodon* (Bonaparte 1967), which probably gave rise to the pattern seen in *S. angustifrons* and all other traversodontids.

The main interest of traversodontids to students of the ancestry of mammals is the fact that they have developed a mammal-like complexity to their postcanine teeth, which involves precise occlusion between upper and lower teeth and a complex pattern of shearing and crushing/grinding seen in few other non-mammalian tetrapods (see Sues and Reisz 1998; Reisz and Sues 2000). Associated with the complex occlusal relations of the traversodontid dentition is the active movement of the lower jaw and teeth in a fore-aft (propalinal) rather than a transverse direction, as occurs in most mammals.

Crompton (1972) in a review of dental morphology and function in gomphodont cynodonts, named three new traversodontid species from the Manda Beds of the Ruhuhu Valley in southwest Tanzania. He included all three species in the genus *Scalenodon*. Two of the new species named by Crompton (1972), *S. hirschsoni* and *S. attridgei*, were collected in 1963 by the British Museum (Natural History)—University of London Joint Palaeontological Expedition; the third species, *S. charigi*, was based on a specimen collected by Parrington in 1933, which had earlier been referred by Crompton (1955) to cf. *Gomphodontosuchus brasiliensis*. In diagnosing the four species attributed to *Scalenodon*, Crompton (1972) utilized only the upper postcanine teeth.

Scalenodon angustifrons is now known to be a relatively primitive traversodontid in which the postcanine teeth display the main features of the traversodont cheek tooth pattern. The three species of *Scalenodon* named by Crompton in 1972 show most of these features, but, with knowledge of the broader range of traversodontid postcanine variation now available, it is clear that they are distinct enough to be placed in separate genera, as has been noted by Hopson (1984) and Abdala and Ribeiro (2003). "*S.*" *hirschsoni* has been included in cladistic analyses of cynodonts by Hopson and Kitching (2001, where it is misspelled as "*S.*" *hirschoni*) and Liu and Olsen (2010) and in cladistic analyses of gomphodonts by Abdala and Ribeiro (2003), Abdala et al. (2006), Kammerer et al. (2008), and Sues and Hopson (2010). Although characters of "*S.*" *hirschsoni* have been included in published data matrices, the type material, with the exception of the postcanines, has yet to be described.

The purpose of this study is to provide a detailed description of the skull and dentition of the known material of "*Scalenodon*" *hirschsoni* Crompton, 1972, and to provide

a new generic name and an expanded diagnosis for this taxon. The other new species referred by Crompton (1972) to *Scalenodon*, i.e., *S. attridgei* and *S. charigi*, will be redescribed, subjected to a phylogenetic analysis, and, if necessary, provided with new generic names in a future paper. Liu and Abdala (2013) have already done this, including both species in the same genus as "*S.*." *hirschsoni*, but I intend to test their conclusions with my own analysis (Hopson in preparation).

The completeness and quality of preservation of the postcanine teeth of "*S.*" *hirschsoni* permit a detailed description of dental wear and a reinterpretation of the functional morphology of the postcanine dentition.

As noted by Sues and Hopson (2010), the monophyly of Traversodontidae has been questioned because some authors (e.g., Crompton and Ellenberger 1957; Hopson 1984, 1985; Sues 1985; Hopson and Kitching 2001; Hopson and Barghusen 1986; Hopson and Sues 2006) have argued that Tritylodontidae, specialized rodent-like herbivores of Early Jurassic to Early Cretaceous age, nests within Traversodontidae, rendering the latter family paraphyletic. Tritylodontidae Cope, 1884 has priority over Traversodontidae Huene, 1936, so if tritylodontids were indeed to fall among the traversodontids, the former name would become the valid name of the group. Despite these uncertainties, I have utilized the name Traversodontidae in this paper, recognizing the uncertainty of its validity, because it is almost universally used by workers on cynodonts.

Materials and Methods

The material described here as "*Scalenodon*" *hirschsoni* was originally considered to pertain to a single individual, catalogued as NHMUK R8577 (Crompton 1972). The holotype includes the snout and lower jaws, the teeth of which were originally in occlusion but were separated during preparation (Crompton 1972, p. 49). However, included among the dissociated skull parts is a fragment consisting of portions of the primary and secondary palates and the pterygoid flanges that duplicates parts preserved in the type skull. The presence of a second individual of "*S.*" *hirschsoni* among the type material raises the question of which incomplete pieces pertain to the individual represented by the holotypic snout (the teeth of which present the diagnostic features of the species) and lower jaws and which may pertain to a second individual. All are from the same locality, and though they vary in color from reddish-brown to dark gray-brown, some specimens (notably the fused dentaries) are reddish in some parts and dark gray in others, canceling the value of such color differences in distinguishing individuals.

For purposes of description of the skull and lower jaws of "*S.*" *hirschsoni*, all identifiable fragments, with the exception of the duplicated palatal elements, are herein considered to pertain to the type skull, which consists with absolute certainty only of the snout plus orbital region and the lower jaws. In addition, an isolated right jugal has a reasonably good fit with the rear of the right maxilla, once weathering and some breakage are taken into account. An isolated braincase with attached right zygomatic arch lacks an identifiable contact with the anterior part of the skull; however, in terms of size and non-duplication of parts, it is likely that the braincase pertains to the type specimen. A number of unidentified small fragments cannot be assigned to either individual and are not further discussed. The poorly preserved distal portion of a left humerus may pertain to either individual.

The second individual is about equal in size to the type specimen. Though less complete, it is better preserved than the type and possesses more of the primary palate and pterygoid flanges.

Systematic Paleontology

Therapsida Broom, 1905
    Cynodontia Owen, 1861
    Eucynodontia Kemp, 1982
    Cynognathia Seeley, 1908
    Gomphodontia Seeley, 1894
    Traversodontidae Huene, 1936
    Mandagomphodon gen. nov.

Etymology: *Manda*, for the Manda Beds from which the material was collected, and, from the Greek, *gomphios*, molar, and *odon*, tooth; *gomphodon* is a commonly used suffix in generic names of gomphodont cynodonts.

Holotype: The Natural History Museum, London, NHMUK R8577, anterior half of skull, most of right dentary and dentigerous portion of left dentary. Also referred to the type are a right jugal and a partial braincase with attached right zygomatic arch.

Referred Specimen: The Natural History Museum, London, NHMUK: PV R11974, partial palate including primary and secondary palate and left pterygoid flange.

Horizon: Lifua Member of Manda Beds.

Locality: Locality U12 of the British Museum (Natural History)—University of London Joint Palaeontological Expedition of 1963, Ruhuhu Valley, southwest Tanzania, between the Hiasi and Njalila streams, just south of the Rutukira River; the most northerly of the Expedition's localities west of the Njalila (Crompton 1972, p. 43). Cox (1991, p. 768, Fig. 1) shows a map of these localities, including U12.

Age: The fossiliferous middle to upper parts of the Lifua Member of the Manda Beds are considered to be of Anisian (Middle Triassic) age (Wopfner 2002).

Diagnosis: Traversodontid cynodont with three upper and probably two lower incisors, all of which are enlarged (except possibly the first upper incisor) and markedly procumbent; the upper canine is separated from the incisors by a very shallow paracanine fossa; the postcanine tooth rows diverge only slightly from the midline axis; the presumed lower canine (third dentary tooth) inclines forward, nearly paralleling the procumbent incisors. Upper postcanines with rectangular crowns that are oriented perpendicularly, not obliquely, to the midline axis; transverse crest of uppers relatively low and anteroposteriorly broad, with three main cusps, the labial cusp separated from the central and lingual cusps by a deep U-shaped (rather than V-shaped) notch; prominent anterolabial and anterolingual cusps present; anterior and posterior cingula well-developed, labial cingulum absent. Lower postcanines with a robust anterior transverse ridge consisting of two large cusps that are relatively low and anteroposteriorly broad; large anterolabial and posterolabial accessory cusps. Suborbital flange of jugal appears to be absent.

Remarks: *Mandagomphodon hirschsoni* is a very unusual traversodontid because of its unique mixture of plesiomorphic and highly autapomorphic features. It differs from *Luangwa* and *Traversodon* in lacking a strong sigmoid curvature to the lower border of the dentary (this feature in *S. angustifrons* is uncertain) and from all three of these genera in lacking great height of the zygomatic arch above the tooth row. In both of these features it resembles *Massetognathus*. Its upper postcanine teeth lack an external cingulum, which occurs in the three apparently primitive genera noted above, but like *S. angustifrons*, it possesses an anterolabial accessory cusp in front of the lower transverse ridge. *Luangwa, Boreogomphodon*, and *Nanogomphodon* have a transverse cingulum on the anterior face of the lower transverse ridge, but its homology with the single anterolabial cusp of *Scalenodon* and *Mandagomphodon* is uncertain.

Description

Skull

This description is based on the type snout and the associated jugal, braincase, and zygomatic arch, which probably pertain to the same individual (Figs. 14.1, 14.2, 14.3). Details are added from the isolated palatal region pertaining to a second individual (Fig. 14.2).

The type snout of *Mandagomphodon hirschsoni* has been dorsoventrally compressed and its dorsal midline shifted to the right. The anterodorsal surface has suffered the greatest
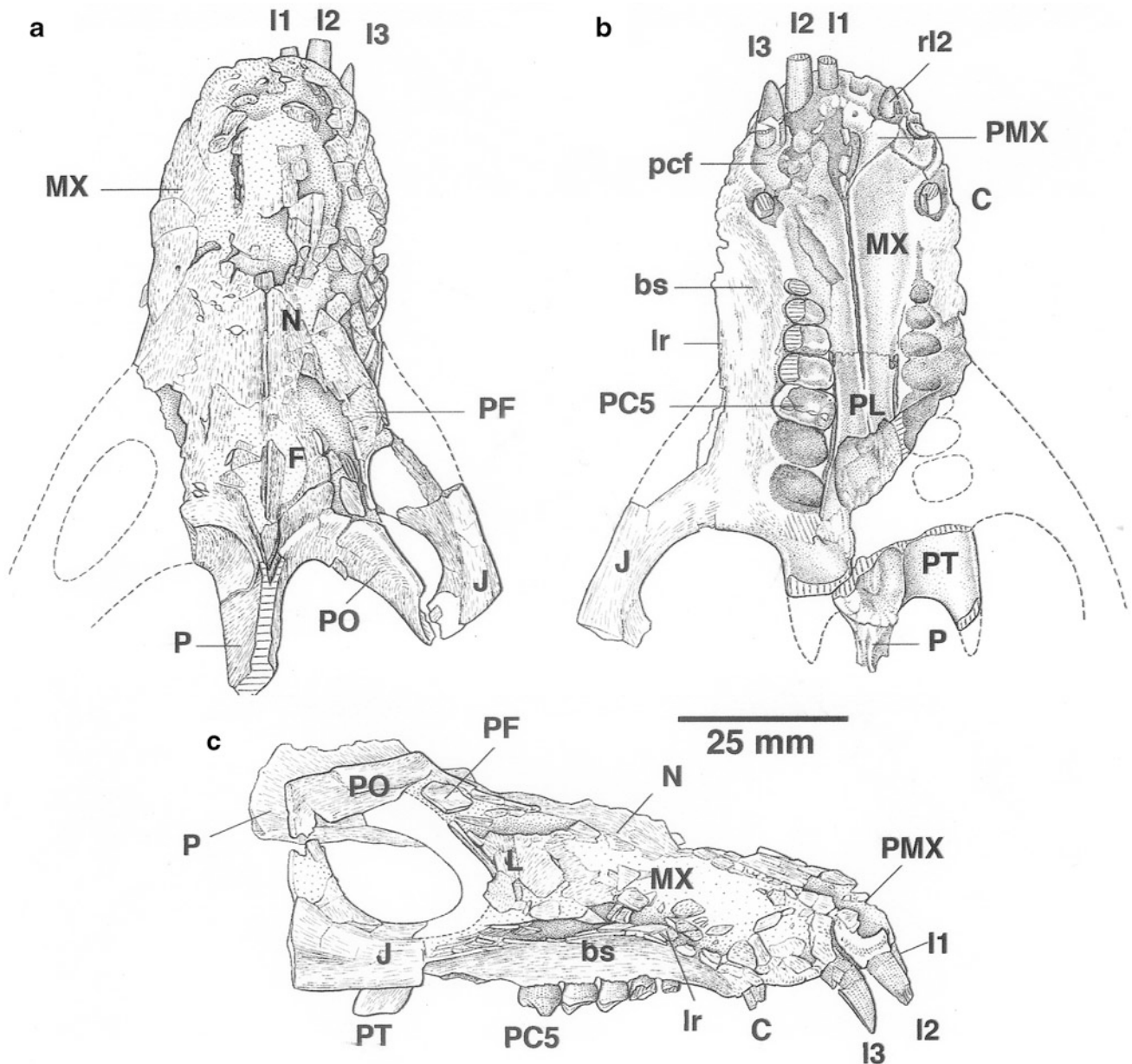
Fig. 14.1 *Mandagomphodon hirschsoni*, Crompton 1972. Anterior portion of holotype skull, NHMUK R8577. **a** dorsal view; **b** ventral view; **c** right lateral view. *bs* buccal shelf, *C* canine, *F* frontal, *I* incisor, *J* jugal, *L* lacrimal, *lr* lateral ridge, *MX* maxilla, *N* nasal, *P* parietal, *PC* postcanine, *pcf* paracanine fossa, *PF* prefrontal, *PL* palatine, *PMX* premaxilla, *PO* postorbital, *PT* pterygoid, *rI* replacing incisor

collapse, which has obscured the external nares except along their anteroventral margins. The bone on the left side of the snout is only moderately damaged, whereas that on the right side is shattered into numerous fragments. The anterior margin of the right orbit has been pushed down and back so that the restored orbit is an asymmetrical oval with its long axis oriented posterodorsally.

The ventral surface of the snout has suffered much less damage than the dorsal surface. Lateral compression has caused the rear of the secondary palate to buckle upward into the choanal passage, which has pulled the posterior halves of the maxillary postcanine tooth rows closer together. The undistorted secondary palate of the referred specimen is therefore wider than that of the type. Sutures cannot be distinguished on either specimen except on the palate.

The anterior end of the premaxilla, above the first two procumbent incisors, is very shallow; more posteriorly, the premaxilla curves back and up above the large third incisor. It forms a distinct edge on the margin of the narial opening, suggesting it was overlain by the septomaxilla, no part of
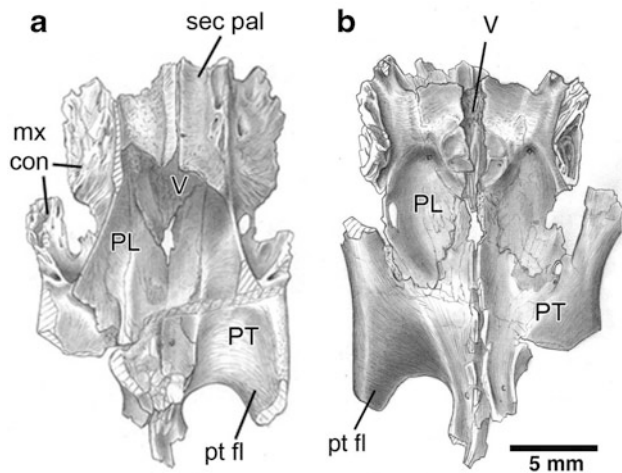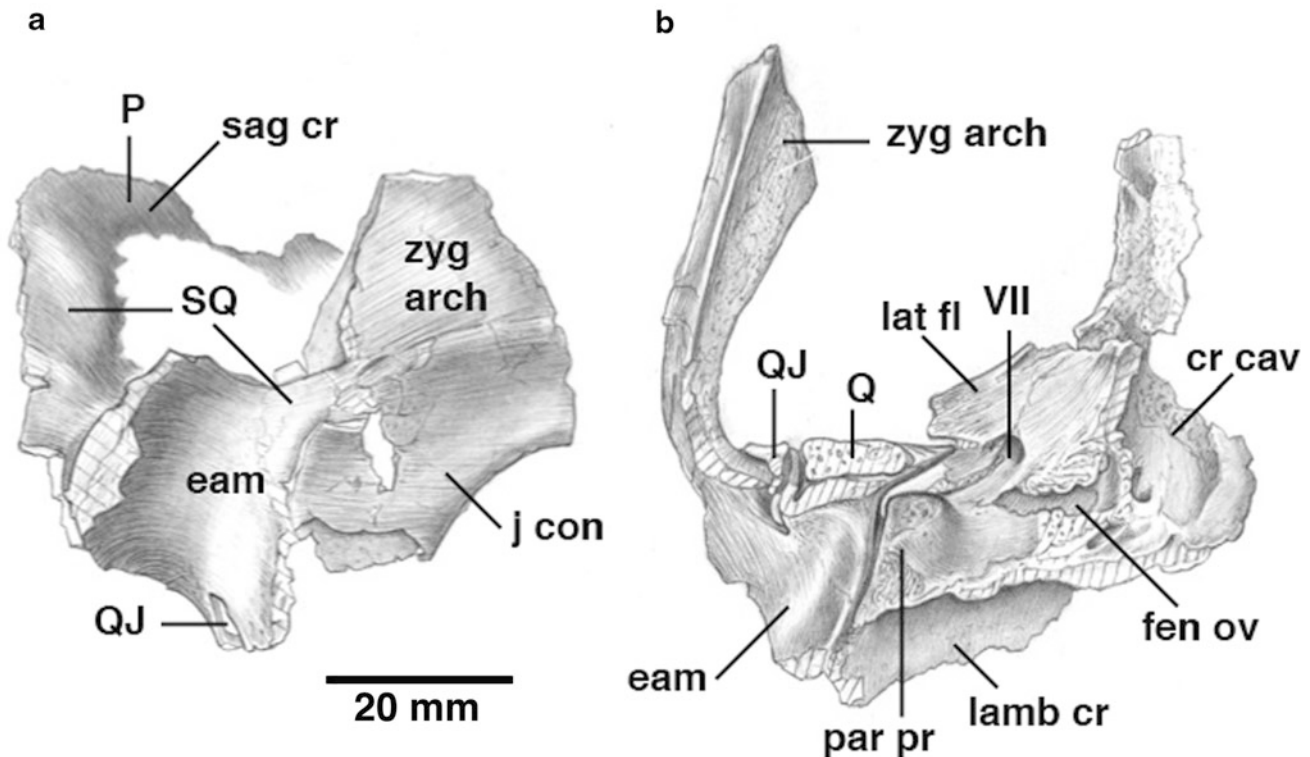
Fig. 14.2 *Mandagomphodon hirschsoni*, Crompton 1972. Ventral view of referred specimen, NHMUK: PV R11974, isolated portion of the palatal region. **a** ventral view; **b** dorsal view. *mx con* portions of palatine and pterygoid that overlie posterior part of maxilla, *PL* palatine, *PT* pterygoid, *pt fl* pterygoid flange, *sec pal* secondary palate, *V* vomer

which is identifiable. On the palatal surface, the premaxilla forms a short shelf behind the first two incisors and is pierced by a small foramen behind the first incisor. More

laterally, the posterior margin of the premaxilla is uncertain, but it appears to form the medial border of the alveolus for the third incisor. It presumably forms the bar between the incisive foramina and definitely forms their lateral margins. Whether the paired premaxillae meet behind the incisive foramina, or whether the posterior rim is formed by the maxillae, cannot be determined with certainty.

The maxilla undoubtedly forms the greater part of the lateral surface of the snout, but it is heavily damaged dorsally and its sutures with other facial elements cannot be determined. Laterally, it supports a rounded longitudinal ridge that extends back from the slight swelling for the canine root to pass below the orbit, where it merges into the suborbital portion of the jugal. Above this ridge on the better-preserved left side, a shallow depression lies between the low canine swelling and the lacrimal region; such a depression is seen in most gomphodonts. Below the longitudinal ridge, the maxilla bends sharply inward to form a moderately broad, concave overhang lateral to the cheek teeth, termed the buccal shelf by Sues and Hopson (2010). On the right side, between the canine and fifth postcanine, the overhang is wider than on the left because an elongated piece of laterally displaced maxilla appears to form an outer extension of the right shelf (Fig. 14.1c). The less damaged

Fig. 14.3 *Mandagomphodon hirschsoni*, Crompton 1972. Fragment of braincase and right zygomatic arch referred to holotype skull, NHMUK R8577. **a** Lateral view, **b** ventral view. *cr cav* cranial cavity, *eam* external auditory meatus of squamosal, *fen ov*, presumed position of fenestra ovalis, *j con* contact surface on squamosal for jugal, *lamb cr* lambdoidal crest of squamosal, *lat fl* lateral flange of prootic, *P* parietal, *par pr* paroccipital process of the opisthotic, *Q* quadrate, *QJ* quadratojugal, *sag cr* sagittal crest, *SQ* squamosal, *zyg arch* zygomatic arch of squamosal, *VII* hollow containing foramen for facial nerve

surface on the left shows that the shelf was much narrower. The concavity of the overhang is seen best lateral to the diastema, where it forms a shallow but distinct depression behind the canine. Lateral to the last postcanine, the maxillary overhang expands outward to contact the jugal in the base of the zygomatic arch. Anterior to the left canine is a small foramen in the side of the maxilla, as is usual in cynodonts. The maxilla extends forward as far as the lateral margin of the alveolus of the third incisor. In palatal view, the maxilla forms a convex-outward ridge that extends forward from the canine alveolus. On the palatal side of the ridge is a very shallow oval depression, preserved on both sides, that lies anterior and slightly medial to the canine alveolus. As will be discussed below, the depression appears to be homologous to the paracanine fossa of other cynodonts, which houses the tip of the lower canine.

The palatal suture between premaxilla and maxilla appears to extend posterointernally from the lingual side of the third incisor to the posterior part of the incisive foramen. As noted above, it is unclear whether the premaxilla or the maxilla forms the posterior border of the foramen. In ventral view, the maxillae form a concave-upward secondary palate that lies between the canines and the postcanine tooth rows, with left and right maxillae meeting on the midline in a low narrow ridge. Behind the canine is a long diastema formed by a prominent rounded ridge that passes posteromedially to meet the first postcanine. The asymmetrical distortion of the palatal region has pushed the right postcanine dentition several millimeters closer to the midline than is the left. The maxilla meets the palatine in the secondary palate in a transverse, slightly interdigitating, suture at the level of the posterior third of the third postcanine. From the major palatine foramen in the lateral part of the palatine just behind the suture, a shallow groove extends forward on to the maxilla.

Portions of the left nasal are preserved anterior to the orbit, but no sutures with surrounding bones are preserved to indicate the limits of the nasal. On the midline, the medial edges of the nasals are raised as a ridge that is continuous with a prominent midline ridge on the frontals.

The frontals appear to be depressed between the orbits. They are bounded laterally by raised ridges formed by the postorbitals and presumably the prefrontals. The prominent midline ridge on the frontals extends into the narrow cleft between the posteriorly-converging postorbitals. The contact with the parietals cannot be seen.

The prefrontals are probably included in the raised ridges lateral to the frontals and also in the orbital wall, but they are too fragmentary for reliable identification.

Fragments of bone anterior to the right orbit and within the orbital rim undoubtedly pertain to the lacrimal, but no sutures or foramina are preserved to corroborate this.

Most of the right postorbital, including the postorbital bar, and the cranial portion of the left postorbital are preserved. The postorbital bar extends posterolaterally and slightly downward to form the posterodorsal quadrant of the orbital rim. Its dorsal surface is rounded in section, but ventrally it extends down and back as a deep tapering flange. Medially, this postorbital flange extends back as a vertical lappet overlying the lateral surface of the parietal. The postorbital of *Mandagomphodon hirschsoni* appears to be unusually deep, although a thorough comparison with other advanced cynodonts is not possible at present. A less prominent vertical lappet forming the rear of the postorbital bar was noted by Hopson and Kitching (2001) in the probainognathian *Lumkuia fuzzi*, which they interpreted as marking the area of attachment of the anteriormost portion of the temporalis muscle. Among gomphodonts, such a deepening of the postorbital bar is absent in *Massetognathus* (Romer 1967, Figs. 3, 10), but present in *Traversodon* (personal observation), where it is less prominent than that of *M. hirschsoni*.

The anterior end of the sagittal crest of the parietal is preserved between the cranial lappets of the postorbitals. The narrow crest continues on the isolated braincase back to the divergence of the lambdoidal crests. The dorsal part of the sagittal crest is missing, except for about 12 mm at its posterior end. Evidence of a parietal foramen is absent.

The right jugal is preserved as an isolated fragment consisting of the suborbital region and most of the postorbital process. It appears to have a contact with the posterolateral process of the maxilla lateral to the rear of the last postcanine. An elongate near-horizontal process on the maxilla fits into a groove on the anteromedial end of the jugal. In this orientation, the postorbital process of the jugal is directed toward the postorbital process of the postorbital and the anteromedial process of the jugal is directed toward the anterolateral process of the pterygoid, which it almost contacts behind the maxilla, as is usual in gomphodonts. The anterior end of the jugal extends about 4 mm laterally beyond the contact with the maxilla where it forms a vertical bar about 6.5 mm deep. The ventral margin of this bar is a natural sharp-edged ridge that underlies the posterior two-thirds of the orbit; it is slightly convex, but lacks evidence of a descending flange, which in traversodonts lies below the posterior half of the orbit. It is likely that the anterior extension of the jugal bar contacts the longitudinal ridge of the maxilla, as is usual in gomphodonts.

The palatines are preserved both on the type skull (Fig. 14.1c) and the isolated palatal region (Fig. 14.2). The latter specimen preserves the dorsal surface of the palatine, which is usually hidden by external skull bones. In both specimens, the palatine portion of the secondary palate is about 14 mm in length. In the little-distorted palatal

specimen, the palatine portion of the secondary palate is 14 mm wide, whereas in the more laterally compressed type skull, in which it is buckled upward, it is 10.5 mm wide. On the lateral margin of the palatine, shortly behind the transverse suture with the maxilla, is a conspicuous foramen, the major palatine foramen, from which a shallow groove extends forward. Two smaller, elongate foramina lie behind this foramen and in the palatal specimen, a tiny foramen lies slightly medial to the posteriormost foramen. A pair of slender ridges extend back and slightly outward from the posterolateral margins of the secondary palate, bounding the posterior parts of the maxillae laterally and the lateral walls of the choanal passage medially. In the roof of the choana, the palatines curve medially above the fused vomers in the primary palate, nearly meeting on the midline. Posterior to the secondary palate, the palatines meet the pterygoids in the roof of the choanal trough and contribute to the anterior parts of the low palatal ridges that converge slightly toward the rear. In the isolated palatal specimen, the contact surfaces with the medial surfaces of the maxillae are large thin plates that extend dorsolaterally from the margins of the secondary palate and the more posterior palatine ridges. These plates are slightly concave laterally and bear ridges, grooves, rugosities, and small foramina on their contact surface with the maxillae. They extend above the level of the dorsal surface of the primary palate. Medial to the plates, the palatines in the roof of the primary palate bear a broad longitudinal trough that opens laterally through a notch or foramen, presumably into the nasal cavity.

The fused vomers are preserved only on the palatal specimen, where they form a broad plate in the roof of the air passage above the palatines in the secondary palate. They taper toward the rear but are missing from the roof of the choanal trough, where they are expected to contact the pterygoids between the more lateral palatines.

The pterygoids are best preserved on the palatal specimen, though the base of the right pterygoid flange and the anterolateral process that appears to contact the jugal behind the maxilla are also preserved on the type skull. On the primary palate, the pterygoids bear the rear portions of the low ridges in the choanal roof, which converge slightly toward the rear and end 5 mm apart at the junction of the basipterygoid rami of the pterygoids with the posteromedial margin of the pterygoid flanges. The pterygoid flanges are robust, with flat lateral surfaces that are oriented backwards about 35° from the horizontal. Continuing forward from the pterygoid flange is a robust process with a concave ventromedially-facing surface that overlies the rear of the maxilla dorsolaterally. In the type, this process of the pterygoid, which is exposed in the floor of the orbit, bends outward toward the anteromedial process of the jugal. On its ventral surface in the palatal specimen, this process has a prominent anterolaterally-directed foramen on both sides,

immediately lateral to the concavity for the rear of the maxilla. It is not visible in the type skull where it may be covered by the suborbital flange of the maxilla. A short section of the basipterygoid rami of the pterygoids are preserved on the palatal fragment.

Much of the right squamosal is preserved on the isolated braincase (Fig. 14.3). The cranial process is a narrow triangular sheet of bone that lies against the parietal at the posterior end of the sagittal crest. It extends sharply back from the apex of the sagittal crest to form the lambdoidal crest; in the complete skull the diverging lambdoidal crests would overhang the occiput. The zygomatic process of the squamosal joins the lower end of the cranial process at the V-shaped notch. Although the posterior margin of the lambdoidal crest is damaged, enough is preserved to show that it extended behind and below the base of the zygomatic arch. Continuous ventrally with the lambdoidal crest is a narrow, slightly concave ridge that forms the lateral boundary of the middle ear cavity (and possibly supported a tympanum; Allin and Hopson 1992). On the medial side of this ridge, the squamosal has a vertical surface bounded in front by a medially-directed vertical lappet. The anterior surface of this lappet bears striations, indicating that it was overlain by another bone, most likely the lateral flange of the prootic (which is damaged in this specimen). In life, the space between the preserved distal end of the paroccipital process (which is formed by unfinished endochondral bone) and the distal and anterior squamosal surfaces probably held a cartilaginous distal and anterior extension of the paroccipital process. Lateral to the medial lappet, the squamosal forms a transverse plate that supports on its anterior face the preserved dorsal ends of the quadrate and quadratojugal. The latter bone lies in a deep notch in the squamosal so that it is visible from behind. Posterodorsal to the quadrate region is a broad shallow trough, the external auditory meatus, which is overhung by the outturned dorsal border of the squamosal. The zygomatic arch curves forward and outward from the level of the V-shaped notch. Its posterolateral surface bears a conspicuous sulcus, the external auditory meatus, which extends from the presumed tympanic ridge up, forward, and slightly laterally on the outer surface of the zygoma. The zygomatic arch is very deep, its incomplete dorsal margin perhaps extending as high as the sagittal crest. The lower margin of the squamosal portion of the zygomatic arch is preserved as a very thin, slightly concave, knife-edged plate. On the broken anterior end of the arch, the squamosal is seen to increase in width about 10 mm above its lower edge; this change in thickness is traceable for about 15 mm back on the damaged lateral surface of the squamosal. It is likely that the thinner lower portion of the squamosal was the contact surface for the rear of the jugal, which would have extended back nearly to the jaw joint. As preserved, the anterior end of the zygomatic

arch angles medially too much to meet the suborbital portion of the jugal; it is restored as angled more laterally.

All but the posterior-most part of the sidewall of the braincase and none of the basicranium is preserved; hence the orbitosphenoid, epipterygoid, basisphenoid, parasphenoid, and basioccipital, are not represented. Most of the prootic and opisthotic and the right side of the occiput above the level of the foramen magnum are complete, though sutures are not visible.

The paroccipital process of the opisthotic is sufficiently preserved to show that its anteroventral surface slopes posteroventrally and is composed of finished bone (Fig. 14.3b). Comparison with other cynodonts indicates that this surface forms a partial roof for the middle ear cavity (Hopson 1966; Allin and Hopson 1992). More distally, this surface curves ventrally and slightly anteriorly to end in a ventrally-bulging process formed by unfinished bone. Behind this process is a shallow trough of finished bone that is directed toward the presumed "tympanic" ridge of the squamosal. As noted above, the unossified distal and anterodistal parts of the paroccipital process were probably finished in cartilage, which implies that the ventrally-bulging process was a much larger structure than indicated by its preserved size, perhaps resembling the ossified crista parotica of tritylodontids (Hopson 1966; Sues 1986). At the proximal end of the paroccipital process is a broken mass of spongy bone around an irregular gap where the fenestra ovalis would be expected to lie.

Though sutures are lacking, the prootic of cynodonts usually contributes a thin lappet of bone to the anterior face of the paroccipital process (Parrington 1946; Hopson and Kitching 2001). The concave anterior margin of the paroccipital process forms the posterior rim of the pterygoparoccipital foramen. This foramen is usually walled in front by the lateral flange of the prootic, which extends laterally to contact the lappet of squamosal covering the anterodistal end of the paroccipital process. Here, the lateral flange has been pushed upward and forward by compression so that it lies 3 mm anterior to the squamosal lappet; the latter, however, shows anterior striations presumably marking the contact surface with the lateral flange. A sulcus in the prootic anterior to the proximal end of the paroccipital process contains a small facial foramen.

The triangular occiput is bounded above by the posterior end of the sagittal (parietal) crest and laterally by the posterolaterally-directed lambdoidal crests of the squamosal. The paroccipital process is exposed ventrally, but the foramen magnum and adjacent elements are not preserved. Bulges at the proximal ends of the paroccipital processes probably represent the dorsal parts of the exoccipitals. From them on either side, rounded ridges extend dorsolaterally, dividing the occiput into a single dorsomedian depression and two lateral depressions (of which only the right is preserved). These depressions contain matrix, but the lateral one is undoubtedly floored by the tabular and is penetrated by the small posttemporal foramen. The dorsomedian depression is probably formed by the supraoccipital in its lower half and the postparietal above.

The upper parts of the quadrate and quadratojugal are preserved in place, but their distal, articular portions are broken off. The upper part of the quadrate lies in a sulcus on the anterior face of the squamosal adjacent to the squamosal lappet that abuts the paroccipital process. The preserved part is 5.5 mm wide and 7.8 mm long and 3.4 mm from front to back. The broken surface shows that the outer bone is dense but the inner bone is spongy with fairly large cavities. The medial side of the quadrate is rounded in section whereas the lateral side is flat to slightly concave. Its posterolateral corner lies in front of a vertical groove in the squamosal; this is just above the expected position of the inverted V-shaped emargination that houses the posterior process of the quadrate.

The quadratojugal lies in a deep notch in the squamosal (which, as preserved, is 6.5 mm long) that lies immediately lateral to the quadrate sulcus. The medial face of the notch is flat (matching the flat medial surface of the quadratojugal) whereas the lateral face is flat dorsally but narrows ventrally to form a longitudinal ridge that fits into a matching groove on the lateral side of the quadratojugal. As preserved, the quadratojugal is about 1.0 mm in transverse width and 4.5 mm from front to back.

Lower Jaw

The only preserved parts of the lower jaws are partial dentaries indistinguishably fused at the symphysis (Fig. 14.4). The more complete right dentary consists of the horizontal ramus, which lacks the angular region, and the vertical ramus preserving the lower part of the coronoid process to about the level of the articular process, the latter lacking a small portion of its posterior tip. The left dentary is broken vertically behind the last (seventh) postcanine. The surface bone of the left ramus is largely smooth and undamaged, whereas that of the right ramus has suffered fracturing and some distortion. The medial surface of the right ramus is covered with a layer of fragmented bone embedded in a thin layer of matrix; it is possible that the fragmented bone represents parts of the coronoid and splenial, even portions of the postdentary rod formed by surangular, angular, and prearticular, but this is uncertain.

The total preserved length of the more complete right dentary is 103.3 mm, with an estimated restored length of about 118.3 mm. The fused symphysis has a slightly convex anterior profile and extends a short distance below the ventral margin of the horizontal ramus at the level of
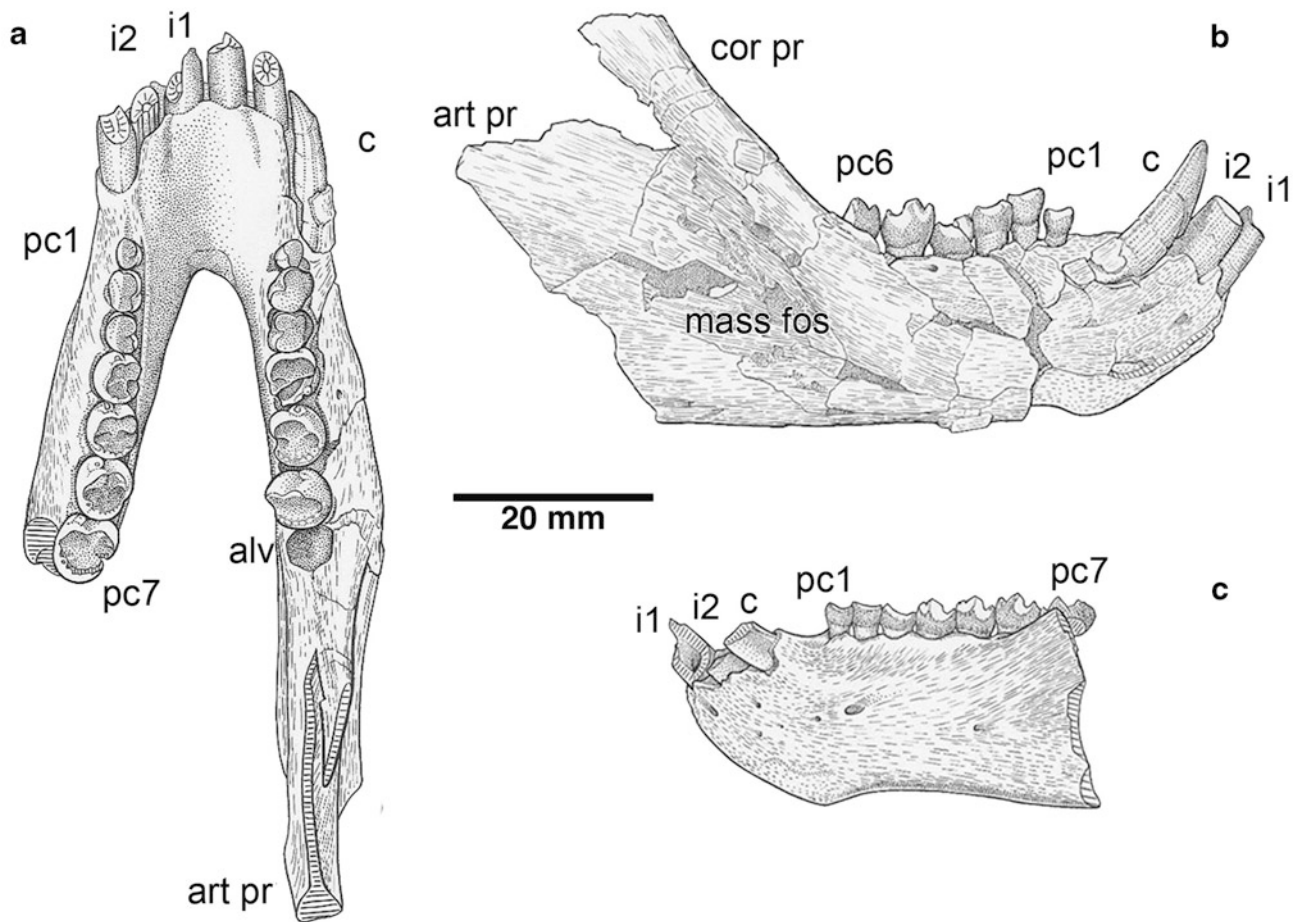
Fig. 14.4 *Mandagomphodon hirschsoni*, Crompton 1972. Holotype lower jaw, NHMUK R8577. **a** Dorsal view of fused dentaries; **b** lateral view of right dentary; **c** lateral view of left dentary. *alv* alveolus, *art pr* possible articular process, *c* canine, *cor pr* coronoid process, *i* incisor, *mass fos* masseteric fossa, *pc* postcanine

the canine/postcanine diastema. The horizontal length of the symphysis is 24.5 mm. The height of the jaw below the diastema is 20.0 mm. Behind the symphysis, the ventral profile of the dentary is slightly concave, with the shallowest part of the horizontal ramus lying below the rear of the second postcanine, where the dentary is 19.6 mm high. The dentary deepens very slightly toward the rear of the tooth row (well shown on the left side) and becomes straight or very slightly convex below the coronoid process (shown only on the slightly damaged right side). The deepest part of the ramus anterior to the rise into the coronoid process, at midlength of the fifth postcanine, is 20.2 mm.

Approximately the lower two-thirds of the horizontal ramus is broadly convex in cross section; but the dorsal third of the ramus forms a shallowly concave, medially inclined surface that extends from the swelling of the canine root back to the base of the coronoid process. This concave surface corresponds to the overhanging concave buccal shelf in the skull, though it is much less prominent. It is likely to have been covered by a fleshy cheek, as has been

interpreted for *Arctotraversodon plemmyridon* (originally ?*Scalenodontoides plemmyridon*) (Hopson 1984).

The lateral surface of the well-preserved left ramus has a few mental foramina, the largest of which lies below the contact between the first and second postcanines and opens anteriorly into a short groove. Slightly anterior to this opening is a much smaller foramen, which also opens anteriorly. Below the rear half of the fifth postcanine, on the thickened anterior margin of the masseteric fossa is a tiny foramen that opens toward the rear. On the symphyseal part of the dentary are three very small mental foramina below the canine and a single larger oval foramen below the gap between the first and second incisors. The relative sparseness of mental foramina in the symphyseal region of *M. hirschsoni* is notable, suggesting that the skin in this region is less tightly connected to the underlying bone than in other cynodonts, in which the symphyseal region is often rugose and more densely covered with small foramina.

The base of the thickened ridge that forms the anterior margin of the coronoid process rises lateral to the sixth

postcanine tooth and extends posterodorsally at an angle of about 40° from the horizontal postcanine tooth row. The coronoid process is preserved to about the height of the articular process of the dentary, some 17.0 mm above the alveolar margin of the tooth row. The lateral surface of the coronoid process forms a concave depression that is deepest just behind the thickened anterior margin and that is bounded below by the thickened ventral border of the dentary. Anteroventrally, this depression is bounded by the thickened masseteric crest, at about the level of the seventh postcanine. The lower part of this depression is the masseteric fossa, the attachment area of the masseter muscle, and the upper part of the depression, on the lateral surface of the coronoid process, is the attachment surface for the temporalis muscle.

Though the rear of the dentary is missing, the preserved portion above the missing angular region forms a thin posterodorsally-directed ridge, which is interpreted here as the lower margin of the articular process. If this is correct, then the missing part of the angular region of the dentary is about 20.0 mm long and about 17.0 mm high. On the medial side of the dentary behind the tooth row is the trough for the postdentary jaw bones, which are not preserved. The trough is bounded below by the thickened ventral border of the dentary. Its dorsal margin extends obliquely up and back above the missing angular region, behind which it continues back on the underside of the articular process as a transversely-widened surface that presumably supported the rear of the postdentary rod. This widened surface ends at a near-triangular break, the dorsal part of which represents the broken posterior end of the coronoid process. Neither the coronoid nor the splenial bone can be distinguished on the inside of the lower jaw. Below the tooth row a narrow groove extends forward to form a deep sulcus just above the posteroventral margin of the symphysis; this part of the trough was undoubtedly overlain by the splenial, which presumably met its counterpart in the symphyseal sulcus.

When viewed from above, the dentaries diverge at a low angle, thickening posteriorly lateral to the tooth row before rising into the coronoid process. The anterior end of the postcanine row lies slightly internal to the level of the canine, from which it is separated by a short diastema marked by a rounded, posteromedially-directed ridge. The tooth row is curved, concave-outward, and toward its rear overhangs the medial side of the dentary. On the lingual side of the jaw is a continuous shallow groove that lies just below the alveolar margins of the postcanine teeth. Such a groove in other cynodonts has been interpreted as housing the dental lamina.

Dentition

The dental formula of *Mandagomphodon hirschsoni* is I3, C1, PC7/i2, c1, pc7 (abbreviations for upper teeth in upper case, for lower teeth in lower case). The only possible uncertainty involves whether the third lower tooth is the third incisor or the canine.

Upper Incisors (Fig. 14.1)—Of the upper incisors preserved in the type skull, the first and second on the right lack the tips of the crowns, but the third is essentially complete and well-preserved. On the left, the second incisor is in the process of erupting and only its well-preserved tip is exposed. The first and third left incisors are represented by alveoli containing fragmentary roots.

The three upper incisors are all procumbent, being inclined forward about 37° from the vertical. The first upper incisor is the smallest of the three. The tip of its crown is broken off and the cross section on the break is a transverse oval. A small portion of the mesial marginal ridge is preserved. The posterolateral face of the crown appears to possess a flat longitudinal facet that is adjacent to a similar facet on the second incisor. The second incisor has a greater diameter, but is equally procumbent. Its tip is missing on the right, but the erupting I2 on the left has a spatulate tip, with mesial and distal ridges extending down the crown and a raised central area on its lingual face. Its labial face has a broadly rounded transverse surface. On the posteromesial and distal parts of the right I2 are what appear to be longitudinal planar wear surfaces. These presumed wear facets in I1 and I2 suggest that the procumbent first lower incisor occluded between the first and second upper incisors and the second lower incisor occluded against the posterodistal face of I2. The crown of the right third upper incisor is well-preserved and complete to its tip. It is shorter than the restored crown of I2 and slightly less procumbent. It resembles a canine in that its crown is recurved, with sharp mesial and distal cutting ridges that lie parallel to the curved margin of the premaxilla. However, it resembles an incisor in that the lingual side of the crown has slight concavities and a more rounded central surface internal to the marginal ridges, whereas the labial side of the crown is more broadly and smoothly convex than the lingual. Also, although the anterior cutting ridge lies on the mesial side of the crown apically, further toward the base it curves on to the lingual side of the crown and the mesial face of the tooth becomes smoothly rounded in section. This is seen in incisors but rarely in canines. The enamel of the labial face of the crown has a rugose surface of short longitudinal ridges; the enamel on the lingual side is smooth.

The presence in *M. hirschsoni* of three upper incisors that are procumbent and of which some (or all) are enlarged with respect to the primitive traversodont condition also characterizes *Exaeretodon*, *Menadon*, *Protuberum* and *Scalenodontoides*.

Lower Incisors (Fig. 14.4)—The anterior end of the lower jaw has three closely clustered teeth on each side, separated from the first postcanine tooth by a moderate

diastema. Two interpretations of their homologies are possible: there are either three incisors and no canine or two incisors and a semi-incisiform canine. As discussed below, I interpret the third tooth to be a canine; thus, I believe there are only two lower incisors in *M. hirschsoni*. Until now, no gomphodont (excluding *Sinognathus* and tritylodontids, whose gomphodont relationships have been questioned) has been known to possess fewer than three lower incisors.

All of the lower incisors lack the apical portions of their crowns, but because the preserved portions do not taper apically, they appear to have been longer than the upper incisors. The better-preserved right incisors are inclined forward about 35° from the vertical. They are enlarged, about the same diameter as the second upper incisor, but are more robust than the uppers, having an oval cross-section that is longer labiolingually than mesiodistally. In lateral profile they appear to be nearly straight. The first left and two right incisors are broken off relatively low on the crown and show a long exposure of basal dentine, with very thin enamel adjacent to the breaks. The crown of the second left incisor is partially erupted and is broken off just above the level of the alveolus. The cross-section shows a rim of thick enamel, which on the labial face of the erupting crown is strongly rugose and longitudinally-ridged.

Upper Canine (Fig. 14.1)—Both upper canines are in the process of erupting so that the crowns are only partially visible in their much larger alveoli. The apices of both crowns are broken off. The mesial (anterior) part of the right canine appears to be broken off, but the distal (posterior) part of the crown has slightly convex labial and lingual surfaces separated by a distal cutting ridge without serrations. The right canine is more heavily damaged. The preserved enamel on the lateral surfaces of both canines bears longitudinal rugosities. The right canine is slightly procumbent whereas the left is inclined more steeply forward.

Lower Canine (Fig. 14.4)—This tooth is strongly inclined forward, about 30° from the vertical, so that its crown lies very close to that of the second incisor; thus it appears functionally to be part of the incisor series. However, the lower part of the crown curves strongly back so that its embedded root is nearly horizontal in orientation, as indicated by a low swelling below the diastema external to the level of the first postcanine tooth. Furthermore, when the lower postcanines are occluded with the uppers, the tip of the presumed lower canine lies below the shallow depression identified above as the paracanine fossa. Finally, the presumed canine has sharp posterior and anterior cutting ridges that extend to the base of the crown, although this is not necessarily a clear distinction because the crowns of the lower incisors are broken off and show no trace of mesial and distal ridges. However, the third and only complete upper incisor does resembles the lower presumed canine in

having sharp mesial and distal ridges, although its mesial ridge passes lingually to terminate on the medial face of the crown, as often occurs in incisors, though not canines.

The lower canine is strongly recurved, in contrast to the nearly straight crowns of the incisors, and it is interpreted here as being much shorter than the lower incisors, because the latter, though incomplete, are almost as long as the canine, yet show no sign of tapering apically.

Dimorphism between upper and lower canines is rare in cynodonts, though it occurs in *Exaeretodon, Protuberum*, and *Scalenodontoides*, where, however, it is the upper canine that lies adjacent to the incisors and the lower canine that is separated from the incisors by a long diastema; consequently, in these taxa the paracanine fossa, which receives the tip of the lower canine, lies behind rather than in front of the upper canine as it does in *Mandagomphodon*.

Upper Postcanines (Figs. 14.1, 14.5a, 14.6)—The upper postcanine dentition is preserved only on the right side, and consists of five well-preserved teeth implanted in their alveoli and two large alveoli at the end of the tooth row.

The preserved upper postcanines increase in transverse diameter from front to back. The anterior to posterior decrease in wear on the crowns indicates that they erupted in sequence from front to back, the usual eruption pattern in traversodontids. In addition, the color of the enamel darkens posteriorly, from an amber color in PC2-4 to a deep brown in PC5, indicating thicker enamel in the latter. The unworn enamel in PC5 has a pattern of fine dorsoventral ridges.

Postcanine five (PC5) is the least worn of the upper postcanines and thus best shows the main features of the crown. Crompton (1972, pp. 50, 51) presents excellent illustrations of this tooth, describing it through a comparison with the upper postcanines of *Scalenodon angustifrons*.
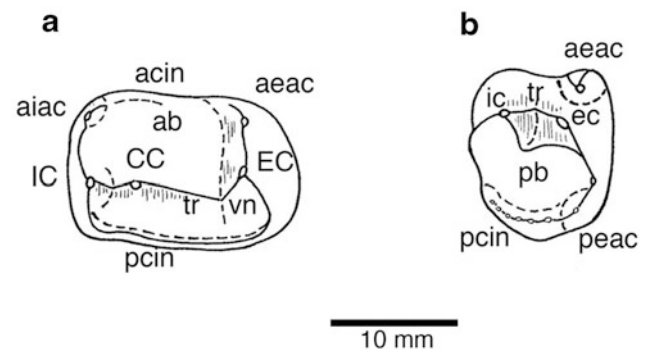
Fig. 14.5 *Mandagomphodon hirschsoni*, Crompton 1972. **a** Upper, and **b** lower postcanines with cusps and other features labeled. *ab* anterior basin, *acin* anterior cingulum, *aeac* anteroexternal accessory cusp, *aiac* anterointernal accessory cusp, *CC* main central cusp, *EC, ec* main external cusp, *IC, ic* main internal cusp, *pb* posterior basin, *pcin* posterior cingulum, *peac* posterior external accessory cusp, *tr* transverse ridge, *vn* V-shaped notch. Modified from Crompton (1972)
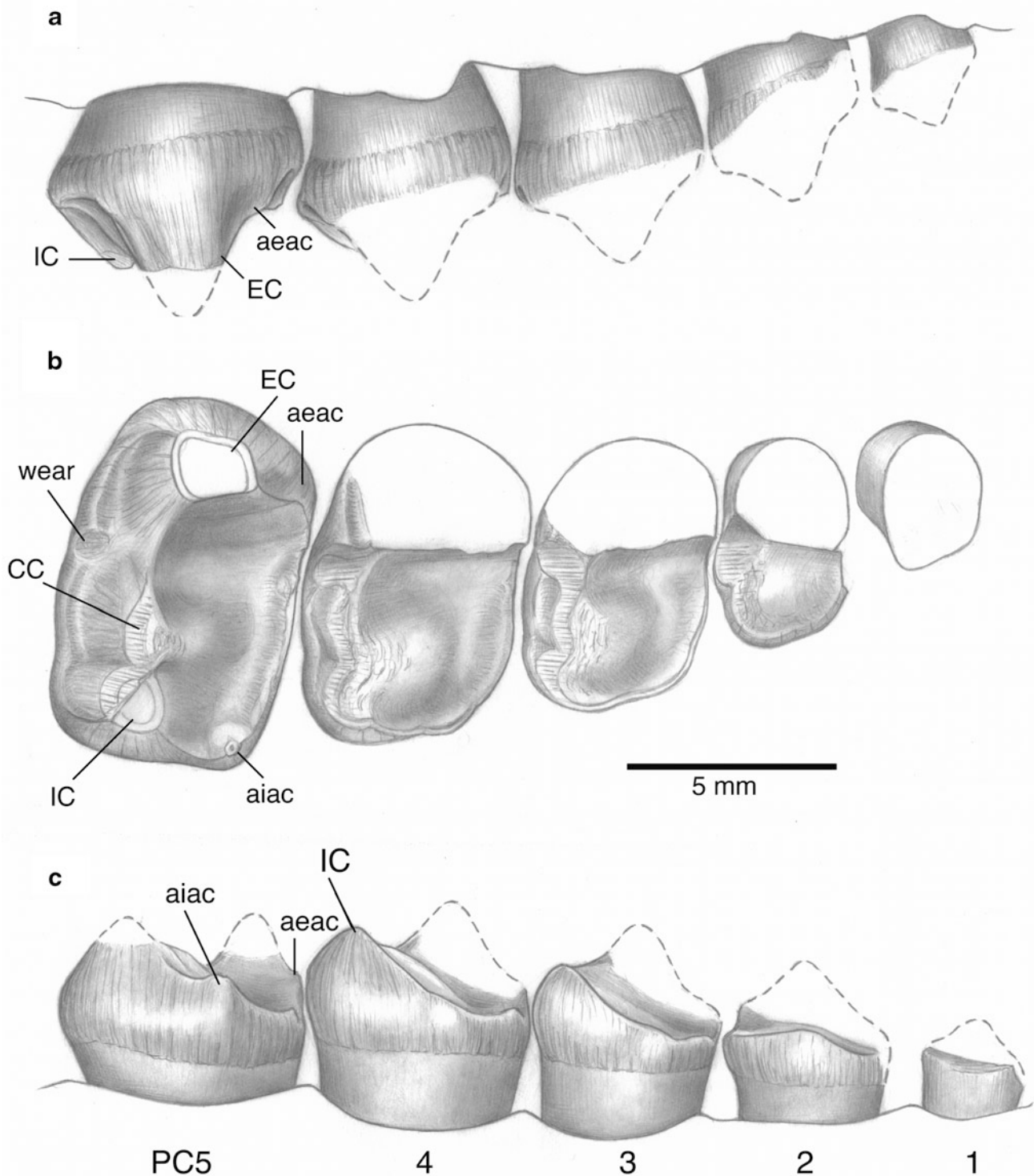
Fig. 14.6 *Mandagomphodon hirschsoni*, Crompton 1972. Right upper postcanines 1–5 of holotype skull, NHMUK R8577. **a** Buccal view; **b** crown view; **c** lingual view (rotated 180° so occlusal surface faces dorsally). *aeac* anteroexternal accessory cusp, *aiac* anterointernal accessory cusp, *CC* main central cusp, *EC* main external cusp, *IC* main internal cusp, *PC* postcanine, *wear* wear facet on posterior cingulum caused by main lower external cusp

I shall present a detailed description of PC5, including wear facets, and then shall describe the crowns of the preceding postcanines and how they have been modified by progressive wear. Functional interpretations will be discussed after the lower dentition is described. Identification of upper postcanine features are shown in Fig. 14.5a.

The fifth right upper postcanine is roughly rectangular in crown view (unlike the elongate oval shape of *S. angustifrons*). It is 9.1 mm in transverse diameter and 5.7 mm in anteroposterior diameter, thus being 1.6 times wider than long. This contrasts with *Scalenodon angustifrons* (Crompton 1955) in which the ratio of width to length of the largest posterior postcanines ranges from 1.6 to 2.1, indicating, as noted by Crompton (1972), an average greater length in *M. hirschsoni*. As also noted by Crompton (1972, pp. 50, 51), that portion of the *M. hirschsoni* crown anterior to the transverse ridge is considerably longer than in *S. angustifrons*, but this is also the case for the portion behind the transverse ridge, which bears a distinct posterior cingulum, as well as for the ridge itself. As in *S. angustifrons*, the transverse ridge is formed by three main cusps joined by a continuous crest that extends from the apex of the main external cusp to the apex of the internal cusp. The internal and central cusps are partly conjoined on the lingual half of the crown and are separated from the taller external cusp by a deep embayment with a broad, nearly semicircular, posterior profile (in contrast to the almost V-shaped profile of *S. angustifrons*). This embayment is referred to in *Boreogomphodon* as a "V-shaped notch" by Sues and Hopson (2010). The labial face of the main external cusp is convex, whereas its lingual face is a vertical, near longitudinal, planar surface. The anterior ridge on the external cusp is an oblique, nearly straight cutting edge that is notched toward its basal end by a small anterior accessory cusp lying on the ridge. Unlike in *S. angustifrons* and *Luangwa drysdalli*, the labial surface of the main external cusp lacks a cingulum.

The anterior basin of the upper postcanine is bounded anteriorly by a low transverse cingulum ridge. This ridge ends labially at the anteroexternal accessory cusp and lingually at a large anterointernal accessory cusp that lies at the junction of the transverse cingulum ridge and the prominent anterior ridge of the main internal cusp. The anterior basin is narrowest lingually, where the main central and internal cusps bulge forward from the transverse crest. Labial to the central cusp, the basin is deeper and extends further back, being bounded posteriorly by the slope up to the deep "V-shaped" notch and laterally by the planar longitudinal surface on the lingual side of the main external cusp. The posterior cingulum is a robust cuspidate ridge that bounds a narrow transverse trough behind the main transverse ridge. The posterior cingulum continues labially and lingually as faint ridges that pass down the rear of the main external and internal cusps toward their apices.

The little-worn enamel of the fifth upper postcanine is relatively thick on the peripheral parts of the crown and very thin within the anterior basin. Wear has removed the lingual enamel from both the main external cusp and its anterior accessory cusp and has worn the enamel on the ridge that extends down the lingual side of the main cusp to join the ridge of the "V-shaped" notch. The thin enamel on the anterior faces of the central and internal cusps appears to be worn through and the apex of the anterolingual accessory cusp shows slight abrasion wear. On the posterior side of the transverse ridge, the central and internal cusps and the posterior slope of the "V-shaped notch" have oblique facets on the thick enamel. The posterior cingulum is notched by wear in the enamel behind the valley separating the central and internal cusps and behind the lingual end of the "V-shaped" notch.

In all of the more anterior upper postcanines, the external cusp has been broken off. The topography of the preserved parts of the crowns becomes progressively lower and more broadly rounded than in PC5. In PC4, wear has truncated the anterior and lingual walls of the anterior basin, leaving a rim of worn enamel around the exposed dentine in the basin, and has entirely obliterated the anterolingual accessory cusp. The anterior faces of the central and internal main cusps are also heavily worn and their apices are smoothly rounded, with dentine extensively exposed on both cusps. On its lingual side, the internal cusp has a raised rim of enamel and adjacent dentine. The posterobasal parts of these cusps preserve enamel with oblique posterodorsally-sloping wear facets bearing anteroposteriorly-oriented striations. The posterior cingulum is worn posteriorly and is notched by wear behind the junction of the central and internal cusps. A deep longitudinal trough truncates the slope and cingulum behind the "V-shaped" notch.

The third postcanine has a more subdued topography than PC4, the central and internal cusps being very low and rounded, with steeper, enamel-covered posterior faces and worn, more gradually-sloping, anterior faces. The lateral part of the anterior basin is deeper than the medial part and is continuous with a deep wear surface with a V-shaped cross-section on the preceding tooth. The enamel across the rear of the transverse ridge bears a continuous oblique wear facet and, more basally, the entire posterior cingulum is worn off, leaving a posterodorsally-sloping facet.

The second postcanine has a featureless surface of exposed dentine surrounded by a rim of enamel lingual to the base of its broken external cusp.

The first postcanine is much smaller than the following tooth and its crown appears to be both worn and damaged, so that no reliable details can be determined.

Lower Postcanines (Figs. 14.4, 14.5b, 14.7)—The lower postcanine dentition is complete on both sides, with seven teeth in place on the left and six in place on the right, plus an isolated right crown that was presumably lost from the empty seventh alveolus and which has been glued back in place. In crown view, the tooth rows are seen to diverge toward the rear, so the labial profile of the tooth rows is slightly concave. In addition, the fourth to seventh teeth incline progressively inward toward the midline. As in the upper postcanines, the
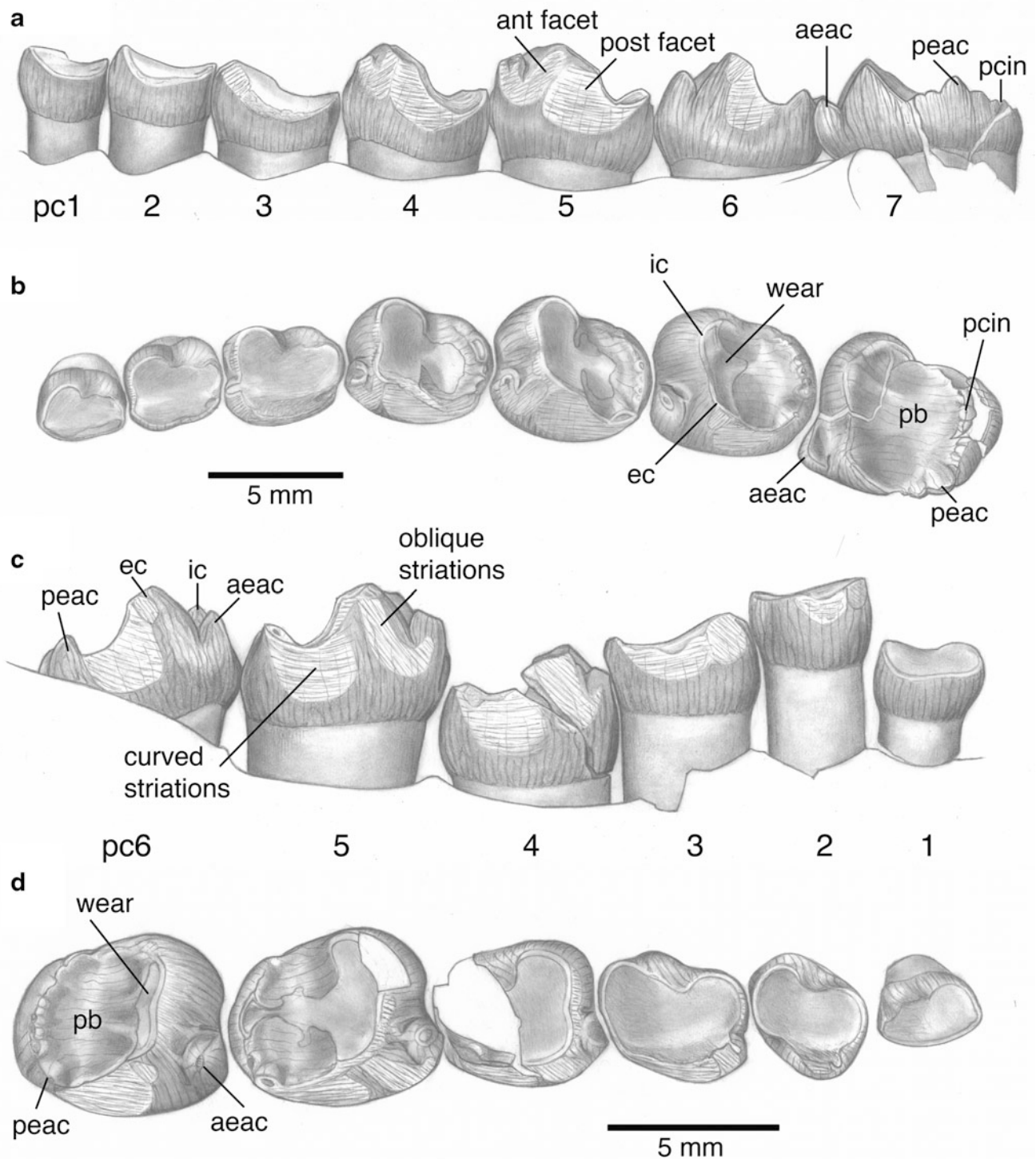
Fig. 14.7 *Mandagomphodon hirschsoni*, Crompton 1972. Lower postcanines of holotype specimen, NHMUK R8577. **a**, **b** Left lower postcanines 1–7 in **a**, external (buccal), and **b**, crown views. **c**, **d** Right lower postcanines 1–6 in **c**, external (buccal), and **d**, crown views. *aeac* anteroexternal accessory cusp, *ant facet* facet on main external cusp and anteroexternal accessory cusp, *ec* main external cusp, *ic* main internal cusp, *pb* posterior basin, *pcin* posterior cingulum, *peac* posterior external accessory cusp, *post facet* facet on lateral surface of crown, *wear* posteroventrally-sloping wear facet on transverse ridge

enamel darkens, therefore, is thicker, in more posterior teeth. The unworn enamel on the posterior teeth is rugose, with a pattern of short irregular dorsoventral ridges.

The description of the crown pattern (see Fig. 14.5b for identification of features) is based on both sixth postcanines, which are little worn, as well as the unworn but damaged left pc7. As with the upper postcanines, the lowers are compared with those of *S. angustifrons*, as was done by Crompton (1972). The crown pattern in *M. hirschsoni*, as in *S. angustifrons*, is typically traversodont, with a tall anterior transverse ridge formed by two cusps and a low posterior basin walled laterally by a narrow concave-upward ridge descending from the anterolabial cusp and behind by a cuspidate cingulum. A large posterolabial accessory cusp forms the posterolateral margin of the rear cingulum, as it does in *S. angustifrons*. Internal to it, the cingulum descends to the posterolabial side of the crown, where it joins a very low, broadly-rounded ridge that bounds the lingual side of the basin. The floor of the basin slopes obliquely downward toward this low ridge, which is soon obliterated in more worn teeth so that the basin becomes open internally.

In both *M. hirschsoni* and *S. angustifrons*, as is usual in Middle Triassic traversodontids, the internal cusp on the transverse ridge is labiolingually wider than the external cusp; the latter cusp, however, is taller and more robust. Both species possess a prominent cusp, very large in *M. hirschsoni*, on the anterolabial face of the transverse ridge. The transverse ridge in *M. hirschsoni* is lower and anteroposteriorly broader than that of *S. angustifrons*, with an oblique rather than nearly vertical posterior slope. The posterior basin in *M. hirschsoni* is consequently proportionately shorter than that of *S. angustifrons*. In *M. hirschsoni*, a low ridge passes from the apex of the lingual cusp down the posterior slope into the basin; its presence is uncertain in *S. angustifrons*.

Wear on the crowns varies slightly on the right and left lower postcanines, with teeth on the right being less worn than the matching teeth on the left. The descriptions of wear will concentrate on the left side, with some observations made from the right. The newly erupted left pc7 shows no signs of wear, but in pc6 a thin posteroventrally-sloping facet extends across both cusps of the anterior transverse ridge. The facet on the labial cusp extends steeply downward from the apex of the cusp into the notch between the two cusps, truncating the thick enamel, which bears longitudinal striations, and extending across a narrow band of exposed dentine. On the near-horizontal labial ridge of the main internal cusp, between notch and apex, the enamel and adjacent dentine are also truncated by wear. Crompton (1972, Fig. 8F) illustrates these wear facets in the right pc6. Wear also extends into the dentine in a broad V down the posterior slope of the transverse ridge below the notch

between the main cusps. Though not totally clear, the enamel on the anterodorsal face of the transverse ridge appears to have faint wear surfaces. As noted below, anterior wear on the transverse ridge is clearly present in more anterior postcanines.

The external face of pc6 shows two planar wear facets in the enamel, a smaller one high on the anterolabial face of the main lateral cusp and a larger one that covers much of the lateral surface of the crown below the concave ridge that descends from the main cusp. The small anterolabial facet, when viewed from above, is angled slightly inward anteriorly; posteriorly it truncates the larger, more longitudinal wear facet. It bears parallel striations that are angled posterodorsally between 20 and 25° from the horizontal. The more posterior facet fades out at the level of the large posterolabial cusp on the heel. It bears striations that tend to be oriented upward posteriorly at a low angle to the horizontal.

The wear on pc5 is much more extensive than that on pc6. The notch between the main anterior cusps is totally obliterated, leaving a single posteriorly-sloping transverse facet with thick enamel in front of the transverse ridge and a long posteroventrally-sloping wear facet on the dentine that extends down into the posterior basin. The wear facet on the posterior slope of the transverse ridge of the right pc5 is illustrated by Crompton (1972, Fig. 7B). The floor of the basin appears to have separate wear surfaces separated by a low anteroposterior ridge that bisects the the basin, a more labial and shallower depression behind the main external cusp and a more lingual and deeper depression behind the main internal cusp.

The enamel on the anterodorsal face of the transverse ridge bears a distinct anteroventrally-sloping wear facet near the crest of the ridge. The facet is anteroposteriorly slightly curved, rather than being planar, and striations are not evident.

On the outer wall of the crown of pc5 are two much larger wear facets than seen on pc6. The anterior facet is roughly V-shaped, with one limb extending anteroventrally and slightly medially down the anterolabial side of the main external cusp and the second limb truncating the entire lateral face of the anterolabial accessory cusp. The tip of this cusp is also worn by apical abrasion. The parallel striations on both limbs of the facet are oriented steeply up and back. A narrow vertical strip of unworn enamel separates this anterior facet from the larger, more posterior, wear facet in the enamel that covers most of the lateral surface of the crown. This facet is planar and longitudinally-oriented, lying below the concave lateral ridge and extending back and upward to truncate the side of the posterolabial accessory cusp. The striations on the anterior part of the facet slope only slightly up and back,

whereas on the posterolabial cusp they slope more steeply up and back.

The fourth lower postcanine possesses the main features of pc5, but wear is more extensive. Truncated enamel extends across the crest of the transverse ridge, which is worn down lower on the crown than in pc5, lying only slightly above the tip of the anterolabial accessory cusp. Enamel wraps around to the posterior side of the internal cusp and merges ventrally into a thin surface of enamel on the lingual margin of the posterior basin. The worn dentine on the posterior slope of the transverse ridge merges into the worn dentine on the floor of the posterior basin. The posterior cingulum ridge bears an elongate oval wear facet that truncates the enamel and an enclosed patch of dentine. The wear on the enamel on the anterior face of the transverse ridge forms a thin facet that extends across both cusps; the facets bear clear anteroposteriorly-oriented striations.

The main labial cusp of the fourth postcanine has on its anterolateral face a facet that bears surface striations that are oriented posterodorsally at an angle of about 35°. It contacts the more posterior lateral facet, forming in crown view a slight angulation with it. The anterolabial accessory cusp has a truncated apex, with an abraded wear facet that slopes down and forward. The lateral surface of the cusp is polished and may bear a few faint striations.

The lateral face of pc4 shows a wear feature not seen on more posterior teeth: the concave ridge passing down and back from the anterolateral main cusp and the lateral face of the posterolabial accessory cusp are so heavily worn that a large exposure of deeply-incised dentine is present. This feature is shown well on the left pc4, but is not ascertainable on the damaged right pc4. Below this wear surface, the enamel on the lateral surface of the crown bears a large planar wear facet that extends from the apex of the main labial cusp to the base of the posterolabial accessory cusp. There are several prominent concave-upward striations low on the facet and fainter striations higher on the facet that appear to extend up and back at low angles. On the anterolateral face of the main labial cusp is a second facet that contacts the lateral facet, forming in crown view a slight angulation between them. It bears surface striations that are oriented posterodorsally at an angle of about 35°.

The crowns of the anterior three lower postcanines are much more worn than pc4 and lack distinct cusps, including the anterolabial and posterolabial accessory cusps. A rim of enamel forms the circumference of each crown, with the entire central portion formed by worn dentine. Though greatly truncated, the transverse ridge remains the highest part of the crown. Its posterior face slopes at a low angle back to the posterior basin, the rear of which rises slightly to form the basin's posterior wall. The dentine-covered floor of the posterior basin slopes lingually and merges with the

lingual embayment of enamel, the surface of which slopes medially at a low angle.

Wear on the labial side of pc1-3 varies between the two tooth rows. On the right side, the labial enamel is less truncated by wear, so less dentine is exposed along the concave cutting ridge; thus, the lateral enamel wear facet is dorsoventrally deeper than on the left. On the right pc3, the lateral enamel facet has striations that show a less consistent trend than on more posterior teeth, but the majority of the striations appear to slope slightly anterodorsally. The smaller facet on the enamel of the anterolabial face of the main labial cusp has striations that are more parallel and slope relatively steeply up and back. These two facets differ from those on more posterior teeth in that they meet at a worn, rounded, surface rather than at a sharp angle. On the left side, where the dorsolabial surface of the crown is truncated by exposed dentine, the lateral enamel facet is narrow dorsoventrally and the orientation of the lateral striations is not clear. On the more anterior facet on the main labial cusp, the parallel striations slope strongly posterodorsally. The linear contact between the two facets forms a distinct angle.

The lateral facets on pc2 on both sides of the jaw are similar to those of pc3, except that the lateral facets are very narrow and the anterolabial facets cannot be distinguished on the smoothly polished enamel. The right pc2 is rotated anterolabially in its alveolus, which could be considered a postmortem event except that the lateral wear facet is restricted to the enamel on the outer side of the anterolabial cusp and the enamel on the more posterior part of the lateral surface is unworn. The shear surface on the main labial cusp of the matching upper postcanine is broken off, so an unusual wear pattern here cannot be determined. As noted above, the crown of pc1 on both sides is so truncated that the labial wear facets are no longer present. However, the enamel on the anterior face of the crown is more rounded and polished than that of pc3, which in turn is more rounded than that of pc4, which still bears traces of planar, sharp-edged wear facets.

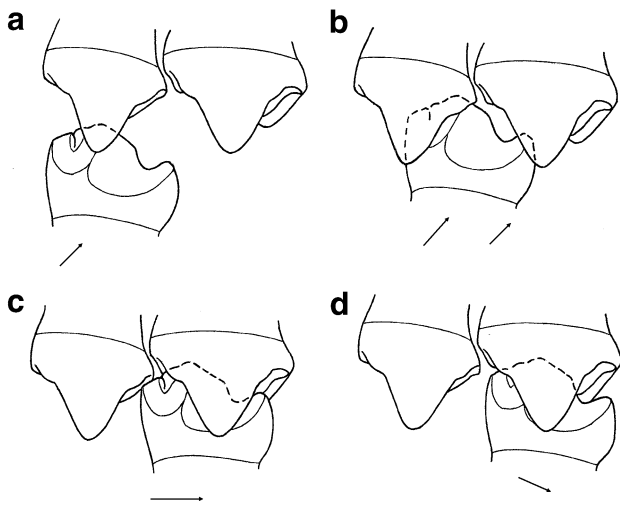## Interpretation of Postcanine Occlusion in *Mandagomphodon hirschsoni*

Several features of the occlusion of upper and lower post-canines of *M. hirschsoni* are evident from the description of the wear facets. These are essentially as noted by Crompton (1972).

1. Resting occlusion in unworn postcanines is with the transverse ridge of the lower postcanine fitted into the anterior basin of the matching upper postcanine and

the transverse ridge of the upper postcanine fitted into the posterior basin of the lower postcanine.

2. The initial movement of the lower jaw for chewing is anteroventrally so that the transverse ridge of the lower postcanine comes to lie immediately below the transverse ridge of the preceding upper postcanine (Fig. 14.8a). The transverse ridge of the lower tooth moves up the posterior side of the transverse ridge of the preceding upper tooth. At the same time, the anterolabial face of the main lower external cusp contacts the main upper external cusp on its posterolingual face, behind the extension of the transverse ridge on to the inner face of this cusp (Fig. 14.8b).

3. The path of the tip of the main labial cusp of the lower postcanine at the beginning of the retractive stroke is to move up and back on the posterior slope of the "V-shaped" notch in the upper transverse ridge. As the tip of the cusp passes up and back into the basin of the following upper postcanine, the anterolabial accessory cusp of the lower also slides up and back on the posterior slope of the "V-shaped" notch. The main labial cusp continues up and back across the anterior part of the basin of its matching upper tooth (Fig. 14.8c); it then shifts down and back along the anterior slope of the "V-shaped notch" of the upper transverse ridge (Fig. 14.8d).

4. The path of the wide main lingual cusp of the lower postcanine at the beginning of the closing and retractive stroke is to move up and back on the posterior faces of the medial and lingual cusps of the upper transverse ridge of the preceding tooth (positions in Fig. 14.8a, b). It continues up and back across the more medial part of the upper basin of its matching tooth (position of Fig. 14.8c), then moves down and back along the anterior slope of the medial and lingual cusps of the upper transverse ridge (position of Fig. 14.8d).

The functional interpretation of these movements is much as described by Crompton in *Scalenodon angustifrons* and *Scalenodon* (now *Mandagomphodon*) *hirschsoni* (1972, Figs. 5–9). The principal shearing surfaces are as illustrated by Crompton (1972, Fig. 6C): (1) a longitudinal shear surface on the inner face of the main labial cusp in the upper postcanine that is paired with a longitudinal shear surface on the labial face of the matching lower crown; and (2) a transverse shear surface on the transverse ridge of the upper postcanine that is paired with a transverse surface on the transverse ridge of the lower postcanine. The functional unit associated with a single lower postcanine is more complex than this because it includes the transverse ridges of two upper postcanines, the one on the matching upper tooth that the lower tooth contacts during resting occlusion and that of the preceding upper postcanine that the lower tooth contacts during dynamic occlusion. That portion of the upper shear surface that lies posterior and somewhat labial to the upper transverse ridge contacts that portion of the lower shear surface that lies on the anterolabial face of the lower transverse ridge of the succeeding lower tooth (for example, the anterior part of pc5 shears against the posterior part of PC4). Only the portion of the upper longitudinal shear surface that lies anterior to the upper transverse ridge shears against the longitudinal labial face of its matching lower postcanine (for example, the lateral face of pc5 shears against the large longitudinal shear surface on the lingual face of the main upper external cusp of PC5).

With respect to the transverse shear surfaces, the wear surface on the rear of the transverse ridge of the preceding upper tooth shears against the anterior face of the transverse ridge of the following lower tooth (for example, the transverse ridge of pc5 shears against the transverse ridge of PC4). The posterior face of the lower transverse ridge also possesses a distinct wear facet that matches wear on the
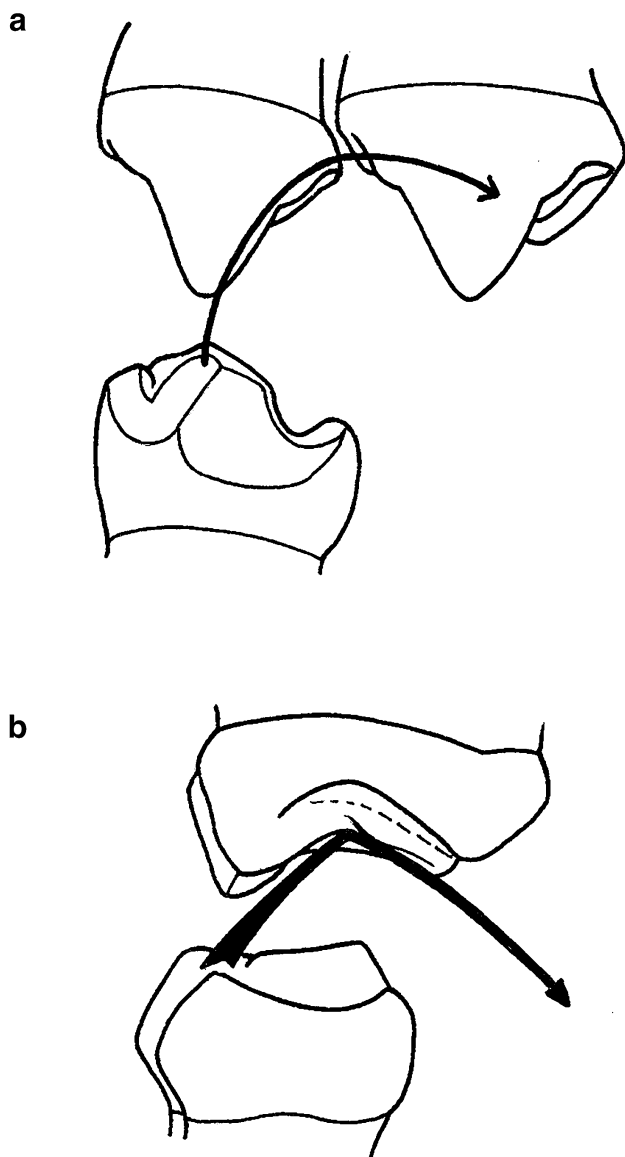

Fig. 14.8 *Mandagomphodon hirschsoni*, Crompton 1972. Stages in the retractive power stroke of a lower postcanine across two adjacent upper postcanines. *Arrows* below each figure show direction of movement at each stage of contact, as indicated by striations on lower tooth. **a** At beginning of the power stroke, the lower postcanine moves posterodorsally so that main external lower cusp contacts internal face of the main external cusp of the anterior upper postcanine. **b** At later stage, the lower tooth is near end of posterodorsal movement in which main external cusp and anteroexternal accessory cusp contact the rear surface of the transverse ridge of the anterior upper postcanine; at the same time, the posteroexternal cusp of the lower postcanine contacts the internal shear surface of the main external cusp of the posterior upper postcanine, creating posterodorsally-sloping striations on the lower cusp. **c** The lower postcanine moves posteriorly, as indicated by near-horizontal striations in the center of the posterolateral wear facet, to reach resting occlusion, at which stage, the main lower cusps occlude in the anterior basin of the upper postcanine. **d** The lower postcanine continues posteriorly and somewhat ventrally beyond resting occlusion so that its truncated transverse ridge (*broken line*) grinds against the anterior face of the medial portion of the upper transverse ridge that is formed by the central and internal main cusps. This movement is indicated by posteroventrally-sloping striations on the anterior portion of the posterolateral wear facet

anterior face of the transverse ridge of its matching upper tooth. Crompton (1972, p. 51) noted that "it is difficult to account for these facets if the power stroke of the lower jaw was directed dorso-posteriorly," although "they could have resulted from the postero-dorsal surface of the transverse ridge of the lower tooth being drawn backwards and downwards across the antero-ventral surface of the transverse ridge of the upper" (Crompton 1972, p. 51, Fig. 9D). However, Crompton pointed out, apparently disapprovingly, that this movement "would have required that the lower postcanines be dragged down an inclined plane". Consequently, he proposed that the same wear facets "would have been formed if the mandible had moved forwards and upwards during dynamic occlusion… so that the leading edge of the transverse ridge of the lowers sheared past the trailing edge of the transverse ridge of the uppers" (Crompton 1972, p. 51, Fig. 9E).

Can any of the wear facets on the postcanine teeth be used to test whether the wear on the rear of the lower transverse ridge and on the front of the upper transverse ridge were made by a posteroventral or an anterodorsal movement of the lower tooth across the upper? It would seem that either direction of movement would produce similar oblique striations. The parallel striations on the anterolateral wear facet of the main labial cusp of the lower postcanines slope strongly up and back, clearly demonstrating that the initial movement of the lower crown was in a posterodorsal direction (Fig. 14.7b, d). Thus, to demonstrate anterodorsal movement of the lower postcanines, one would expect to see equally strong striations on their external wear facets (made by contact with the lingual side of the main upper external cusp) sloping up and forward, parallel to the truncated dorsal surface of the lower transverse ridge (Fig. 14.8a). Variably present and usually faint striations that slope obliquely anterodorsally-posteroventrally do occur on the external longitudinal wear facet of lower crowns, but they are mixed with more horizontally-oriented striations and even posterodorsally-oriented striations. This mixture of differently-oriented, overlapping striations can be interpreted more plausibly as being caused by the lower crown consistently moving in a generally posterior direction, but with an initial posterodorsal direction (indicated by striations on the posterolabial accessory cusp), then a more horizontal direction (indicated by striations on the middle of the lateral surface of the crown), and, finally, a posteroventral direction (indicated by striations high on the lateral surface of the main external cusp). What is lacking among these overlapping striations is a clear set of parallel striations superimposed on the fainter ones but discontinuous from them. This strongly suggests that the reversal in direction of the lower teeth from a backward and downward movement to a powerful forward and upward movement lacks support in the wear facets and striations on the lower postcanines.

I interpret the tooth movements that caused the external striation patterns as follows (Fig. 14.8): (1) during the oblique posterodorsal movement of the lower crown (which is recorded in the striations on the anterolabial main and accessory cusps) the posterolabial accessory cusp of the lower crown contacted the upper longitudinal shearing surface on the inner face of the main external cusp (see Crompton 1972, Fig. 9B), resulting in anteroventrally sloping striations on the posterolabial cusp (Fig. 14.8b); (2) further posterodorsal movement of the lower crown, to a position where the lower transverse ridge moves into the deepest part of the anterior basin of the upper, is represented by the forward continuation of the lateral striations, which now slope slightly anteroventrally to horizontally, on to the middle of the large external wear facet (Fig. 14.8c) on the lower crown (see Crompton 1972, Fig. 9C); (3) the final movement of the rear face of the lower transverse ridge down and back against the anterior face of the upper transverse ridge is represented by the anterodorsal/posteroventral slope (Fig. 14.8d) of the anterior- and dorsal-most striations on the lower crown (Crompton 1972, Fig. 9D). Thus, the evidence of the lateral striations on the lower postcanines suggests a posteroventral crushing/grinding movement, continuous with the posterodorsal and subsequent horizontal and backward movement of the lower crown, rather than a reversal of direction of the lower crown to create an anterodorsal shearing movement of the lower transverse ridge on the upper ridge.

That an oblique downward movement of the lower postcanine can occur toward the end of the occlusal stroke, where it moves down an inclined plane formed by the upper crown, is demonstrated by a variety of living (usually herbivorous) mammals. In Fig. 14.9, the proposed movement of the lower postcanine in relation to the upper postcanine in *Mandagomphodon* is compared with the movement of the lower molar across the upper in the primate *Saimiri* (Kay and Hiiemae 1974, Fig. 9C). In both, the initial phase of upward movement (Phase I) causes shear between tall lower cusps passing internal (or posterior in *Mandagomphodon*) to tall upper cusps. This phase is followed by Phase II, in which the tall lower cusps move obliquely downward and medially (posteriorly in *Mandagomphodon*) across an inclined plane formed by low upper cusps. Kay and Hiiemae (1974, p. 243) argue that "Phase I and Phase II [in primates] are parts of a continuous movement, distinguished only by a change of direction from anteromedial and upward to anteromedial and downward." I believe this interpretation is applicable to *Mandagomphodon*, which differs only in that movement of the lower tooth is posterior rather than medial. The gomphodont also differs from mammals in that it utilizes two upper molariform teeth to achieve the functional results that

a

Fig. 14.9 Comparison of the curved trajectory of a lower molariform tooth across the matching upper molariform(s) in **a** the gomphodont *Mandagomphodon hirschsoni* Crompton, 1972, and **b** the living cebid primate *Saimiri sciureus* (modified from Kay and Hiiemae 1974). Movement of the lower tooth, as indicated by the *arrows*, is in a posterior direction in **a** and in a medial direction in **b**. Thus the cutting component in the gomphodont (*phase* I of Kay and Hiiemae) is due to movement of the anterior face of the transverse ridge of the lower postcanine up and back against the rear of the upper transverse ridge of the preceding postcanine. (The longitudinal shear also contributes to cutting the food.) In the primate mammal, where the lower jaws move transversely, the shear component of *phase* I is due to movement of the external surfaces of the outer cusps of the lower molar up and inward across the inner surfaces of the external cusps of the upper molar. The grinding component (*phase* II of Kay and Hiiemae) occurs in the gomphodont as the lower postcanine moves down and back beyond centric occlusion at the end of the power stroke, so that the posterodorsal faces of the lower main cusps grind against the anteroventral faces of the central and internal main upper cusps. In the primate, the grinding in phase II occurs as the dorsomedial surfaces of the outer cusps of the lower molar pass medially across the ventrolaterally-facing surfaces of the inner cusps of the upper molar. **a** and **b** not to scale

b

mammals achieve with one upper molar. Other implications of these differences are discussed below.

As noted above, as wear of the postcanine crowns of *Mandagomphodon* increases from posterior to anterior, the transverse ridges become increasingly lower in height and all of the tooth cusps are eliminated; furthermore, the distinctness of the wear facets is lost on the anterior postcanines, indicating a loss of direct contact between upper and lower teeth. Also, as noted above, the worn enamel on anterior teeth is more rounded and polished than that of more posterior teeth and wear facets are less clear. The increase in smoothing and polishing of the enamel of anterior teeth is undoubtedly due to abrasion by food between the teeth rather than tooth-on-tooth contact. The occlusal surfaces of these teeth, which are formed entirely

by dentine, are also smoothly rounded, with only slight topography remaining. This nearly complete destruction of the crown topography in anterior postcanines is characteristic of all traversodontids, indeed of all gomphodonts.

The power stroke of the lower jaws of gomphodonts during food processing is in a posterior direction, as attested by the positions of shearing edges and grinding surfaces on the crowns and by the orientation of wear facets and striations on the enamel. Thus, unworn or little worn postcanines appear to function optimally as the lower crown moves backwards across the matching upper crown. Another characteristic of gomphodont postcanines is that they increase in size from front to back, which is a consequence of their serial eruption as the skull and lower jaws elongate posteriorly during ontogeny and consequently create space at the back of the tooth row for eruption of newly-formed teeth. Thus, for optimal function of the postcanine dentition, the length and shape of the retractive power stroke must be determined by the least worn and largest (i.e., longest) teeth, which lie at or near the posterior end of the tooth row. A consequence of the length of the power stroke being adapted to the functional requirements of the longest postcanines is that for shorter more anterior postcanines the power stroke becomes incompatible to optimal functioning. It is now much too long for these teeth to perform useful shearing or grinding. Thus, the distinct occlusal wear facets seen in more posterior teeth become rounded and polished in more anterior teeth because these teeth no longer possess useful tooth-on-tooth contact. It is also likely that the greater length of movement of lower teeth relative to uppers anteriorly along the tooth row would have increased the rate of wear, and hence of obliteration of

the crown surfaces, in comparison to more posterior teeth. As noted above, enamel thickness increases posteriorly along the tooth row, so that the thinner enamel of more anterior teeth probably contributed to an increased rate of wear. However, rather than being a disadvantage, the rapid elimination of the original topography of anterior teeth meant that these teeth could not interfere with the optimal functioning of the little-worn posterior teeth.

The postcanine dentition of *Mandagomphodon hirschsoni*, which shares its main characteristics with most other gomphodonts, functions optimally only in the posterior-most part of the tooth row. The traversodontid postcanine dentition in its functional complexity can be compared with that of mammals. However, the dentitions of most mammals (with the exception of those with planar occlusal surfaces, such as rodents and elephants) function with a transverse rather than fore-aft (propalinal) movement of the lower jaws. Thus, whereas mammalian molars (and premolars) can maintain functional occlusion along the entire tooth row throughout most of an animal's life, and the length of the transverse power stroke can be adjusted to the degree of wear of the tooth crowns, gomphodonts must adjust the length of the longitudinal power stroke, at most, to the last few teeth in the jaw, with the more anterior teeth progressively losing optimal function. Thus, the functional surface and lifetime of use in an herbivorous mammal's cheek dentition is much greater than that of a gomphodont cynodont, which is restricted to a few posterior teeth that appear to lose optimal function fairly rapidly. It also follows that replacement of small, heavily-worn anterior postcanines by unworn teeth of comparable length would not increase the functionality of the dentition if the length of the power stroke remained adapted to optimizing function of the longer posterior teeth.

Tritylodontids, which may have been derived from within Traverodontidae, appear to have circumvented this "functional constraint" by eliminating features that functioned in transverse shear; thus, the postcanine crowns consisted of multiple parallel rows of shearing cusps, with functional boundaries between individual teeth no longer present. Thus, the power stroke no longer needed to be adjusted to the posterior-most teeth and the whole tooth row functioned as a single functional unit.

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