

# Reassessment of the late Triassic symmetrodont mammal *Woutersia*

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Sigogneau-Russell, D. & Hahn, R. 1995. Reassessment of the late Triassic symmetrodont mammal *Woutersia*. *Acta Palaeontologica Polonica* **40**, 3, 245–260.

Since the creation of the taxon *Woutersia mirabilis* Sigogneau-Russell 1983, on a lower molar and two upper molars from the French locality of Saint-Nicolas-de-Port (late Triassic), quite a number of additional mammalian teeth have come to light; among them, are not only some elements undoubtedly belonging to this species, but also 5 teeth interpreted here as representing a second species of *Woutersia*, *W. butleri* sp. n. The peculiarities of this second species, especially in the upper molars, allow in turn the presentation and discussion of another upper molar from the same locality, which had remained an enigma for a long time. Though too large to be attributed to *W. butleri*, this tooth exhibits at a higher degree some characters already detected in the latter species, suggesting that it could still belong to *Woutersia*; but in that case, its sharing of some derived characters with upper molars of docodonts implies at least a certain parallelism between the new family Woutersiidae and primitive Docodonta.

**Key - words :** late Triassic, molars, therians, docodonts.

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## Introduction

Synapsid collections presently known from Saint-Nicolas-de-Port (late Triassic, France) contain more than a thousand teeth (both complete and partial), of which only a part has been studied (last reference: Sigogneau-Russell & Hahn 1994). Most of these teeth represent Haramiyidae (allotherians). The remaining part is distributed among cynodonts, eotherians and therians. This paper is dedicated to some interesting elements belonging

to the latter. Among them is a 'large' tooth, the interpretation of which poses intriguing anatomical and phylogenetic problems.

Abbreviations: M.N.H.N., Muséum national d'Histoire naturelle de Paris; SNP, collection of Saint-Nicolas-de-Port preserved in the M.N.H.N.; RAS, collection of Saint-Nicolas-de-Port preserved in the Musée Royal d'Histoire Naturelle in Bruxelles.

## Taxonomy

Order Symmetrodonta Simpson 1925

Woutersiidae fam. n.

**Diagnosis.** — An early family of Theria whose lower molars, and even more the upper molars, tend to widen labiolingually and increase or develop a cusp on the lingual cingulum, thus extending their role towards a crushing function.

Genus *Woutersia* Sigogneau-Russell 1983

**Emended diagnosis.** — Lower molars compact, with a large lingual median cusp *g*; cusp *e* nearly as large as cusps *b* and *c*; cusp *a* relatively lower than in *Kuehneotherium praecursoris* Kermack *et al.* 1968, and divided longitudinally by two vertical sulci; anterior and posterior labial cingulum present; talonid shorter than in *Kuehneotherium*, with cusp *d* little developed.

Type species: *W. mirabilis* Sigogneau-Russell 1983.

### *Woutersia mirabilis* Sigogneau-Russell 1983

Holotype: SNP 101, left lower molar (Fig. 10a). Attributed material: SNP 52W, right upper molar (Figs 1A, 9A); SNP 74 W, partial right upper molar.

**New attributed material.** — Lower teeth: RAS 975 (Fig. 1B and C), RAS 706 (Fig. 1D and E), both right. Upper teeth: RAS 884, right (Fig. 3A and B); SNP 426, left (Fig. 3C); ?SNP 719, right (Figs 7, 8 and 9D).

**Remarks.** — RAS 706 differs from the type by the total absence of the *d* cusp (a unique case among the known Triassic material); cusp *e* is smaller and cusp *a* is less thick labiolingually; finally, the posterior labial cingulum is weaker. On RAS 975, *d* exists but is more reduced than on the type; on the contrary, the posterior labial cingulum is stronger. Abrasion surfaces have the same orientation in all cases. On RAS 975 there is a clear wear facet along the anterior face of *a*; that on the posterior face is less clear. On RAS 706 (cast) only the weak posterior labial cingulum seems to have been slightly worn.

Among the upper teeth, RAS 884 is less worn than SNP 52W, previously attributed to this species, but resembles it in all characters; the only noticeable difference is that the anterior part of the crown is slightly more transverse and the lingual cingular cusp appears more detached (probably due to less wear). RAS 426 is smaller than both, has no anterior indentation and no cingulum above *B*: it could be a premolar; it is more worn than

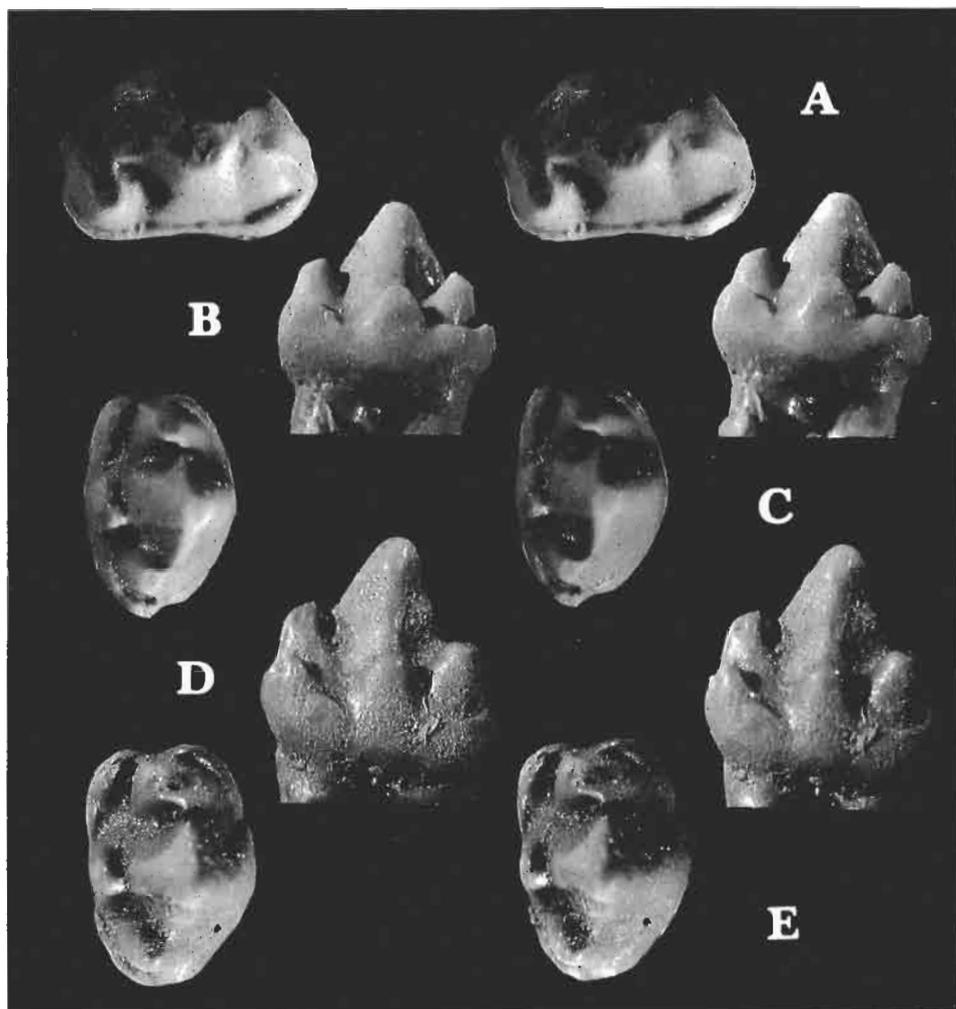


Fig. 1. *Woutersia mirabilis* Sigogneau-Russell 1983, the quarry of Saint-Nicolas-de-Port, France, ?early Rhaetian. □A. Right upper molar SNP 52W in occlusal view (anterior left). □B-C. Lower right molar RAS 975 in lingual (B) and occlusal (C, anterior top) views. □D-E. Lower right molar RAS 706 in lingual (D) and occlusal (E, anterior top) views. Stereophotos D. Serrette, URA 12 CNRS. All  $\times 20$ .

the other two upper teeth. We will discuss SNP 719 in more detail below. A point that was not sufficiently stressed in 1983 concerns the anterior division of cusp A, a constant character of all the upper molars mentioned; it looks nearly as if there were an anterior labial cusp in line with C but less well individualized (a reduced cusp B? in which case the anterior labial cusp would not be equivalent to B); we will discuss this point below.

### *Woutersia butleri* sp. n.

Holotype: SNP 517, right lower molar (Figs 2, 3D and E).

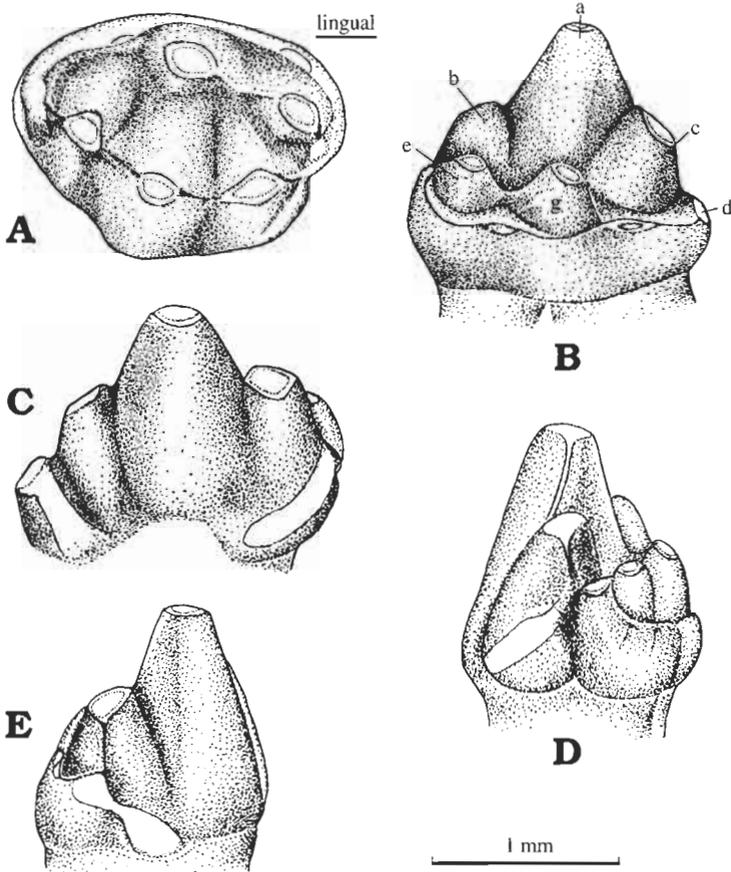


Fig. 2. *Woutersia butleri* sp. n., the quarry of Saint-Nicolas-de-Port, France. ?early Rhaetian, holotype, lower right molar SNP 517 in occlusal (A), lingual (B), labial (C), anterior (D), and posterior (E) views. The white surfaces correspond to abrasion or wear; letters denote cusps.

Type horizon and locality: The quarry of Saint-Nicolas-de-Port, commune of Rosières-aux-Salines, département of Meurthe-et-Moselle, France; late Triassic (early Rhaetian?).

Etymology: *Butleri*, in honor of Dr. P.M. Butler, whose advice and competence have been of particular value during the lengthy incubation of this paper.

**Attributed material.** — Lower teeth: SNP 119, left molar (Fig. 4). Upper teeth: SNP 88 (Figs 5C, D, 9B); SNP 82 (Fig. 5E); SNP 720 (Figs 5A, B, 6 and 9C); all from the right side.

**Diagnosis.** — Teeth of small size (length of type — 1.17 mm; width of type — 0.84 mm, i.e. 2/3 of *Woutersia mirabilis*); *c* less lingual relative to *a*; *b* and *c* bigger with respect to *a*.

**Description.** — The type tooth is moderately worn and lacks the roots. The description given for the type specimen of *Woutersia mirabilis* SNP 101 generally applies here, except for the specific diagnostic characters, and for the lingual cingulum, which completely encircles *g* and *e*.

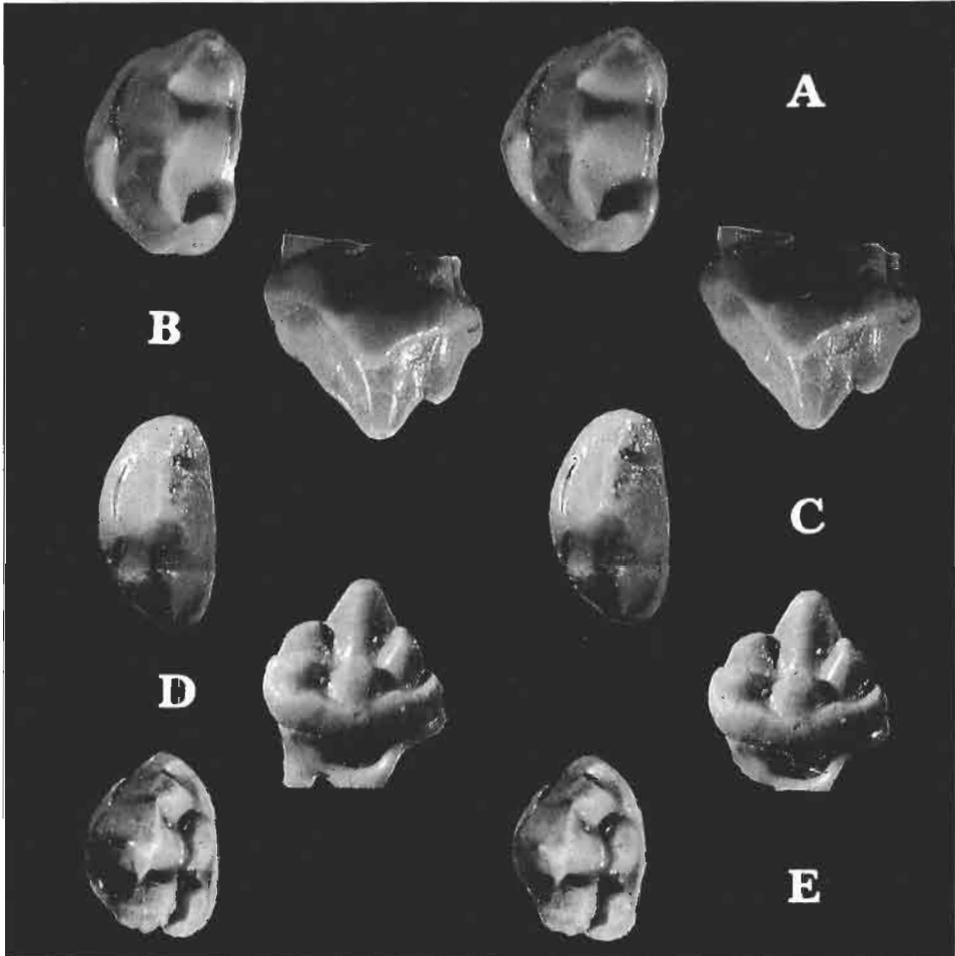


Fig. 3. □A-C. *Woutersia mirabilis* Sigogneau-Russell 1983, the quarry of Saint-Nicolas-de-Port, France, ?early Rhaetian. A-B. Upper right molar RAS 884 in occlusal (A, anterior bottom) and lingual (B) views. C. Upper left ?premolar SNP 426 in occlusal view (anterior top). □D-E. *Woutersia butleri* sp. n., the quarry of Saint-Nicolas-de-Port, France, ?early Rhaetian. Holotype lower right molar SNP 517 in lingual (D) and occlusal (E, anterior bottom) views. All  $\times 20$ .

The cusps are similarly abraded in both teeth, but here, that affecting *d* extends down to the labial cingulum, which is worn; similarly, the anterior labial cingulum is also abraded, while these two cingula remained intact on SNP 101, which is slightly more fresh. Besides that, there are no clear wear surfaces on SNP 517 (perhaps there is a narrow strip of wear on the labial face of *c*).

The second lower molar attributed to this species (SNP 119) is unfortunately incomplete, *a* and *b* having been broken; but the roots are partly preserved. It differs from the type tooth by the absence of the cingulum around *g* and *e* (the situation is thus more like that of SNP 101, or RAS

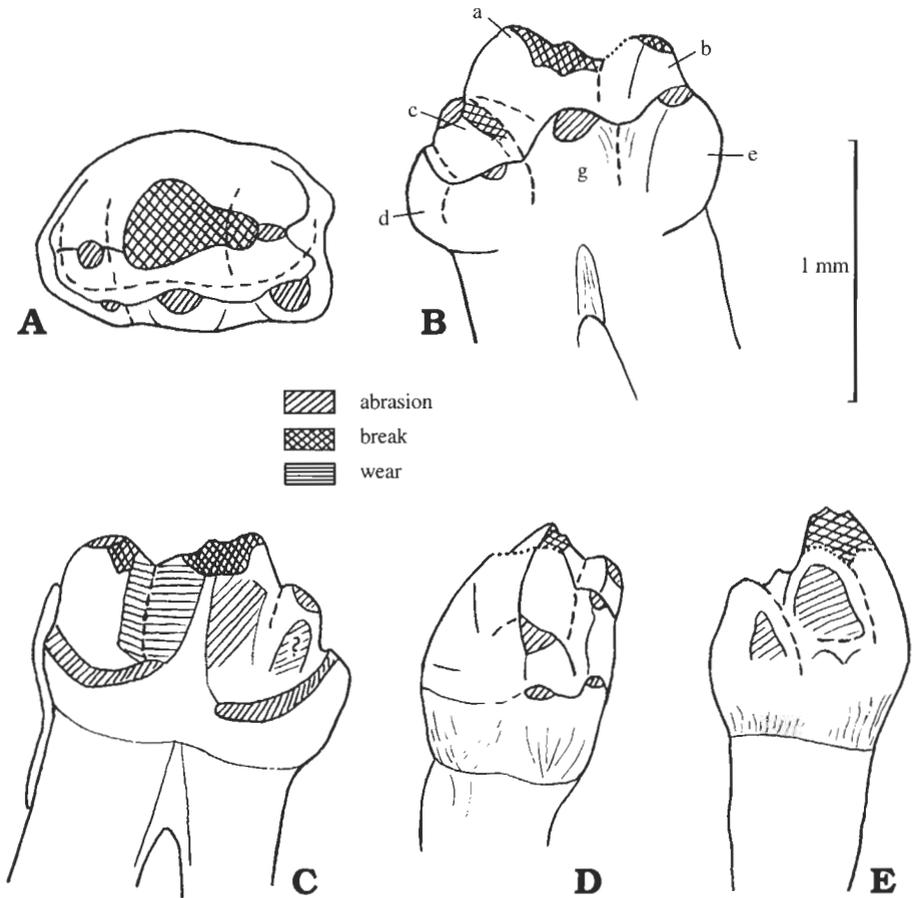


Fig. 4. *Woutersia butleri* sp. n., the quarry of Saint-Nicolas-de-Port, France, ?early Rhaetian, lower left molar SNP 119, in occlusal (A), lingual (B), labial (C), anterior (D) and posterior (E) views.

975 and 706); also these two cusps are less convex lingually, and the labial cingula are less protruding. But the same type of abrasion of these cingula as on SNP 517 is to be observed. The wear surfaces sketched on the drawings are not always clearly delimited. By its morphology, this tooth thus resembles more the type of *Woutersia mirabilis*, but the size is that of SNP 517 and we consider the peculiarities of the lingual cingulum as an intraspecific variation for *W. butleri*.

The morphology of the referred upper teeth leads to interesting remarks. SNP 82 could be a premolar: there is no anterior indentation, as on SNP 426, and the labial cingulum does not extend above B; however, the angulation between the three main cusps is slightly stronger and C appears to have been somewhat more detached. Wear has touched the anterior face of A and the anterolingual cingulum, a crest linking the latter and B as in SNP 52W.

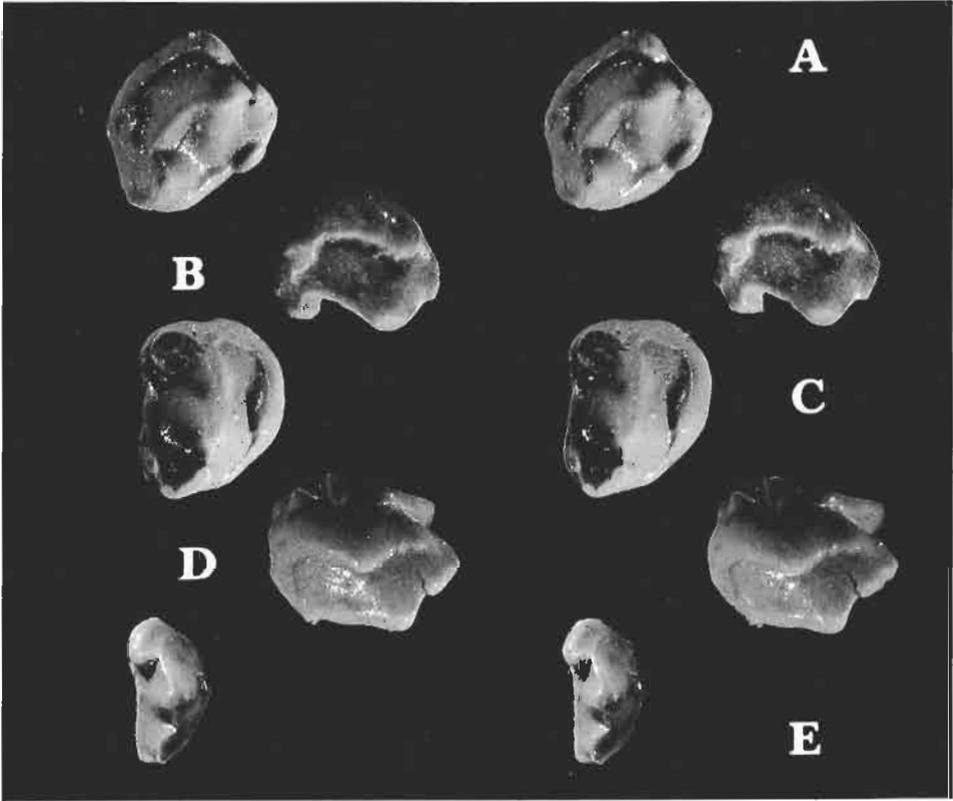


Fig 5. *Woutersia butleri* sp. n., the quarry of Saint-Nicolas-de-Port, France. ?early Rhaetian. A–B. Right upper molar SNP 720 in occlusal (A, anterior left) and lingual (B) views. C–D. Right upper molar SNP 88 in occlusal (C, anterior top) and lingual (D) views. E. Upper right ?premolar SNP 82 in occlusal view (anterior top). All  $\times 20$ .

SNP 88 is very similar to SNP 884 (hence slightly more angular than SNP 52W) in morphology and wear; the latter has mildly affected the anterior part of the lingual cingulum, an abraded crest linking the latter to *B*.

Finally, on SNP 720, this tendency toward a stronger angulation and dissymetry between the anterior and posterior parts is exaggerated, the latter part being shorter and the anterior indentation longer; the tooth is thus almost concave labially and, of course, relatively wider than the other upper molars: this transition from SNP 52W to SNP 720 is well visible on Fig. 9. The labial cingulum fades above *B* but the lingual cingulum is stronger than on the upper molars attributed to *Woutersia mirabilis* and, most important, the lingual cingular cusp *Z* is even more detached than on SNP 88. No wear is discernible except a round facet anteriorly on the lingual cingulum as in SNP 88.

This tooth thus differs from SNP 88 (as well as from RAS 884 and SNP 52) by its more rounded contour in occlusal view; but it also clearly

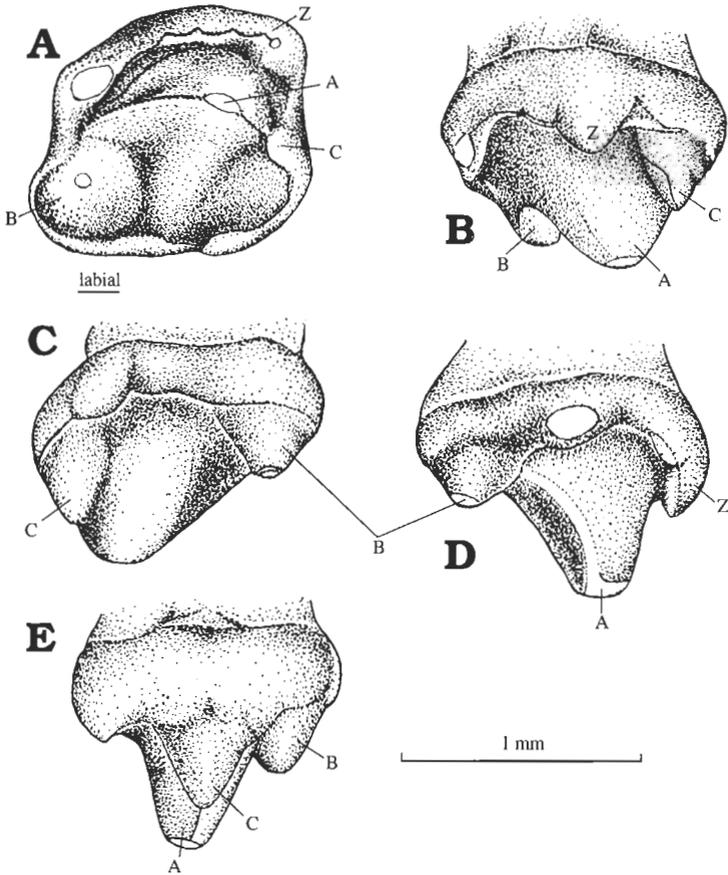


Fig. 6. *Woutersia butleri* sp. n., the quarry of Saint-Nicolas-de-Port, France, ?early Rhaetian, upper right molar SNP 720 in occlusal (A), lingual (B), labial (C), anterior (D) and posterior (E) views. The white areas correspond to abrasion or wear.

possessed a protrusion of the anterior root (unfortunately broken very low) on the lingual face, while on the last two teeth, the two roots are subequal and obliquely oriented relative to the long axis of the crown.

It seems reasonable to interpret SNP 720 as a posterior molar of *W. butleri*, which would testify to a tendency, in the concerned taxon, to develop wider molars than in other contemporaneous therians.

## Discussion of SNP 719

The preceding remarks allow the consideration of SNP 719, a unique tooth that was at the origin of this paper and whose interpretation was long a mystery. It consists of a 'large' crown (lg — 1,78 mm; w — 1,62 mm), supported by two anteroposteriorly-flattened roots, but the anterior root

is lingually divided by a vertical sulcus anticipating the individualisation of a lingual element, and it seems that the situation was the same on the posterior root, unfortunately broken very short.

In occlusal view, the crown presents a grossly heart-shaped and slightly dissymmetrical aspect. Medially, there exist two unequal cusps (*A* and *C*), twinned (i. e., pressed one against the other) through almost the whole height of *C* and situated in the posterior half of the tooth; they are lingually as well as labially separated by a sulcus. Cusp *A* shows an anterior extension as in the upper molars of *Woutersia*. Anteriorly, a crest extends between the main cusp *A* and a wide cingulum, which terminates antero-labially in a low cusp, labially displaced with respect to *A*: this can be interpreted as the remains of, or equivalent to, cusp *B*. From *B*, the cingulum continues anteriorly then lingually, forming vague festoons, then rises lingually in a stout cusp (*Z*) situated immediately behind the level of *A*, hence behind the median axis of the tooth; a ridge links the two cusps *A* and *Z*. Posteriorly the cingulum decreases before disappearing at the level of *C* (as on SNP 720), but it reappears a little farther along to totally disappear labially at mid-length of the tooth.

The tips of the cusps are only slightly abraded. But wear has strongly affected the anterior and posterior main crests (cusps *C* and *A*); in this last case, the shelf thus formed reaches the labial cusp *B*. Finally the cingula are slightly rounded and depressed by a distinct oval facet situated immediately lingual to *B* (but not linked to it by a crest), and by another one, smaller, at the anterior base of the lingual cusp. Moreover, the dorsal face of this cusp *Z* shows a marked depression, which seems to be the result of a small enamel fracture that was worn smooth while the animal was still alive.

Study of the teeth described above leads to a first interpretation: SNP 720, attributed to *W. butleri*, appears to be intermediate, in morphology and mode of wear, between RAS 884 or SNP 52W, attributed to *W. mirabilis*, and SNP 719; in the latter, the lingual cusp *Z* is even more detached, *B* more reduced and the labial cingulum interrupted. SNP 719 could then be a posterior molar of *Woutersia mirabilis*, a species in which the tendency noted in *W. butleri* to develop wider molars posteriorly would have been carried farther (which appears clearly in Fig. 9).

However, no molar is known of *Woutersia mirabilis* with the morphology (and size) intermediate between SNP 52W or RAS 884, and SNP 719; this raises a doubt concerning the attribution of the latter tooth to that species (could it represent a third species of *Woutersia*?) or even to that genus. Also, posterior molars of *Kuehneotherium* tend to be shorter than the middle ones. This would be true for *Woutersia butleri* SNP 720 also; but it would have to be the opposite for *W. mirabilis* if SNP 719 belongs to this taxon.

The only other tooth to which SNP 719 would appear comparable is the last upper premolar of a docodont (Fig. 10C, D); the latter possesses two main appressed labial cusps, a lingual cingulum with a detached cusp (*X*

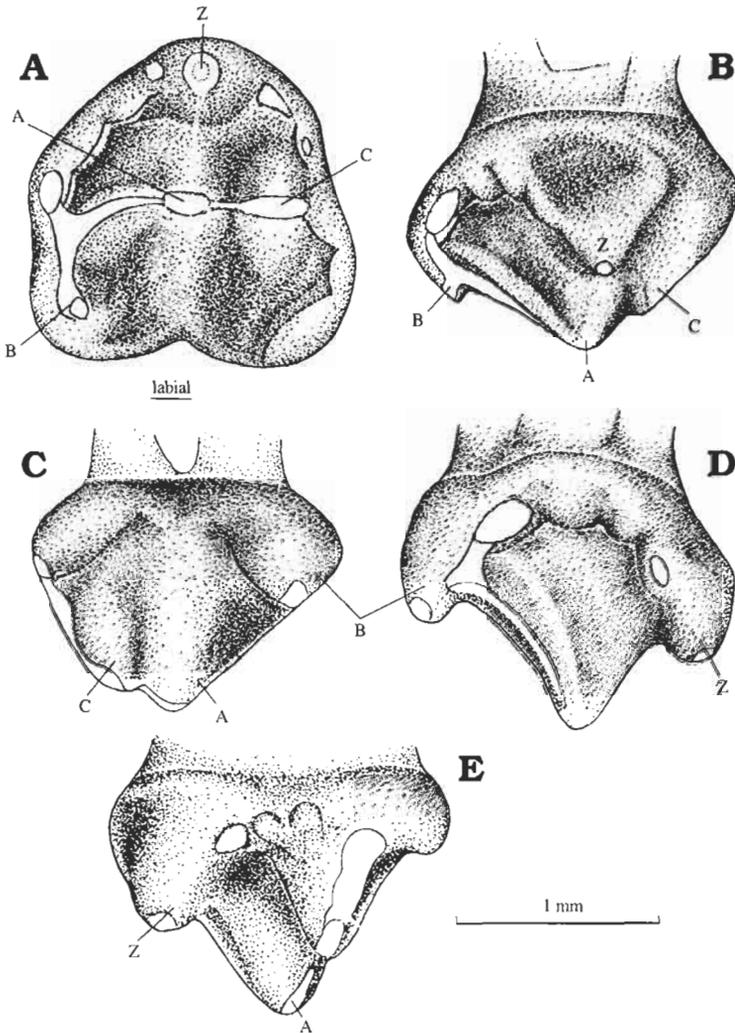


Fig. 7. ?*Woutersia mirabilis* Sigogneau-Russell 1983, upper right molar SNP 719 in occlusal (A), lingual view (B), labial (C), anterior (D) and posterior (E) views. The white areas correspond to abrasion or wear.

in Krusat 1980), a crest linking A and X, and an anterolabial cusplule B (E in Krusat 1980). The main differences concern the contour, which is more regular here while it is anterolingually concave in *Haldanodon* (Krusat 1980) or *Docodon* (Simpson 1929); also in the latter the cusps are disposed in a more dissymetrical triangle. In addition, the lingual cingulum here is thicker and more rounded, and B is displaced labially relative to A. With a docodont molar the contrast is even stronger, first in the contour, due to the doubling of cusp X, which itself contributes to the development of an anterior or posterior basin: all that can be seen on SNP 719 is a suggestion of an anterior basin; in fact, among docodont molars, those of *Simpsono-*

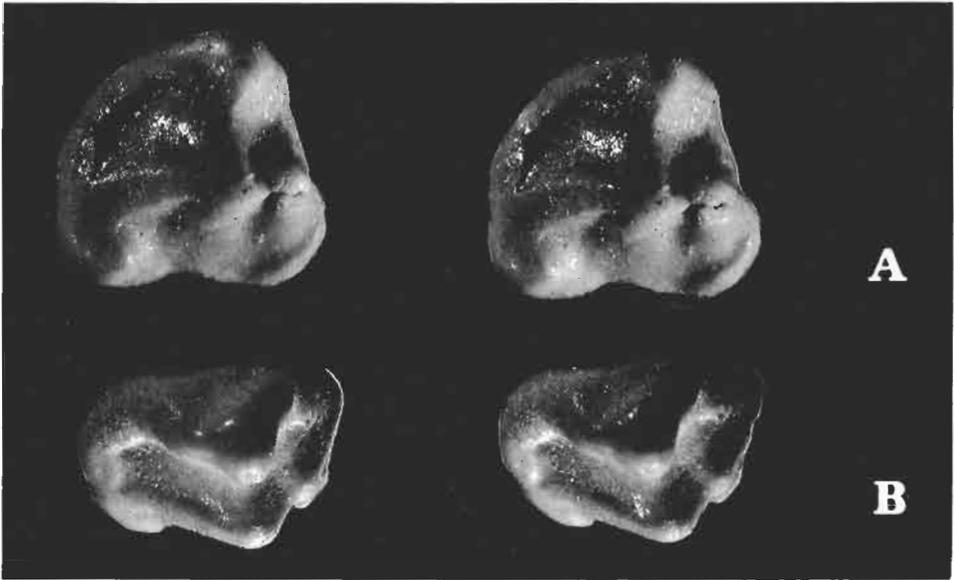


Fig. 8. ?*Woutersia mirabilis* Sigogneau-Russell 1983. Right upper molar SNP 719 in occlusal (A, anterior left) and lingual (B) views:  $\times 20$ .

*don*, where 'the characteristic pinched waist seen in *Docodon* or *Haldanodon* is lacking' (Kermack *et al.* 1987) are the closest, in shape, to SNP 719. Moreover, the labial cingulum is, on our tooth, interrupted at the level of C, which is not the case on the docodont molars, but is clearly seen only on the penultimate premolar of *Docodon*. But cusp B (E), still developed on SNP 719, is, in docodonts, very reduced (a little less in *Haldanodon* than in the other genera) to a small outgrowth of the cingulum. Also there does not seem to be a mediolabial indentation on the premolars and molars of docodonts, as on SNP 719. Finally, these docodont teeth are supported by three roots (though, in *Haldanodon* at least, P<sup>3</sup> may have only two roots, the posterior one being incompletely divided).

As concerns wear, one does not see, on SNP 719, the set of facets observed in *Haldanodon* (Krusat 1980) or *Docodon* (Jenkins 1969; Gingerich 1980), nor are there, on the enamel, ridges and striae forming secondary cutting edges; only a crenulation of the enamel on the anterolabial part of the tooth can be observed. Conversely, the crests of A and C, abraded on SNP 719, are not affected by wear in *Docodon*, and in *Haldanodon* the wear only appears anteriorly.

One could interpret these differences (in morphology and wear) as indicating that we have, with this tooth, the beginning of the docodont line (docodonts are not, so far, known before the middle Jurassic), where the functional specialisation reached by later forms is not yet realized. As Kermack *et al.* (1987) put it: 'any common ancestor of *Docodon* and *Simpsonodon* must have lived prior to the middle Jurassic, possibly considerably earlier'. On the other hand, the close resemblance of SNP 719

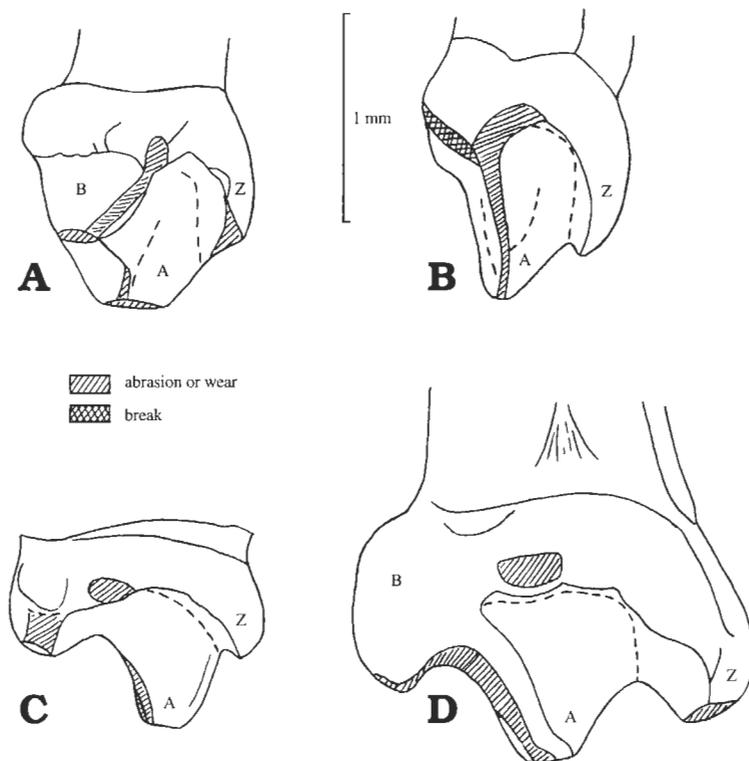


Fig. 9. Upper right molars of *Woutersia* in anterior view. □A. *W. mirabilis* Sigogneau-Russell 1983, holotype SNP 52W. □B-C. *W. butleri* sp. n., SNP 88 and SNP 720. □D. ?*W. mirabilis* SNP 719.

to SNP 720, and also to the other upper molars mentioned above, seems to indicate that we have a continuous morphological series.

## Conclusion

To conclude, three hypotheses can be proposed:

(1) Are all these upper molars studied in this paper not therian but docodont? In this case we would have a docodont represented only by upper molars and the therian *Woutersia* by lower molars, which is not very likely.

(2) If 719 is an upper molar of *Woutersia*, could this genus itself be an early docodont rather than a therian? This would entail, as a consequence, the relation of the former order to the Theria rather to the Eotheria as usually believed. This interpretation, supported by P.M. Butler (personal communication 1993) is, in our opinion, not easily tenable: it would imply that cusp *g* (Krusat 1980) of the lower molars of docodonts is homologous to cusp *c* of symmetrodonts (= posterior accessory cusp of Butler 1939),

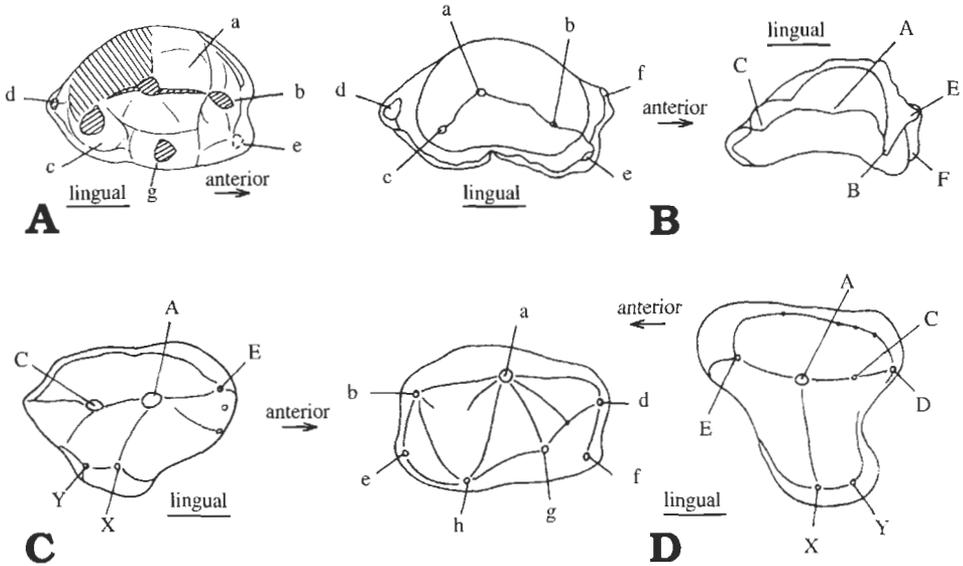


Fig. 10. □A. *Woutersia mirabilis* Sigogneau-Russell 1983, holotype, left lower molar SNP 101 in occlusal view; × 25, from Sigogneau-Russell 1983. □B. *Kuehneotherium praecursoris* Kermack *et al.*, lower (left) and upper (right) molar in occlusal views; × 40 (from Kermack *et al.* 1968, modified). □C. *Haldanodon expectatus* Krusat 1980, right P<sup>3</sup> in occlusal view; × 53 (from Krusat 1980, modified). □D. Schematic representation of lower (left) and upper (right) molars of *Haldanodon expectatus* in occlusal view (from Krusat 1980).

which itself is not cingular in origin, but generally considered as a main cusp homologous to the metaconid of later therians. Study of the lower dentition of the docodonts (milk teeth, premolars) is not in favour of such an interpretation, already refuted by Patterson (1956). In fact, little in the lower teeth of *Woutersia* supports a docodont relationship: only the incipient subdivision of cusp *a* posteriorly is a shared derived character between the two. But the labial convexity of this same cusp *a* in our genus is reminiscent of that of therians and is different from that in eotherians and docodonts; also, cusp *c*, at least, is encircled by the lingual cingulum (Krusat's *g* is on the cingulum in docodonts: Fig. 10D); cusp *b* is shifted lingually and well developed (while aligned with *a* and not so well individualized even in *Haldanodon*), the kuehnecone is situated in the middle of cusp *a* and not posteriorly, cusp *d* is situated medially and not labially; all these characters oppose therians (and *Woutersia*) on the one hand and eotherians as well as docodonts on the other. In fact, in our opinion, every known dental trait links the last two groups. And if some early therians like *Woutersia* developed — as a convergence with docodonts — prematurely wide upper molars, this does not correspond to a correlative development of a triturating zone on the lower molar as in docodonts (the talonid is even less developed in *Woutersia* than in *Kuehneotherium*: Fig. 10B); the lingual cingular cusp *Z* would fit between two lower molars as

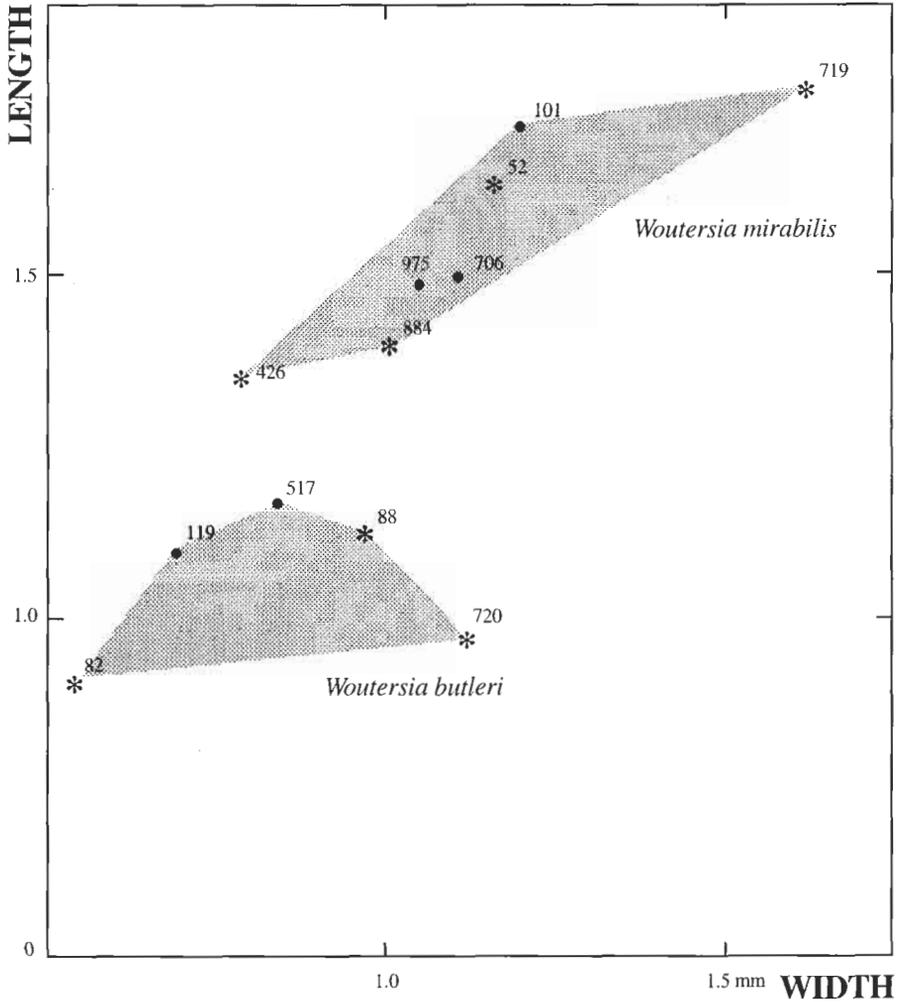


Fig. 11. Distribution of the teeth studied in this paper according to their measurements. Dots for lower teeth; asterisks for upper teeth.

the homologous zone in the latter genus. All that can be inferred is that these teeth of *Woutersia* tended to have a crushing as well as a cutting action, conversely to most symmetrodonts, but were not submitted to transverse masticatory movements.

(3) Finally, the upper tooth SNP 719 may not belong to *Woutersia* but represent alone an early docodont? This is a tempting interpretation, but its similarities to SNP 720, a tooth attributed to *W. butleri*, do not seem to support it.

In consequence, we tentatively refer SNP 719 to *Woutersia mirabilis*, and we consider the genus as a member of the Theria belonging to a new family of symmetrodonts, the Woutersiidae, paralleling the later docodonts

in the upper teeth morphology (twinning of A and C, development of a lingual expansion and cusp), and specialized in the tendency to promote a crushing molar action.

## Acknowledgments

The authors are grateful to Dr. Bultynck and Dr. P. Godefroit for having allowed and facilitated access to the collection in their care as well as for the loan of specimens. Stereophotos D. Serrette, URA 12 CNRS.

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## Resumé

Depuis la création du taxon *Woutersia mirabilis* Sigogneau-Russell 1983 (Mammalia, Theria), sur une molaire inférieure et deux molaires supérieures en provenance du gisement français de Saint-Nicolas-de-Port (Trias supérieur), un grand nombre de dents mammaliennes supplémentaires ont été mises au jour. Parmi celles-ci se trouvent non seulement quelques éléments appartenant indubitablement à cette espèce, mais aussi 5 dents interprétées ici comme représentant une seconde espèce de *Woutersia*, *W. butleri* sp. n. Les particularités de cette seconde espèce, spécialement au niveau des molaires supérieures, ont à leur tour permis d'interpréter une autre molaire supérieure du même gisement restée longtemps une énigme. Cette dent, dont la morphologie exagère certains

caractères décelés chez *W. butleri*, tout en étant beaucoup trop grande pour cette espèce, pourrait cependant appartenir au même genre; mais, si cette attribution est exacte, le partage de certains caractères dérivés avec les dents supérieures de Docodontes implique au moins un certain parallélisme entre la nouvelle famille Woutersiidae et les Docodontes primitifs.

## Streszczenie

Nowe znaleziska izolowanych zębów retyckich Synapsida ze stanowiska Saint-Nicolas-de-Port we Francji, obok licznych Haramiyidae i cynodontów, dostarczyły nowych okazów symetrodontów. Pozwalają one na uzupełnienie diagnozy typowego gatunku rodzaju *Woutersia*, *W. mirabilis* i wydzielenie nowego gatunku *W. butleri* oraz rodziny Woutersiidae wykazującej paralelizmy w morfologii górnych zębów do późniejszych symetrodontów a także specjalizacje do funkcji miażdżenia w pokroju trzonowców.