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Thegosis – A critical review

Christopher G. Murray, MDSc(Melb), MSc(Lond), CertPros(Texas), AFAAMP, FRACDS*
Gordon D. Sanson, PhD(WA)†

Abstract

The evidence for tooth sharpening has been examined and it has been concluded that there is no evidence for a posterior tooth sharpening mechanism which is independent of masticatory function and improves the efficiency of that function.

Anterior tooth sharpening may occur in some species as behavioural activity but it is not accepted that this sharpening is directed towards the production of new incisiform weapons as distinct from the improvement of existing caniniform weapons, or more efficient tools for the manipulation of food. Thegosis (from the Greek, *thego* to whet or sharpen) is a term which could be used to describe the sharpening of anterior teeth under specific often socially context driven situations. Stress is accepted as a cause of non-masticatory tooth to tooth contact as is the suggestion that excessive tooth grinding and clenching is pathological and stress related. Bruxism and pathological thegosis are suggested synonymous terms for this activity.

Key words: Thegosis, bruxism, dental microwear, jaw mechanics.

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Introduction

Following Ronald Every's last publication describing his theory of thegosis in 1975[1] there has been sparse but continuous mention of his concepts in the literature of disparate fields. Some authors have acknowledged and accepted the theory without question, while others have directly or indirectly provided contradictory evidence, but there has been no compilation of this body of work or analysis of its effect on the validity of the thegotic concept.

Anderson stated, 'since 1960 the physiology of thegosis has received intensive, if cheerlessly lonely, research which, by not being restrained within just one scientific discipline, has largely escaped them all, and certainly has escaped dentistry, for which it has the utmost significance'.[2] A list of references accompanied Anderson's letter but their reading suggests a theory based on observation rather than a hypothesis proven by replicable research. It may be that the multidisciplinary nature of the thegotic literature has served to limit scientific debate, but it may also be because it has not been taken very seriously, possibly because of the lack of data to support it.

Scally paraphrased Every whom he stated suggested that 'nocturnal jaw movements, beyond and opposite those of mastication and oblique to those of incision, were a universal phenomenon in man'.[3] Based on the matching of thegotic facets he suggested that current concepts of the management of myofascial pain be discarded and that alternative treatment, based on thegotic theory, is appropriate. Aspects of the suggested treatment protocol are outlined by Scally.[4] In that guest editorial he stated that 'it is the irregularities in the thegotic path that constitute a significant degree of (dental) trauma for some individuals when they attempt to sharpen their teeth' and he further suggested that the aetiology of much of myofascial pain dysfunction and temporomandibular joint dysfunction related to thegotic activity. He considered that thegotic behaviour is normal while bruxism is an inappropriate concept.

Klineberg considered the aetiology and management of bruxism and mentioned that 'its management is poorly understood by dentists' and he considered that their focus on a local dental cause had led to much unnecessary irreversible dental treatment with little impact on the incidence of bruxism.[5] Klineberg defined and reviewed bruxism and emphasized his view that malocclusion was not a trigger for bruxism and supported that view with reported scientific evidence. He then introduced 'thegosis' as a term describing a biological basis for tooth wear, rather than a pathological basis. He stated that 'restorations must be compatible with

*Prosthodontist, Melbourne, Victoria; Senior Visiting Specialist, Austin and Repatriation Medical Centre, Heidelberg, Victoria.
†Associate Professor, Department of Ecology and Evolutionary Biology, Monash University, Victoria.

adjacent tooth wear patterns'. Interestingly, and in contradiction to thegotic theory, he stated that 'thegotic facets arise from tooth grinding action with the jaw placed in a latero-protrusive position, and drawing back into intercuspal position with the teeth firmly in contact' Neurological experiments were mentioned which may be of relevance in supporting thegotic theory but the evidence provided was based on supposition and is unconfirmed. A concise summary of the signs and management of bruxism followed which is unrelated to thegotic theory and in parts is contradictory. The effects of stress on modern man was linked to a presumed inherited predisposition to keep teeth sharp.[5]

A palaeontological view was provided by Archer in which he supported Every's views.[6,‡] He utilized an aggressive Australian Rules footballer as an example of thegotic action. He differentiated healthy thegosis from pathological bruxism but agreed with the proposition that thegotic damage could occur in individuals with 'variations in their anatomy'. The relief of tension was considered the appropriate means of reducing the damage. Archer stated that 'thegotics is an exciting integration of palaeontology, morphology and behaviour'.[6] Thegotic theory has been used to assist in the description of an extinct platypus.[7,8]

The practical application of thegotic theory to dental practice and to the science of palaeontology legitimized its status. It is, therefore, imperative that thegotic theory be supported by a body of research, which at present is not apparent. This paper does not attempt to deal with all aspects of thegosis as it impacts on tooth to tooth contacts, dental restorations, the management of craniomandibular dysfunction, and the use of dental facets in the description of extinct taxa. Rather it addresses that part of the thegotic literature which presumes to establish the case for thegosis and papers which provide alternate views. A consideration of these papers should encourage thegosis to be viewed in a more objective manner and may indicate areas for further research.

The thegotic literature

Every[9] in the very first article that can be linked to the thegotic literature stated that 'most mammals sharpen their teeth' and cited this statement as evidence for later assertions.[10] Except for a very few, perhaps special cases, there is no evidence presented that most mammals sharpen their teeth and it is inappropriate for these papers to continue to be cited as evidence for tooth sharpening in mammals. Every[10] considered that sharpening was needed for the use of the teeth as tools and weapons and based this argument on another unsupported statement about the behaviour of our extinct ancestors. He considered that the mandibular movements which accompanied tooth sharpening were frequently greater than needed for sharpening and these extreme movements produced symptoms of facial and temporomandibular joint discomfort and dental damage. He considered that this tooth sharpening mechanism represented a powerful aggressive instinct which had been repressed in man, but still occurs in sleep. It is suggested that the observations and opinions which led Every[10] to conclude that 'on, or related to, the occasion when man is under stress, he will sharpen his teeth' are confounded. By proposing a theory that humans grind their teeth in order to sharpen them because of some atavistic trait, and that this is often done under stress, he obscured the possibility that some humans under stress respond by grinding their teeth which incidentally ends up 'sharpening' them. This may seem a fine point but has greater significance if a body of clinical and scientific work is predicted and legitimized by this proposition.

Every[10] expanded his tooth sharpening hypothesis to detail its function in the development of teeth as weapons and tools. He also provided details of his view of intercuspal relations, mandibular movements, and the particular action of the lateral pterygoid muscle which he considered was responsible for a forceful lateral excursion of the mandible which occurs during tooth sharpening. The concept of segmentive biting function was also introduced in the context of the evolutionary and structural development of a dental weapon, and associated aggressive behaviours were incorporated in his theory.

Thegosis (from the Greek, *thego* to whet or sharpen) was introduced in 1970 as an alternative term for attrition.[11] The history of the introduction of this term is important. Every[11] defined attrition as a loss of tooth substance caused by rubbing upper and lower teeth together in the absence of food: 'That is to say, it is caused by non-masticatory movements with the teeth in contact'. Every[11] consistently argued that teeth do not contact during normal masticatory movement: 'Attrition (thegosis) does not occur during chewing and swallowing because masticatory and incisive strokes are terminated, presumably by proprioreceptive reflex, just short of contact between opposing teeth'.[11] Clearly Every equated attrition and thegosis though he provided no actual evidence that tooth contact did not occur during normal mastication, while Anderson showed that it did.[12] Every[11] preferred the term thegosis because it was more appropriate to an evolutionary adaptive phenomenon. Unfortunately

‡Archer M. Inhuman and human thegosis: 500 million years of the function of parafunction. Unpublished observations, 29 August 1994.

this was another example of a concept based on presumption rather than fact. The importance and significance of the use of this terminology is that when a thegotic facet is identified (equals attrition facet *sensu lato* Every[10]) it is now interpreted by definition as the product of a deliberate sharpening action, which leads to circular argument. It must be stressed that this interpretation is not based on any independent data.

Every[11] first provided detailed evidence for his proposition in 1970 and presented three cases. The first case mainly examined canine wear in the baboon and is partly concerned with the arguments relating to loss of the canine in humans and, therefore, a new role for the segmentive bite of the incisors. However, the loss of canines in humans is not logically followed by the fact that humans must sharpen the incisors. The analysis of the dentition of two individuals one from New Guinea and the other from New Zealand is deduced from his ideas of thegosis. The dentitions were interpreted from a preconceived theory and yet were presented as inductive evidence for the theory.

Thegotic (attrition) facets were further defined by Every and Kuhne in terms of nine characteristics of the facets which distinguish them from abrasion facets.[13] The paper does not provide any information based on experiment that explains what precise action produces thegosis facets. It is clear that the cause of the thegosis facet is inferred. Every and Kuhne emphasized that thegosis was not found in all mammalian taxa, in all members of a population, or in all teeth of a dentition. The significance of this, if true, is yet to be determined and differs from the emphasis in Every's 1970 paper[11] in which he stated that 'mechanisms to perfect and maintain this sharpness through progressive wear have evolved as important characteristics of mammals'.

Every[14] formalized his ideas concerning the effect of thegosis on tooth form with a new terminology for mammalian teeth. This terminology was explicitly functional in its interpretation. Particular forms of cusps or facets were identified in terms of morphological and functional characteristics where the function was inferred from the morphology. The derived name is, therefore, theory laden which implies it functions in a particular way even though there may be no independent evidence that it actually does. The paper itself provided no additional evidence for the theory of thegosis, it is presumed in a short preface and introduction.

Scally, Tunicliffe and Every examined extant lower animal classes for thegotic activity and considered such activity existed.[15-18] Their evidence was the presence of 'thegotic' for which could be read 'attrition' facets, and following the arguments presented above, they concluded that thegosis occurred and was therefore phylogenetically ancient. Presumably this evidence was considered to be important in supporting the argument that 'most mammals are genetically programmed to sharpen their teeth as tools or weapons'.[8] However, the evidence presented was neither convincing nor detailed. Even if the evidence had been convincing it is unclear how observation of 'thegosis' in phylogenetically unrelated phyla with no homologues to teeth and dentitions could be applied to explaining an analogous phenomenon in mammals. Of particular concern is the common theme that the animals examined were subjected to some specific behavioural situation primarily involving stress. Tunicliffe[17] noted that, 'Sounds analogous to thegotic tooth chattering of mammals under stress, are evoked, under comparable circumstances . . . To interpret these oral behaviours and morphologies in a nonfunctional context violates basic evolutionary principles, an anomally stressed by Every'. This appeal to 'evolutionary principles' to validate such an argument is flawed and the dangers of this adaptionist view have been seriously questioned by evolutionary biologists.[19]

What is of greater interest is the observation that all the proposed examples of thegotic action, whether in the experiments referred to above, or in hippopotamus, warthogs, pigs, peccaries or baboons are provoked under stressful situations. In the latter animals, the teeth that are generally accepted as being ground before some inter- or intra-specific behaviour are not food processing teeth. It is also interesting that the shattering noise of the pig may act as much as a warning as anything else. One side effect would be to sharpen the teeth. It would be difficult to unequivocally determine which is cause and effect, particularly in fossil animals, and that is one of the central problems with Every's proposal.[10,11]

Every emphasized the importance of tooth sharpness and argued that, without a sharpening mechanism, 'the precision scissorial blade unit could not have evolved'.[1] Two features of the associated new mandibular movement are described. First, the addition of a horizontal component and second, the occurrence of a forceful grinding contact of one tooth against another. Morphological variations according to the abrasive content of the diet were considered to occur.

Thegotic facets were again considered in guinea pigs and the presence of parallel striations on these facets is mentioned. The presence of an acute angled leading edge and the necessity to sharpen this edge when it becomes rounded and blunted was detailed. The statement was made that, 'marks on the teeth, therefore, run from lingual to buccal in a mandibular molar and (relatively) buccal to lingual

in a maxillary'.[1] No evidence was provided for these directional presumptions.

The difficulty of studying occlusal relationships was acknowledged and extrapolations of thegotic theory to the reptilian antecedants of mammals was made.

The alternative literature

Mills considered that attrition facets on molars were the result of chance tooth-tooth contacts on the balancing side.[20] This varied from Every's thesis[10-,11] that the contacts are part of a tooth sharpening mechanism. Anderson[12] confirmed that during chewing the mandible made more medially directed movements and that upper and lower teeth frequently contact.[12]

Berkovitz and Poole demonstrated differences between the worn molar teeth of ferrets fed on different foods.[21] Their work indicated that animals can adapt their dentitions to most effectively cope with different diets and it can be implied that thegosis would not be diet specific for a particular animal. They argued that normal wear produces a degree of sharpness appropriate to a particular diet.

In an extensive paper, Osborn and Lumsden disputed Every's tooth sharpening hypothesis as applied to mammalian molar dentitions.[22] They argued that the attrition facets on molar teeth were probably produced by contacts during normal mastication. They considered that it was doubtful that any molar tooth needed to have sharper edges than those produced by normal masticatory action.

These authors explained the development and actions of mammalian molar tooth surfaces and they reviewed the relevant literature.

They concluded that:

1. Tooth-tooth contact was necessary to cut food completely. With a scissorial action a relief was needed to prevent food being caught between the cutting blades and this would be achieved either by an increased rate of dentinal wear when compared with enamel or by rolling the blade. Thegosis would reduce efficiency by removing the relief.

2. Sharp edges and flat surfaces, such as those which might be produced by thegosis, could reduce the efficiency of crushing.

Osborn and Lumsden[22] examined five types of molar teeth and suggested that:

1. The attrition facets of the carnassial teeth of carnivores were sharp edged and to a large degree self sharpening. Thegosis was not needed to maintain efficiency.

2. Omnivores and herbivores tended to adopt a diet and a mode of mastication which is most suited to the state of their dentition. Thegosis would tend to flatten the tooth surfaces and reduce the efficiency of retention which was vital for dividing, crushing and tearing.

3. The sharpness of the enamel edges of selenodont molars were formed after initial contact on erupting and by casual contacts late in the masticatory cycle, rather than by the intentional sharpening strokes of thegosis.

4. In horses, differential abrasion leads to a roughened surface, and flattening the surface by thegosis would drastically reduce the efficiency of the mechanism used to divide grass ('a rolling crush'). The physical properties of enamel, dentine and the diet must be matched and if this alters, as with a domestic diet, the horse is unable to cope with the high enamel ridges which developed due to abnormally rapid abrasion of the dentine. If there were a natural mechanism for levelling these ridges (thegosis) a veterinary surgeon would not have to file the molar teeth.

5. In rodents, abrasion provides the retention needed for a rolling crush and again thegosis would not be useful.

It was also suggested that 'thegotic facets' may be the result of occlusal forces in the middle of the tooth row, and these forces may create premature contacts which become faceted.

The point is made that a considerable waste of tooth substance and effort is needed to sharpen teeth and the result is reduced efficiency. Osborn and Lumsden[22] considered 'that molar thegosis, like bruxism in man, should be considered pathological behaviour'.

Teaford and Walker[23,24] addressed the question of the motion of the tooth sharpening mechanism which Every had postulated as being opposite to that normally used in mastication. The permanent teeth of guinea pigs are erupted and worn *in utero* so that dental microwear in the presence and the absence of food should be distinguishable. The chewing movements of the guinea pig are known and the cheek teeth reflect those movements through differences in the amount of dentine versus enamel wear.[25-31] Teaford and Walker found that adult cheek teeth had a high frequency of striations and enamel chipping while in stillborn animals enamel chipping but not striations were present. This demonstrated that striations were caused by something ingested after birth, and not tooth-tooth contact. Enamel-dentine wear differences on adult guinea pigs and stillborn animals were similar and it was concluded that the teeth of guinea pigs were prepared for postnatal life through prenatal wear. The movements that produce the wear were the same as used in mastication and not the opposite as postulated by Every.

Gordon[32] reviewed the literature relating to the assessment of jaw movement direction from dental

microwear and stated that 'to date no behavioural study of recorded mastication in a living mammal has yet turned up firm evidence of non masticatory thegosis'. Gordon's study of wear on gorilla molars confirmed the work of Covert and Kay,[33] Costa and Greaves,[30] and Teaford and Walker[23] that Ryan's directional model,[34,35] based on analysis of asymmetric microwear scratches, was incorrect. Ryan's model tended to support thegotic movement but it appears that the model was invalid under *in vivo* conditions, and that problems exist with the model itself.

Although this paper is principally concerned with establishing the presence of thegotic wear in molar teeth, activity in anterior teeth is related, and the mechanism of canine honing in the baboon has been extensively examined.[8] Walker concluded that the wear on the baboon canine surfaces 'clearly takes place in the movement of jaw closing'.[36] He supported this opinion by observation of a noticeable Greaves effect and by consideration of scratches in the dentine caused by small pieces of enamel prism.

Discussion

Every,[1] in his psychiatrically oriented dental clinical practice, observed many instances of tooth wear in humans producing planar facets with sharp edges and he termed these attrition facets.[11]

Every[10] recognized that behavioural factors were relevant and that this sharpening activity was frequently associated with stress. He concluded that the behaviour was functional in order to produce sharp edges and decided that the sharpening activity occurred to develop and maintain an inherent weapons system, the teeth, and also to sharpen the masticatory tools for the efficient mastication of food.

Every[14] changed the name of the attrition facets to thegotic facets and coined the term 'thegosis' for the tooth sharpening process. The presence of thegotic facets, therefore, indicated the existence of thegosis. The thegotic facets were considered to be formed during an equal and opposite movement to mastication, to be shiny, circumscribed, flush, to exhibit parallel striations and to match facets in the opposing dental arch.

The evidence for the existence of thegosis was largely drawn from the behaviour of stressed animals, including man, producing thegotic facets and the observation of thegotic sounds associated with non-masticatory tooth to tooth contacts. Thegotic facets were also observed in animals of unknown behavioural status and in animals from other phyla.

Every also used his dental observations to provide evidence for his theory of the development of a segmentive bite in man, and considered that this was an evolutionary advance.

Assumptions by Every[11] and later supporting authors[5,6] concerning the nature and genesis of thegotic facets are challenged. It appears that masticatory tooth to tooth contacts do occur[12] and are capable of producing the discrete facets observed on molar teeth. There is little doubt, based on the evidence provided, that the mandibular movement which produces these facets is the same as that which occurs during mastication, and not an equal and opposite movement as is repeatedly stated in the thegotic literature. Parallel striations are also not an integral part of tooth-tooth thegotic contact but indicate the incorporation of ingested material between the tooth surfaces.[23] The mechanics of thegosis have, therefore, been shown to be invalid and the next question which must be answered is that of the existence of evidence of a tooth sharpening mechanism.

Every,[11] with his observations of baboon canine honing, developed an attractive theory for the sharpening of anterior teeth as social or defensive weapons which has been supported, although the mechanism by which this activity occurs varies from his description. It does appear reasonable to extrapolate this theory to the human species and Archer[6] has accepted this proposition.[11]

However, the thegotic literature exhibits confusion concerning the presence of ancestral 'genetic programming' to sharpen teeth for weapons and food. The early view of a powerful repressed aggressive instinct in humans and an important characteristic of mammals with very few exceptions had been reported by Scally, as 'a universal phenomenon of man'.[3] These views conflict with the chronologically intermediate opinion that thegosis is not found in mammalian taxa, in all members of a population, or in all teeth of a dentition.[13] This confusion is not surprising, and can be explained by the absence of evidence for 'genetic programming' in the literature.

There is no evidence that any animal sharpens its teeth independently of the masticatory process in order to improve the efficiency of that process. Every's earlier papers[9,10] were largely confined to his theory of weapon sharpening, and in 1970 he wrote that humans do not directly sharpen their teeth as tools of mastication or grasping.[11] However, in 1971 he expanded his theory to include the sharpening of the molar teeth for masticatory purposes in herbivores, lagomorphs, horses and rodents, presumably based on the presence of 'thegotic' facets.[13] The paper of Osborne and Lumsden[22] has been reported, and their conclusion that it is doubtful that any molar needs to have sharper edges than those produced by normal masticatory action convincingly challenges Every's tooth sharpening and grasping theory.

Further evidence of the absence of thegotic activity for masticatory purposes is found in the demonstrable differences in the tooth wear patterns of an animal fed different diets.[21] Thegotic molar tooth sharpening would have been expected to maintain a constant functional molar morphology.

It can be accepted that anterior tooth sharpening occurs as a behavioural response to stress and the evidence for thegosis is predominantly from stressed animals or from animals of unknown stress status. The palaeontological evidence is difficult to interpret but may well represent stressed animals as the wear observed may be associated with their time and manner of death.

In a specialized dental practice treating individuals with symptoms of cranio-mandibular dysfunction, such as that of one of the authors of this paper, the majority of patients are significantly stressed. It has been observed that these individuals exhibit an increased level of tooth-tooth attritional activity as is indicated by excessive dental trauma and destruction, and by the other symptoms described by numerous authors, including Klineberg,[5] as applying to bruxism. It is generally considered that bruxism constitutes a pathological condition and the mechanism for treating that condition has been outlined by Klineberg. The authors suggest that the link between an anterior tooth sharpening predisposition in normal humans and bruxism in stressed individuals is clear. Bruxism and pathological thegosis are synonymous and, as has previously been demonstrated, their mechanics are identical. They demonstrate excessive and abnormal tooth-tooth contact.

Every's proposition[11] that the development of a segmentive bite in humans constitutes evolutionary progression needs to be addressed. Human occlusions may exhibit different forms of anterior guidance during mandibular occlusal excursions and variations in the amount of wear needed to achieve a segmentive bite will be required. The authors submit that there is little evidence that a segmentive bite confers a significant advantage, but would agree that it is appropriate in many dentitions and that restorative treatment should reflect the individual dento-facial morphology. Excessive dental wear which results in marked dental destruction and a segmentive bite should be considered the result of pathological thegosis, or bruxism.

Thegosis appears to be an invalid concept when applied to the sharpening of posterior teeth in order to improve masticatory efficiency. Facets produced on these teeth are probably secondary to anterior dental sharpening for behavioural reasons or the result of tooth-tooth contacts occurring in normal mastication.

Research examining the microwear patterns resulting from different diets[37] and from non-masticatory contacts may be useful in further elucidating the aetiology of facets on posterior teeth and the examination of subtle differences in tooth wear[38,39] may permit more accurate inferences of tooth use in fossil mammals.

Conclusion

'Thegotic' and alternative literature has been reviewed and examined with a view to establishing the validity of thegosis as a behavioural and functional concept in man and other animals. It has been concluded that:

1. Thegotic facets are formed during the same mandibular movements that occur during mastication.

2. Parallel striations on thegotic facets are not an integral part of the formation of those facets.

3. There is evidence for the sharpening of anterior teeth as a social weapon and this activity could appropriately be called 'thegosis'.

4. There is no evidence for the genetic programming of a mechanism to sharpen teeth for weapons and the mastication of food.

5. There is no evidence that any animal sharpens its molar teeth independently of the masticatory process in order to improve the efficiency of that process.

It is acknowledged that tooth-tooth forceful contact, unrelated to masticatory contact, is a response to stress. It is proposed that, under conditions of excessive emotional tension, excessive tooth clenching and grinding occurs and this activity is pathological. Bruxism and 'pathological thegosis' are synonymous terms for this activity.

It is considered that a segmentive bite in man may be the result of either thegosis or pathological thegosis depending upon the effect of that activity on a particular occlusion. Dental treatment should seek to maintain the smooth occlusal paths established by the attritional activity.

References

1. Every RG. Significance of tooth sharpness for mammalian, especially primate, evolution. In: Szalay FS, Krager S, eds. Approaches to primate paleobiology. Contributions to primatology. Basel: Karger, 1975;5:293-325.
2. Anderson DMcC. The importance of thegosis. J Craniomandib Prac 1983;2:21-2.
3. Scally KB. Reintroducing an alternative paradigm for myofascial pain-dysfunction syndrome. NZ Med J 1985;98:706-7.
4. Scally KB. Bruxism: a worn out concept. J Prosthet Dent 1991;9:183-5.
5. Klineberg I. Bruxism: aetiology, clinical signs and symptoms. Aust Prosthodont J 1994;8:9-17.
6. Archer M. Our oral arsenal: a natural legacy of primate aggression. Aust Nat Hist 1988;22:474-5.

7. Archer M, Jenkins FA Jr, Hand SJ, *et al.* Description of the skull and non vestigial dentition of a Miocene platypus (*Obdurodon dicksoni* n.sp.) from Riversleigh, Australia, and the problems of monotreme origins. In: Augee ML, ed. Platypus and echidnas. Sydney: Royal Zoological Society of New South Wales, 1992:15-27.
8. Archer M, Murray P, Hand SJ, *et al.* Reconsideration of monotreme relationship based on the skull and dentition of the Miocene *Obdurodon dicksoni*. In: Szalay F, Novacek MJ, McKenna MC, eds. Mammal phylogeny: Mesozoic marsupials. New York: Springer-Verlag, 1993:75-94.
9. Every RG. The significance of extreme mandibular movements. Lancet 1960;2:37-9.
10. Every RG. The significance of extreme mandibular movements. Lancet 1965;1:685-8.
11. Every RG. Sharpness of teeth in man and other primates. Postilla 1970;143:1-30.
12. Anderson DJ. The incidence of tooth contacts in normal mastication and the part they play in guiding the final stage of mandibular closure. In: Anderson DJ, Matthews B, eds. Mastication. Bristol: Wright, 1976:237-41.
13. Every RG, Kuhne WG. Bimodal wear of mammalian teeth. In: Kermak DM, Kermak KA, eds. Early mammals. Zoological Journal of the Linnean Society, Suppl 1, Vol 50. London: Academic Press, 1971:23-7.
14. Every RG. A new terminology for mammalian teeth. Parts 1 and 2. Christchurch: Pegasus Press, 1972:1-65.
15. Scally KB. Thegosis in the sea urchin *Evechinus chloroticus* (Val.) (Echinodermata: Echinoidea). J Dent Res 1973;52:583.
16. Tunicliffe GA. Preliminary observation of the phylogenesis of thegosis. J Dent Res 1973;52:583.
17. Tunicliffe GA, Every RG, Scally KB. Audiospectrographic analysis and behavioural significance of thegotic sounds. J Dent Res 1974;53:709.
18. Scally KB, Every RG, Tunicliffe GA. Thegosis in the red spiny lobster *Jasus edwardii* (Crustacea: Decapoda: Palinuridea). J Dent Res 1974;53:709.
19. Gould SJ, Lewontin RC. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proc Roy Soc London 1979;B205:581-98.
20. Mills JRE. A comparison of lateral jaw movements in some mammals from wear facets on the teeth. Arch Oral Biol 1967;12:645-61.
21. Berkovitz BKB, Poole DFG. Attrition of the teeth in ferrets. J Zool Lond 1977;183:411-8.
22. Osborn JW, Lumsden AGS. An alternative to thegosis and a reexamination of the ways in which mammalian molars work. N Jb Geol Palaont Abh 1978;156:371-92.
23. Teaford MF, Walker A. Prenatal jaw movements in the guinea pig. *Cavia porcellus:* evidence for patterns of tooth wear. J Mamm 1983;64:534-5.
24. Teaford MF, Walker A. Dental microwear in adult and still-born guinea pigs (*Cavia porcellus*). Arch Oral Biol 1983;28:1077-81.
25. Ainamo J. Prenatal occlusal wear in guinea pig molars. Scand J Dent Res 1971;79:69-71.
26. Berkovitz BKB. Ontogeny of tooth replacement in the guinea pig (*Cavia cobya*). Arch Oral Biol 1972;17:711-8.
27. Byrd KE. Mandibular movement and muscle activity during mastication in the guinea pig. J Morph 1981;170:147-69.
28. Greaves WS. The inference of jaw motion from tooth wear facets. J Paleont 1973;47:1000-1.
29. Rensberger JM. An occlusion model for mastication and dental wear in herbivorous mammals. J Paleont 1973;47:515-28.
30. Costa RL, Greaves WS. Experimentally produced tooth wear facets and the direction of jaw motion. J Paleont 1981;55:635-8.
31. Young WG, Robson SK. Jaw movements from microwear on the molar teeth of the koala *Phascolarctus cinereus*. J Zool 1987;213:51-61.
32. Gordon KD. The assessment of jaw movement direction from dental microwear. Am J Phys Anthropol 1984;63:77-84.
33. Covert HH, Kay RF. Dental microwear and diet: implications for determining the feeding behaviours of extinct primates, with a comment on the diet of *Sivapithecus*. Am J Phys Anthropol 1981;55:331-6.
34. Ryan AS. A preliminary scanning electron microscope examination of wear striation direction on primate teeth. J Dent Res 1979;58:525-30.
35. Ryan AS. Wear striation direction on primate teeth: a scanning electron microscope examination. Am J Phys Anthropol 1979;50:155-68.
36. Walker A. Mechanisms for honing in the male baboon canine. Am J Phys Anthropol 1984;65:47-60.
37. Teaford MF, Tylenda CA. A new approach to the study of tooth wear. J Dent Res 1991;70:204-7.
38. Maas MC. A scanning electron microscopic study of *in vitro* abrasion of mammalian tooth enamel under compressive loads. Arch Oral Biol 1993;39:1-11.
39. Salounias N, Hayek LC. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. J Zool Lond 1994;229:421-45.

Address for correspondence/reprints:
Dr C. G. Murray,
Suite 1,
4th floor,
20 Collins Street,
Melbourne, Victoria 3000.