



DENTAL ANOMALY IN *BRACHYODUS* FROM LA FUYE, EARLY MIOCENE, FRANCE

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Abstract: Dental remains of the large anthracothere, *Brachyodus*, from the French Faluns (Touraine, Anjou) and the Sables de l'Orléanais, show a broad range of morphological variation, in particular in the degree of enamel wrinkling, the strength of enamel beading on crests and cingula, the form and volume of styles in the upper molars, and occasionally the addition of accessory cusps or cusplets, notably in the P4/. A third lower molar from La Fuye is highly unusual however, in possessing a greatly enlarged entoconid and posthypocristid which radically alter the appearance of the tooth. The specimen is described and compared with other third molars of *Brachyodus*. It possibly represents a case of teratogeny related to localised injury to, or alteration of, the odontoblast and ameloblast complexes. It is less likely to reflect inbreeding which is hypothesised to result in some cases of anomalous dental formation. Aspects of occlusion and life history of the individual from La Fuye are explored.

Key words: dental anomaly, teratogeny, molar, anthracothere, Artiodactyla, Early Miocene, France

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Introduction

Dentognathic remains of the bothriodont anthracothere *Brachyodus* are common in western France in deposits correlated to MN 3 and MN 4 (Early Miocene) (Ginsburg and Chevrier 2005, Gagnaison et al. 2023). The author has measured and photographed over 1,300 teeth (many of which are associated in jaws). Overall, the dental remains are well preserved with only one specimen showing obvious signs of anomalous development of the crown. It is a lower third molar from La Fuye that possesses an aberrant second lophid that markedly alters the outline of the tooth. Another specimen (Musée du Savignéen 98-2, 37), a left M3/, also from La Fuye, has a normally developed crown, but the wear pattern is anomalous, in that the protocone and the mesial part of the lingual cingulum are far more deeply worn than the other cusps.

The other anthracothere teeth from the Faluns are variable in the degree of enamel wrinkling, which ranges from fine to coarse, in the development of small tubercles of enamel on crests and cingula and in the form and volume of the styles in the upper molars, but overall, the assemblage is remarkably homogeneous.

The aim of this paper is to describe the aberrant anthracothere tooth from La Fuye, to compare it with

normally developed teeth and to try to throw light on why it was developed the way that it did (genetic or accidental?)

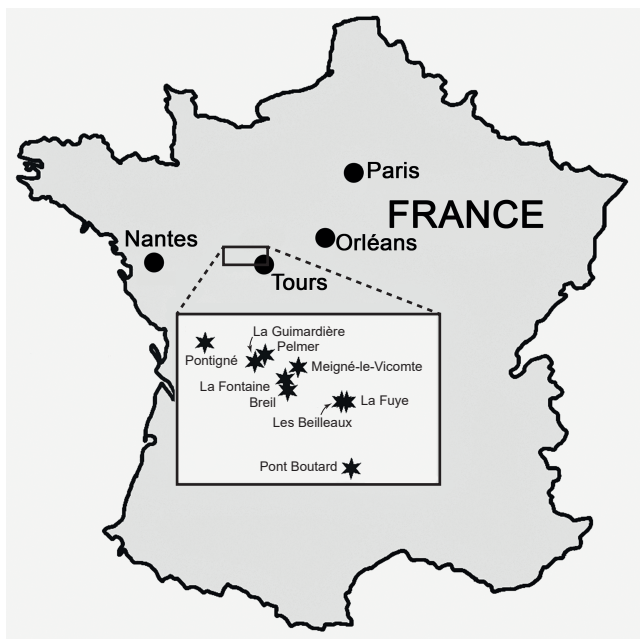
Material and methods

Fossils described in this paper are listed in Table 1 (Text-fig. 1). Measurements of the teeth were taken with sliding calipers to the nearest tenth of a mm. Images were captured with a Sony Cybershot Camera and then treated with Photoshop Elements15 to remove unwanted background, to reduce trembling and to modify the contrast.

Access to the various collections was organised by the Musée du Savignéen, Savigné-sur-Lathan (J.-C. Gagnaison).

Tooth designation

Abbreviations of teeth are as follows: I, i – incisors, d – deciduous cheek tooth, M, m – molars, P, p – premolars. Upper case letters are upper teeth, lower case letters are lower teeth. To avoid misprints of upper and lower case letters, that are difficult to detect, the meristic position of each tooth is given in relation to a forward slash (/) which represents the occlusal plane. Thus M3/ signifies an upper third molar, the number being above the forward slash, and m/3 signifies a lower third molar, the number being beneath the forward slash. lt – left, rt – right.



Text-fig. 1. Map of France showing the location of fossiliferous localities mentioned in this paper.

Systematic palaeontology

Family Anthracotheriidae LEIDY, 1869

Genus *Brachyodus* DEPÉRET, 1895

Type species. *Brachyodus onoideus* (GERVAIS, 1859).

Genus diagnosis. (amended from Pickford 1991) Large anthracotheres with pentacuspidate upper molars, central upper incisors tusk-like, pointing forwards and downwards, lower second incisors spatulate; I1/ and i/2 sexually dimorphic; i/3 to lower canine diastema short; upper canine to P1/ and lower canine to p/1 diastemata very long.

Brachyodus onoideus (GERVAIS, 1859)

Text-figs 2–13, 19

Holotype. Musée d'Orléans 05 (2016-0-3-75, 314), right mandible fragment with p/4–m/3. (Cast in MNHN).

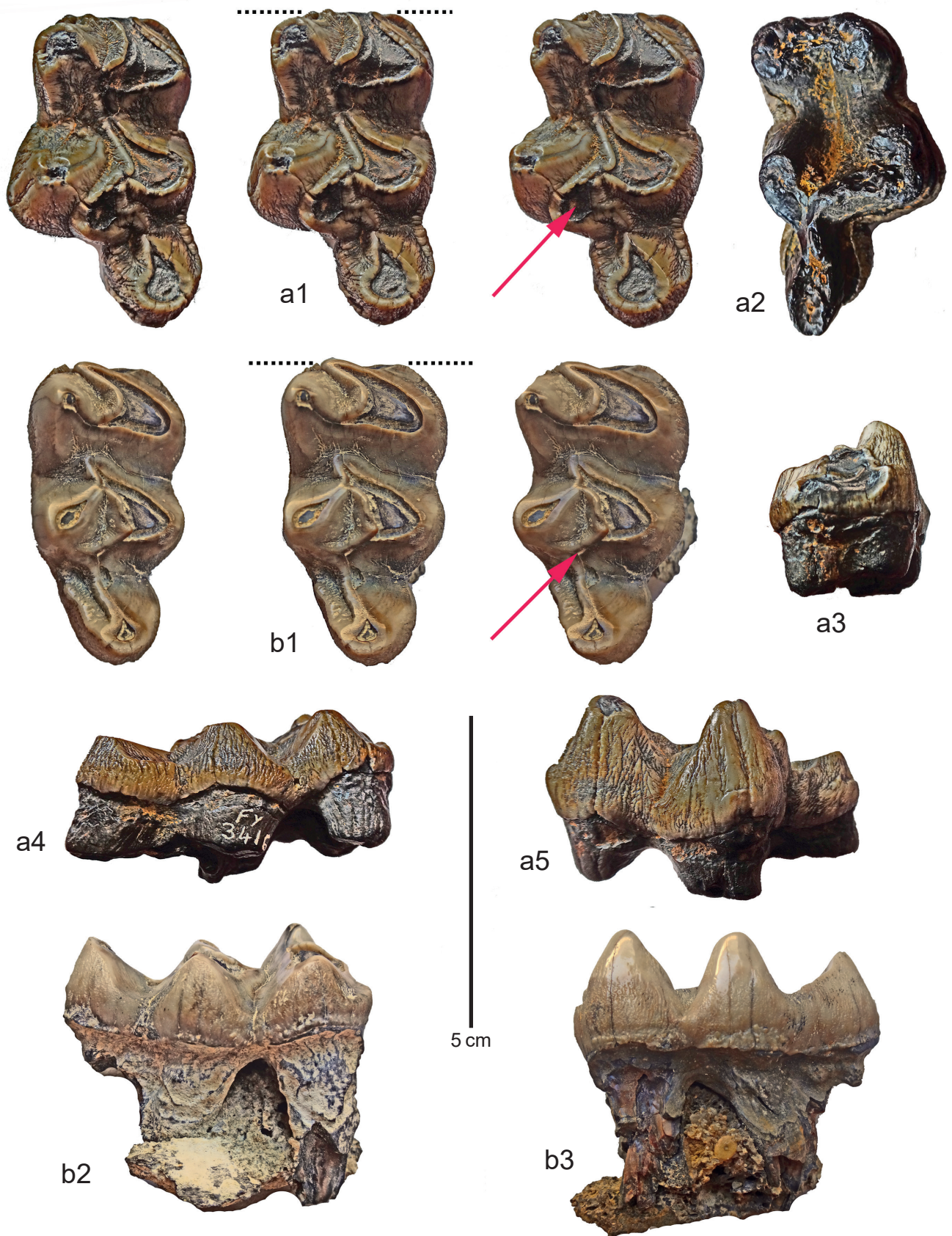
Type locality. Neuville-aux-Bois, France.

Correlation. MN 3b.

Description and comparison. Coll. Sinturet FY 3416 is a moderately worn right m/3 of *Brachyodus onoideus* from La Fuye, France. The crown is normally developed on its buccal side, but on the lingual side the entoconid is considerably larger than usual and it projects markedly lingually, thereby adding ca. 25 % to the breadth of the tooth. The posthypocristid is also greatly enlarged, both mesio-distally and bucco-lingually, such that it extends to the lingual margin of the tooth (arrow in Text-fig. 2a1). In lingual aspect, the base of the entoconid is seen to extend slightly beneath the rest of the cervix (Text-fig. 2a5) which, in normally developed teeth of *Brachyodus*, is usually relatively straight from mesial to distal as in two specimens from La Guimardière (Coll. Gain 20585a; Text-fig. 2b3)

Table 1. List of material studied and measurements (in mm). MDL – mesio-distal length, BLB – bucco-lingual breadth. To complete the list of material from La Fuye, specimens from the site measured by Dineur (1982, sometimes cited as 1981) but not seen by the author, are included (in italics).

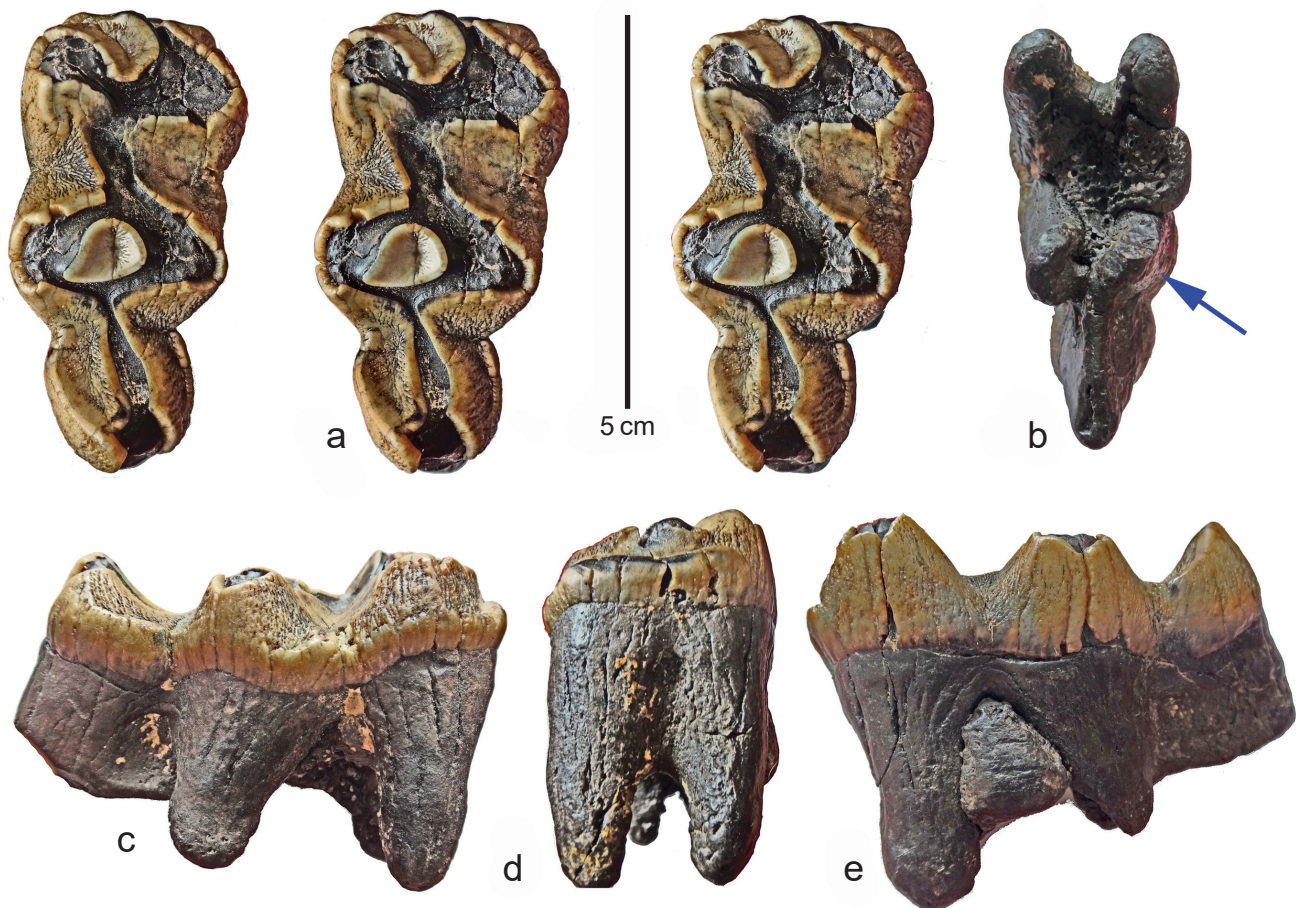
Collection / Catalogue no.	Locality	Tooth	MDL	BLB
Coll. Gagnaison FY 3	La Fuye	i/2 rt	13.7	12.4
Coll. Gagnaison FY 4	La Fuye	i/2 rt	22.6	22.7
Coll. Gagnaison FY 2	La Fuye	i/2 rt	19.6	20.5
Musée du Savignéen 36	La Fuye	p/4 lt	26.2	22.0
Musée du Savignéen 98-2, 49	La Fuye	p/4 lt	26.7	20.0
Musée du Savignéen 98-1, 50 Levé, I81	La Fuye	m/3 lt	55.4	27.6
Coll. Sinturet FY 3416	La Fuye	m/3 rt	51.0	25.5
Musée du Savignéen 98-1, 50 Levé I81	La Fuye	P4/ lt	22.9	27.3
Musée du Savignéen 51	La Fuye	P4/ lt	25.4	31.5
Musée du Savignéen sans #	La Fuye	P4/ rt	25.0	31.2
Coll. Sinturet FY 3106	La Fuye	M2/ lt	37.4	41.4
Coll. Sinturet FY 3106	La Fuye	M3/ lt	–	43.0
Coll. Chevrier FY 557	La Fuye	M3/ lt	39.2	42.2
Musée du Savignéen 98-2, 37	La Fuye	M3/ lt	42.0	44.3
Coll. Guével FY 82	La Fuye	d/3 rt	24.0	14.7
<i>Coll. Faillie</i>	<i>La Fuye</i>	<i>m/1 lt</i>	<i>33.1</i>	<i>21.9</i>
<i>Coll. Faillie</i>	<i>La Fuye</i>	<i>P3/</i>	–	<i>21.1</i>
Coll. Gain 20585a	La Guimardière	m/3 rt	45.4	25.0
Coll. Sinturet Bx 3235	Les Beilleaux	m/3 lt	60.0	28.3
Coll. Sinturet # 65	Faluns sensu lato	m/3 rt	57.0	29.4
Musée du Savignéen FS 86	Faluns sensu lato	M3/ lt	42.3	46.7



Text-fig. 2. Right m/3s of *Brachyodus onoideus*. a: Anomalous specimen Coll. Sinturet FY 3416 from La Fuye; a1 – stereo occlusal views, a2 – radicular view, a3 – mesial view, a4 – buccal view, a5 – lingual view. b: Normally developed specimen Coll. Gain 20585a from La Guimardière; b1 – stereo occlusal views, b2 – buccal view, b3 – lingual view. Dotted lines define the contact facet between m/2 and m/3 and the arrows show the dentine lake associated with the posthypocristid. Scale bar = 5 cm.

and Les Beilleaux (Coll. Sinturet Bx 3235; Text-fig. 19d). The hypoconid and entoconid in FY 3416 are separated by a

shallow valley, as is usual in *Brachyodus* (Text-fig. 2b1) but, unusual for the genus, the preentocristid does not fuse with



Text-fig. 3. Coll. Sinturet 65, a heavily worn right m/3 of *Brachyodus onoideus* from an imprecise locality in the French Faluns. **a:** stereo occlusal views, **b:** radicular view (arrow shows the entoconid root), **c:** buccal view, **d:** mesial view, **e:** lingual view. Note the proximity between, and subequal dimensions of, the two roots that support the second lophid. Scale bar = 5 cm.

the prehypocristid. The protoconid and metaconid are of the habitual morphology for *Brachyodus*, as is the hypoconulid (talonid) but they are slightly twisted with respect to the rest of the crown.

The roots of the tooth reflect the crown dimensions, such that the root supporting the entoconid is much enlarged (Text-fig. 2a2) in comparison with those that support the other cusps. Comparison of the root system of FY 3416 with those of other m/3s of *Brachyodus*, indicate that the entoconid root has been displaced lingually leaving a wide space between the two roots that support the second lophid. Another specimen in the Sinturet collection (# 65; Text-fig. 3) shows the normal condition of the two roots, which are subequal in dimensions and are close together.

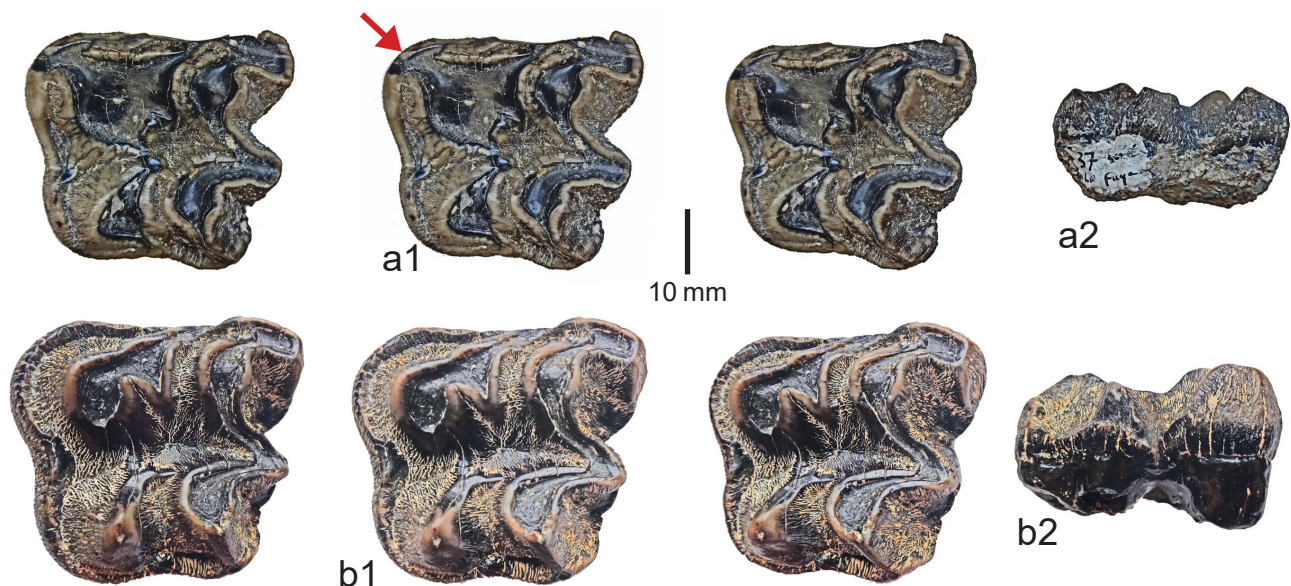
Interpretation. The basic structural elements of the crown of the m/3 from La Fuye are the same as those in other specimens of *Brachyodus*, comprising five cusps arranged into three lophids, accompanied by a well-developed mesial cingulum (Text-fig. 2a3). The protoconid and metaconid comprise the mesial lophid, the hypoconid and entoconid form the second lophid and the hypoconulid forms the centrally placed talonid at the rear of the tooth.

What differs in the tooth from La Fuye is the great enlargement of the posthypocristid (arrows in Text-fig. 2a1) and the entoconid relative to the normal dimensions of the other cusps, with the result that the mesial lophid

is slightly twisted with respect to the second lophid, and the hypoconulid is displaced slightly lingually from its usual orientation in *Brachyodus*. As a result, the pattern of wear in this tooth is somewhat different from what it is in other specimens of the genus. A further consequence of the anomaly was an increase in the dimensions of the root that supports the entoconid (compare Text-figs 2a2, 3b) accompanied by its displacement lingually.

A left M3/ from La Fuye (Musée du Savignéen 98-2, 37; Text-fig. 4a) has a normally developed crown, but the wear pattern differs widely from the usual situation in *Brachyodus* as shown in Musée du Savignéen FS 862 (Text-fig. 4b). The protocone is markedly more worn than the paracone, metacone and metaconule, and there is a deep gully worn into the mesial part of the protocone and lingual cingulum.

Dental occlusion, maleruption and life history. Despite the anomalous enlargement, the slight anterior displacement and minor anticlockwise twist of the entoconid, the m/3 from La Fuye shows almost normal occlusal wear on its other main cusps, with large dentine lakes developed on the protoconid, hypoconid and hypoconulid, and a smaller one on the metaconid (Text-fig. 2a1) (the last facet is somewhat damaged by post-fossilisation breakage). The entoconid, in contrast, has only a small dentine lake at its apex, indicating that it was not in occlusal antagonism with the mesostyle of its corresponding upper third molar, or



Text-fig. 4. Moderately worn upper third molars of *Brachyodus onoideus* from France. **a:** Musée du Savignéen 98-2, 37, left M3/ from La Fuye, with anomalously heavy wear on the protocone and the mesial part of the lingual cingulum (arrow). **b:** Musée du Savignéen (2012-FS-862) left M3/ from the Faluns sensu lato, showing the more usual wear pattern seen in other material of *Brachyodus onoideus* from the Faluns. 1 – stereo occlusal views, 2 – buccal views. Scale bar = 10 mm.

that cusp-to-cusp contact was minimal or very occasional. In normally developed m/3s, the apex of the entoconid would be as deeply worn as that of the metaconid if not slightly more deeply worn (Text-figs 2b1, 3a).

A significant difference in wear pattern is that, in the specimen from La Fuye, the dentine lake developed on the junction of the posthypocristid with the prehypocristid is much enlarged when compared to the corresponding part of a normally developed tooth (red arrows in Text-fig. 2). Indeed this part of the tooth from La Fuye appears to have been occluding with the mesostyle of the M3/, instead of the entoconid as would have been the case in a normally developed crown. This suggests that the tooth was not parallel to the other cheek teeth, but was twisted anticlockwise by about 20°, thereby indicating a mild degree of maleruption.

The stage of wear in FY 3416 indicates that the individual survived to fully adult status, but died prior to senility. The protoconid, hypoconid and hypoconulid are worn to about one third of the height of the cusps, suggesting that it survived for a significant period (several years) following the complete eruption of the third molars. Thus, it is inferred that the dental anomaly did not adversely affect the life history of the individual concerned.

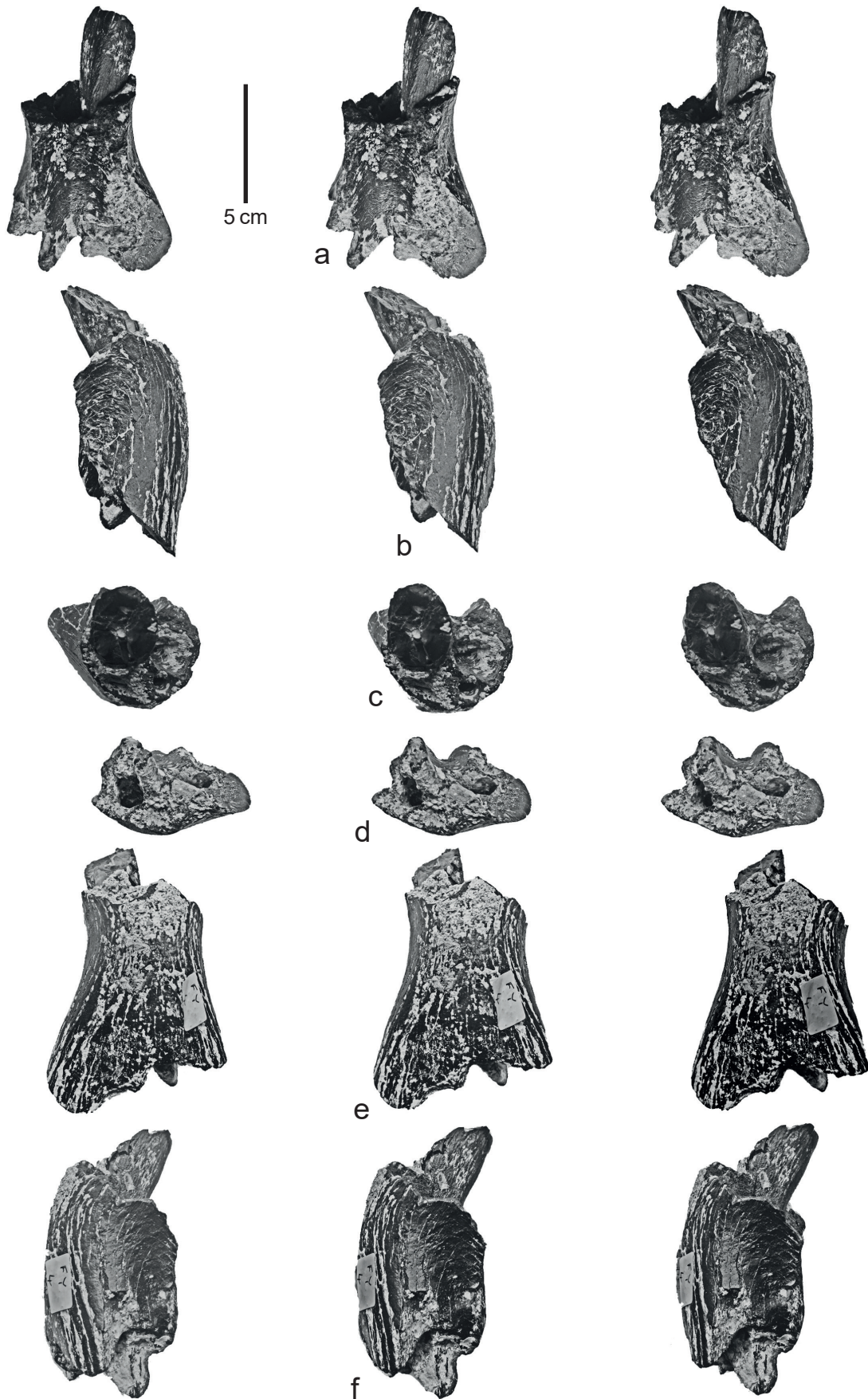
In the context of this paper, a left M3/ (Musée du Savignéen 98-2, 37) also from La Fuye, is of interest because, even though it has a normally developed crown, its wear pattern is anomalous, in that the protocone and the mesial part of the lingual cingulum are far more deeply worn than the other cusps (Text-fig. 4a). The metaconule is also more deeply worn than is usual in this genus. This wear pattern is markedly divergent from the normal wear pattern observed in other third molars of *Brachyodus* from France, that are at a comparable stage of wear (Text-fig. 4b).

Other fossils of *Brachyodus* from La Fuye. In the Gagnaison collection (FY4; Text-fig. 5) there

is a damaged mandibular symphysis from La Fuye of a male individual of *Brachyodus onoideus*. The root and a small part of the crown of the right second incisor are preserved, and on the left side of the jaw, parts of the alveoli of i/1 and i/2 are present. In posterior view the anterior ends of the mandibular canals are visible on both sides, and on the lateral surfaces of the symphysis, beneath the diastema, there are shallow fossae, bordered anteriorly by the swelling that houses the roots of the i/2s. Damage to the superior margin of the bone has removed any evidence concerning the presence or absence of the i/3. The specimen represents a male individual.

Coll. Gagnaison FY 3 (Text-fig. 6), is a right i/2 (female) of *Brachyodus onoideus* from La Fuye. The apex is slightly worn where it contacted the upper central incisor, and there are grooves on the root beneath gingival level; shallow ones close to cervix worn into the roots during the life of the individual, and deeper, more irregular ones further down the root due to post-mortem damage. The crown is labio-lingually compressed and the mesial and distal edges are sub-parallel. The root is conical, tapering to a point and slightly curved from cervix to apex. The apical part is moderately bent towards the distal side.

Coll. Gagnaison FY 2 (Text-fig. 7), is a right i/2 (male) of *Brachyodus onoideus* from La Fuye. Its dimensions are appreciably smaller than those of the corresponding tooth in the symphysis described above (FY 4). The main wear facet is on the anterior and apical part of the crown, due to contact with the upper central incisor. The distal crest is prominent apically but fades out towards cervix. The root is robust and shows a longitudinal groove along its posterior side close to where the i/3 root would lie (Text-fig. 7a). There is a narrow and shallow horizontal groove worn into the root immediately beneath the cervix that was developed during the lifetime of the individual. The latter groove is especially evident on the mesial side of the tooth (Text-fig. 7e).



Text-fig. 5. Stereo images of Coll. Gagnaison FY 4, mandibular symphysis of *Brachyodus onoideus* from La Fuye, containing the root of the right i/2 and the damaged alveoli of the left i/1 and i/2. a: occlusal views, b: right lateral views, c: anterior views, d: posterior views, e: ventral views, f: left lateral views. Scale bar = 5 cm.



Text-fig. 6. Coll. Gagnaison FY 3, right i/2 (female) of *Brachyodus onoideus* from La Fuye. a: stereo lingual views, b: mesial view, c: labial view, d: distal view. Scale bar = 10 mm.

Musée du Savignéen 98-2, 49 (Text-fig. 8), is a left mandible fragment of *Brachyodus onoideus* from La Fuye with damaged p/4 and roots of p/2–p/3. The p/4 is deeply worn and is missing part of the protoconid. It has a strongly developed preprotoconid cristid that reaches mesiolingually where it terminates against the mesial cingulum. The postprotoconid cristid is deeply worn but was directed distolingually where it fuses with a raised part of the lingual cingulum. There is a clear lingual cingulum extending between the ends of the pre- and postprotoconid cristids, and the enamel is lightly wrinkled.

Musée du Savignéen 36 (Text-fig. 9), is a deeply worn right p/4 of *Brachyodus onoideus* from La Fuye. The lingual cingulum is prominent and rises posteriorly to join the postprotoconid cristid as in the p/4 described above (Musée du Savignéen 98-2, 49). The main difference between these teeth is the slightly greater breadth of Musée du Savignéen 36. There are two robust roots, the anterior one conical and tapering apically, the distal one comprised of two coalescent columns that give the root an 8-shaped section with the apices separated from each other (Text-fig. 9c).

Coll. Guével FY 82 (Text-fig. 10), a right d/3 of *Brachyodus onoideus* from La Fuye, is moderately worn. Its overall morphology recalls that of a permanent p/4, but the enamel is thinner, and the distal complex behind the protoconid is more extensive, with a prominent, tall entoconid and a lower hypoconid forming a transverse complex that is separated from the protoconid by a transverse depression. The pre- and postprotoconid cristids are sharp and terminate at the lingual side of the crown, the preprotoconid cristid ending at a minute metaconid. The lingual cingulum extends along the entire length of the tooth rising to meet the postprotoconid cristid and curling round the base of the entoconid to join the distal cingulum. Buccally the cingulum is weaker but it extends mesially and eventually joins the lingual cingulum at the mesiolingual corner of the tooth.

There are three upper fourth premolars of *Brachyodus onoideus* from La Fuye (Musée du Savignéen 51 (Text-fig. 11a); 98-1, 50 Levé, I81 (Text-fig. 11b); and sans # (Text-fig. 11c)). The most notable aspect of these teeth is the enormous degree of variation that they express. Musée du Savignéen 51 has a weak preprotocrista that terminates before reaching the mesial cingulum, and there is no sign of a metaconule.

In contrast, Musée du Savignéen 98-1, 50 Levé, I81, and Musée du Savignéen sans #, each possess a well-developed preprotocrista that reaches the mesial cingulum as well as a prominent metaconule. In Musée du Savignéen 98-1, 50 Levé, I81, the metaconule is mesio-distally compressed and narrow, whereas in Musée du Savignéen sans # the metaconule is large and circular. There are also differences in the strength of the postprotocrista, which is well developed in the first two specimens, but very weak in the third one with the large metaconule. The barrel on the buccal surface of the metaconid is strong in the first tooth, but weak in the third one. All three teeth are almost completely surrounded by a cingulum, with minor weakening of the structure on the buccal side.

The second specimen (Musée du Savignéen 98-1, 50 Levé I81) is distinctly smaller than the other two (Tab. 1), which raises the possibility that it belongs to *Brachyodus intermedius* MAYET, 1908, rather than to *Brachyodus onoideus* (see metric analysis).

Coll. Sinturet FY 3106 (Text-fig. 12), is a left maxilla fragment of *Brachyodus onoideus* containing the M2/ and the anterior half of M3/. The M2/ is deeply worn to the stage that the protocone and paracone are no longer distinguishable from each other. The paracone, metacone and metaconule in contrast, are only moderately worn, which suggests that the heavy wear on the protocone may be anomalous. The parastyle and mesostyle are voluminous, but the metastyle is barely distinguishable at the end of the postmetacrasta. The protocone and metacone each have a strongly developed barrel extending from the apex of the cusp towards the cervix, fading out as it goes. The metaconule has clear pre- and post-cristae that are oriented mesio-buccally and disto-buccally respectively, terminating in the midline of the crown. The mesial, lingual and distal cingula are narrow and continuous, and the buccal cingula are present but weak at the bases of the paracone and metacone. The enamel is finely wrinkled.

The morphology of the mesial loph of the M3/ is like that of the M2/ described immediately above. Being less worn, it is possible to see that the protocone and paracone are closely appressed against each other, being separated by a narrow groove which would be obliterated with a medium amount of wear. The barrel on the buccal surface of the



Text-fig. 7. Coll. Gagnaison FY 2, right i/2 (male) of *Brachyodus onoideus* from La Fuye. a: stereo posterior views, b: distal view, c: stereo anterior view, d: apical view, e: mesial view. Scale bar = 20 mm.

paracone is well developed, as is the cingulum at the base of the cusp.

Coll. Chevrier 557 (Text-fig. 13), a left M3/ of *Brachyodus onoideus* from La Fuye, is lightly worn, with small wear facets on the parastyle and paraconule, but none on the other cusps and styles. As a consequence the specimen preserves all the morphological details of the crown in pristine condition. The roots are missing but in radicular view, it is possible to discern the distal extension of the root beneath the metacone (Text-fig. 13e) which reveals that the

tooth is a third molar, and not a second molar (which lacks such an extension).

The protocone and paraconule are separated from each other distally by quite a broad groove, but they coalesce along the preprotocrista. The postprotocrista is low and weak, but the postparaconule crista is clear and descends towards the median transverse valley, but not encroaching into the valley. The preparaconule crista descends mesio-buccally, reaching the mesial cingulum close to the parastyle. The paracone has a buccal barrel that fades out towards the



Text-fig. 8. Musée du Savignéen 98-2, 49, left mandible fragment of *Brachyodus onoideus* from La Fuye, with damaged p/4 and roots of p/2–p/3. a: stereo occlusal view, b: lingual view, c: buccal view. Scale bar = 5 cm.

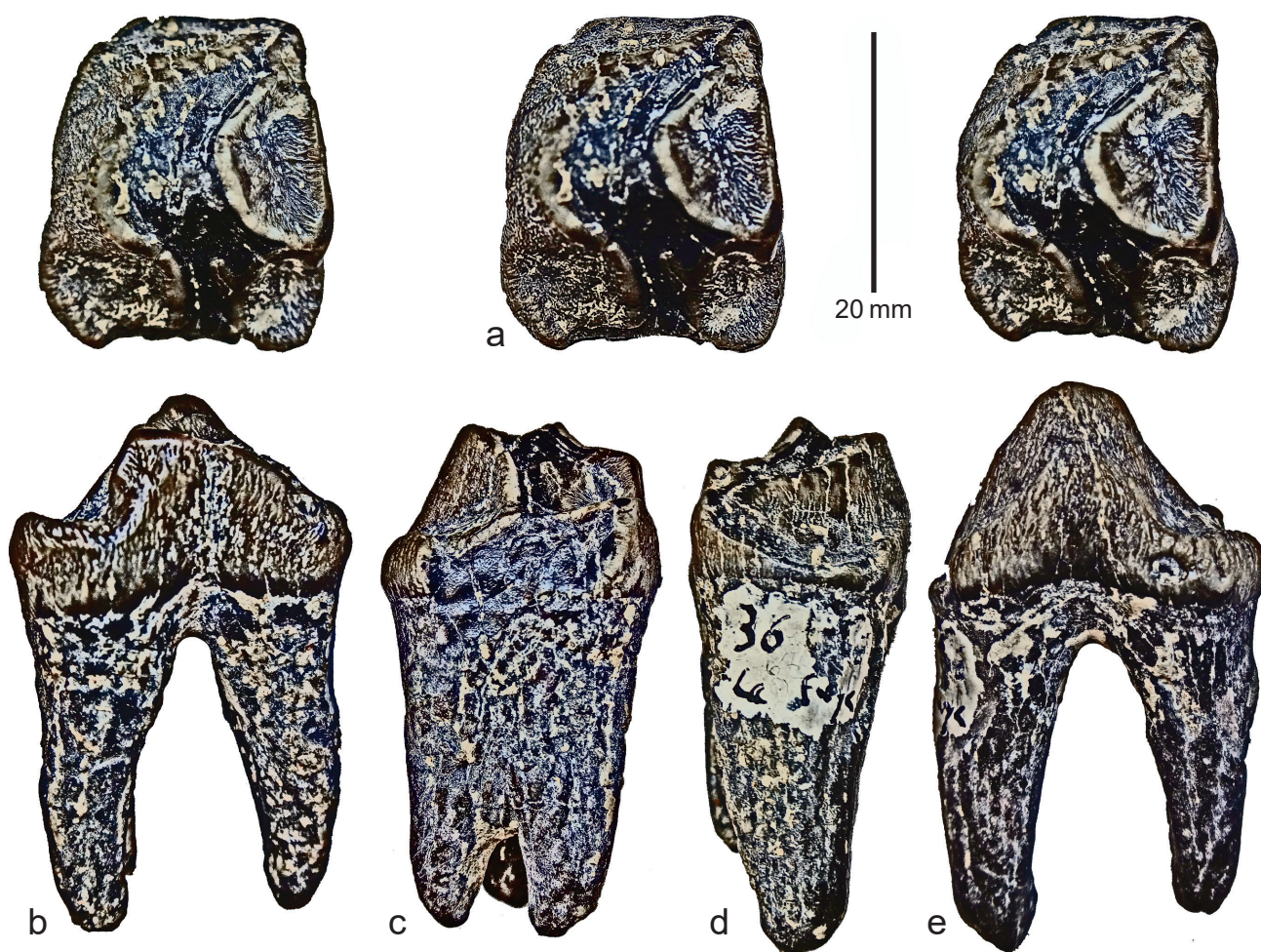
cervix and the barrel on the metacone is weakly expressed. The parastyle and mesostyle are well developed and bulbous at their bases, but are pinched in where they approach the paracone and metacone. The metaconule has clear pre- and postcristae which lead towards the midline of the crown. The metacone is angled in such a way that the postmetacrista is almost in the midline of the tooth, whereas the premetacrista is close to the buccal edge of the tooth, near the mesostyle. There is a strongly developed mesial, lingual and distal cingulum, which contrasts with the narrower cingulum on the buccal side of the crown. The enamel is wrinkled.

Metric analysis. In his unpublished PhD Thesis, Dineur (1982, sometimes cited as 1981) listed measurements (lingual length, buccal length, mesial breadth and distal breadth) of the teeth of *Brachyodus*. The main article dealing with the dimensional variation in *Brachyodus* from France was published by Dineur and Ginsburg (1986). The measurements of the M3/s used in the latter paper correspond to the lingual length and mesial breadth (Text-fig. 14). Concerning the lower third molars, Dineur and Ginsburg

(1986) were unable to decide to which species four of the specimens belonged, and they proposed two explanations; that they were either small specimens of *B. onoideus*, or large specimens of *B. intermedius*. They appear not to have considered the possibility of a third taxon in the sample.

Because of the dimensional and morphological diversity of the dental sample of *Brachyodus* from La Fuye, it was decided to perform a metric analysis of available fossils from the French Faluns, in order to determine the species to which the teeth belong (Text-figs 15–18). Most of the teeth plot within the range of metric variation of *Brachyodus onoideus*, but two specimens (a P4/ and an m/3) are somewhat smaller than the others and possibly represent the species *Brachyodus intermedius* or a species intermediate in dimensions between *B. onoideus* and *B. intermedius*. The M3/ with the peculiar wear pattern from La Fuye, plots within the range of metric variation of the larger of the two named species, *Brachyodus onoideus*.

It is noted that the bivariate plots (Text-figs 15–18) suggest that there are possibly four size groups (species?) of *Brachyodus* in the Faluns, one of which is larger than



Text-fig. 9. Musée du Savignéen 36, right p/4 of *Brachyodus onoideus* from La Fuye. a: stereo occlusal views, b: lingual view, c: distal view, d: mesial view, e: buccal view. Scale bar = 20 mm.

Brachyodus onoideus, but not yet formally diagnosed due to inadequacies of the fossil record (no suitable holotype available), the other is intermediate in dimensions between *B. onoideus* and *B. intermedius*. Alternatively, but perhaps less likely, is the hypothesis that the four metric groups could represent two species in which there was a large body size difference between males and females.

The balance of the metric evidence is that the anomalous tooth from La Fuye (Coll. Sinturet FY 3416) and a small P4/ (Musée du Savignéen 98-1, 51) belong to the size group that is intermediate in dimensions between *Brachyodus onoideus* and *Brachyodus intermedius*. The upper third molar with a peculiar wear pattern (Musée du Savignéen 98-2, 37) and the other teeth from the site plot into the range of variation of *Brachyodus onoideus*.

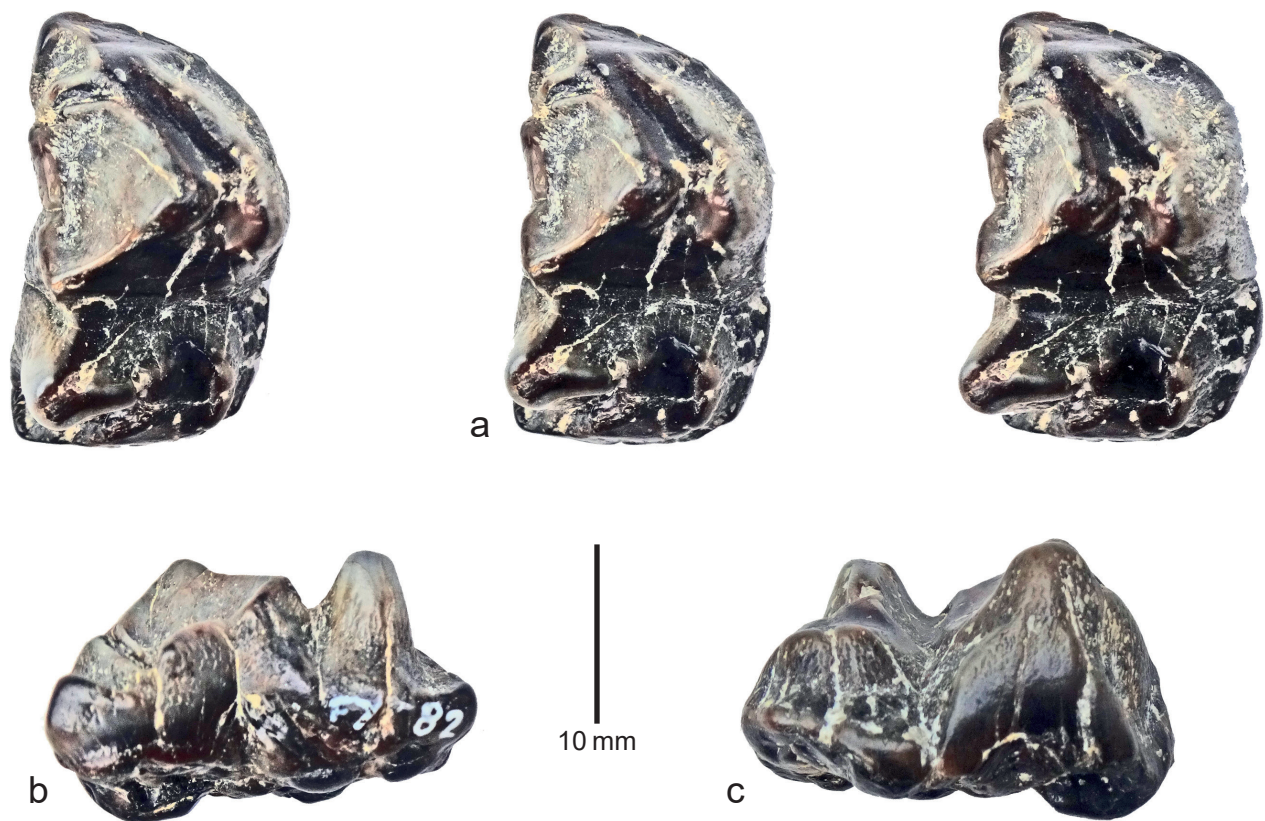
Discussion

Dental anomalies are rare in the fossil record, but have been recorded in a variety of mammals, as discussed by Ducrocq et al. (1995). These authors documented the occurrence of dental anomalies in several upper molars of anthracotheres (*Siamotherium krabiense* SUTEETHORN et al., 1988) from the Eocene of Thailand. The Krabi specimens

developed additional cusps in the upper molars. Because the anomalies were present in several individuals, the preferred hypothesis of the authors was that they were probably due to inbreeding (i.e., a high degree of endogamy).

Unlike the Krabi fossils, the abnormal m/3 of *Brachyodus* from La Fuye does not possess extra cusps, but it does show great enlargement of the entoconid and abnormal development of the posthypocristid, which almost forms an extra cuspid between the hypoconid and entoconid. However, examination of other specimens of *Brachyodus* reveals that the lingual end of the posthypocristid is sometimes slightly swollen, producing a dentine lake in moderate wear (Text-fig. 2b1). The specimen from La Fuye has taken this tendency to an extreme, but has not produced an extra cuspid.

It is not possible to identify precisely what was the underlying cause of this dental anomaly, although localised alteration to the odontoblast and ameloblast complexes (Simmer et al. 2010) was likely to have been involved. An anomalous bend between a tooth and its root is known as dilaceration (Asokan et al. 2004) and can be caused by trauma or by the development of a cyst close to the developing tooth. However, the tooth from La Fuye shows a normal relationship between the crown and its root, so it is unlikely



Text-fig. 10. Coll. Guével FY 82, right d/3 of *Brachyodus onoideus* from La Fuye. a: stereo occlusal views, b: lingual view, c: buccal view. Scale bar = 10 mm.

to represent a case of dilaceration. Nor is the anomaly likely to be due to displacement of the developing cusp within its bud because the anomaly relates to the increased dimensions of the entoconid and alteration of its position relative to the other cusps of the tooth, rather than to modification of its form.

What is highly unusual about the specimen (FY 3416) from La Fuye is the fact that the dental anomaly affected only a limited part of the crown and root. It involved an increase in the volume of enamel secreted by the ameloblasts that produced the entoconid and the posthypocristid, in contrast to the ameloblasts that produced the others parts of the crown which developed normally. A volumetric increase of up to 25 % was involved, one result of which was enlargement of the posthypocristid which, as a consequence, induced a lingual and slight mesial shift of the enlarged entoconid.

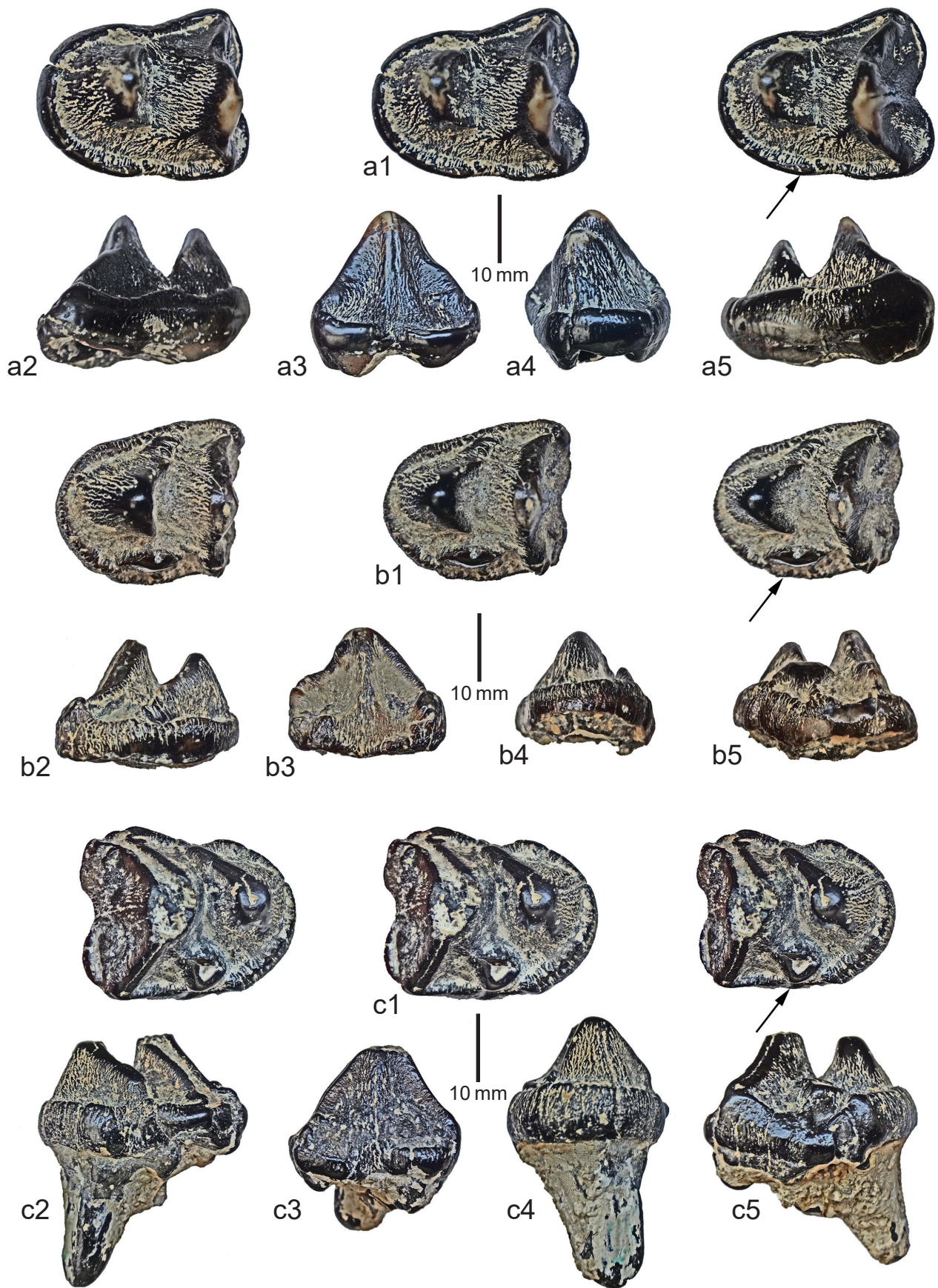
As was pointed out by Simmer et al. (2010), during growth of teeth “the shape of the enamel layer covering the crown is determined by five growth parameters: the (1) appositional growth rate, (2) duration of appositional growth (at the cusp tip), (3) ameloblast extension rate, (4) duration of ameloblast extension, and (5) spreading rate of appositional termination”. These factors determine the shape of the “crown once developmental processes have determined the morphology of the latent dentin surface upon which it grows”. Not only do these factors control the shape of the crown, but they also affect its dimensions.

However, the prior shape and size of the underlying dentine mass produced by odontoblasts is of primordial importance, the subsequent ameloblast activity adding

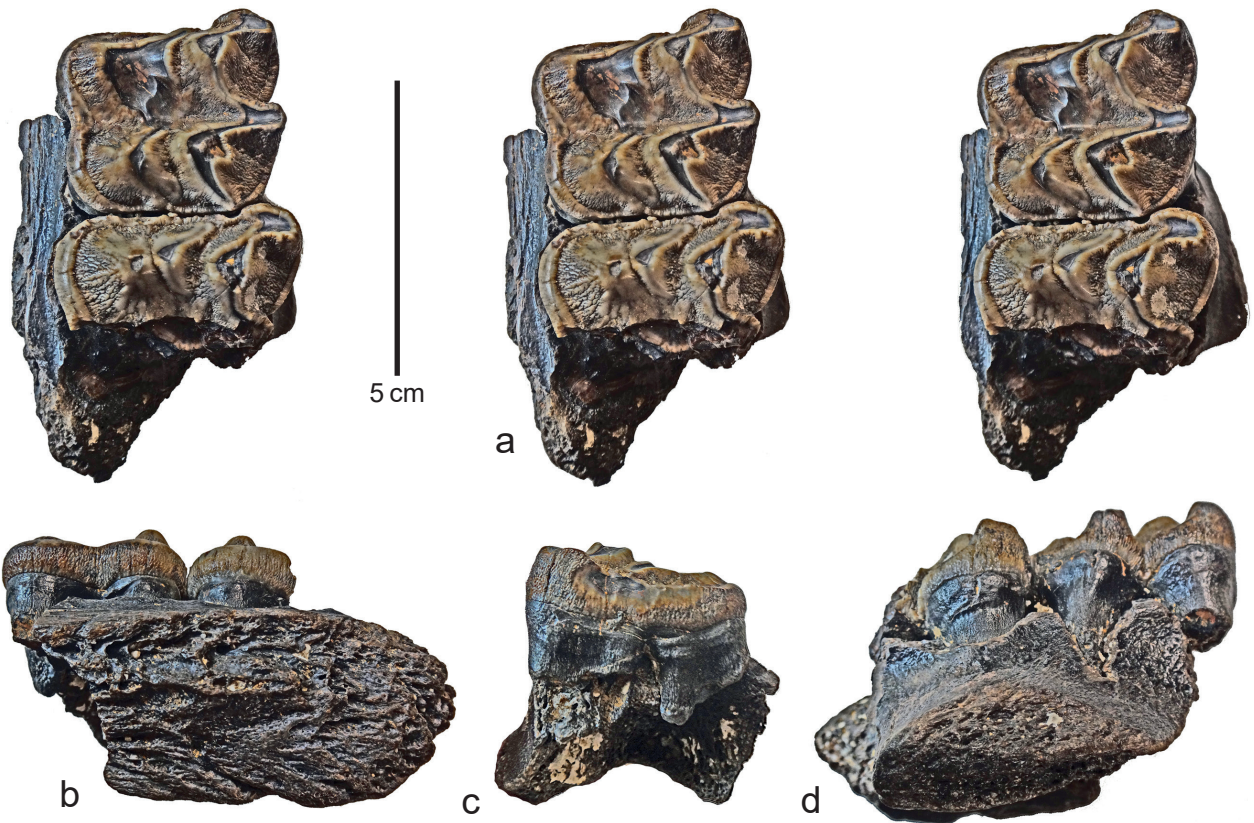
detail to the shape and size of the cusp, rather than being the root cause of its anomalous dimensions and positioning. It is therefore likely that the teratogenic tooth from La Fuye experienced anomalous growth of the dentinal masses of the entoconid and posthypocristid at the odontoblast stage of development, upon which ameloblast secretions subsequently added details. If so, then the anomaly would have been produced during the equivalent of developmental stage 4 in the closely related genus *Bothriogenys* SCHMIDT, 1913 (Sallam et al. 2016: fig. 9). During this stage, the individual still retained its deciduous dentition but had already erupted its m/1 and m/2. This would correspond to a late juvenile or young adult phase in the individual’s life history. The individual from La Fuye then survived into mature adulthood, as shown by the medium stage of occlusal wear of the m/3.

The fact that, in FY 3416, the two roots that support the cusps of the second lophid are positioned far apart from one another (Text-fig. 2a2), contrasting strongly with the roots in normal specimens that are close together and of sub-equal dimensions (Text-fig. 3b), indicates that there may have been a cyst or other anomalous soft-tissue growth in the interior of the mandible.

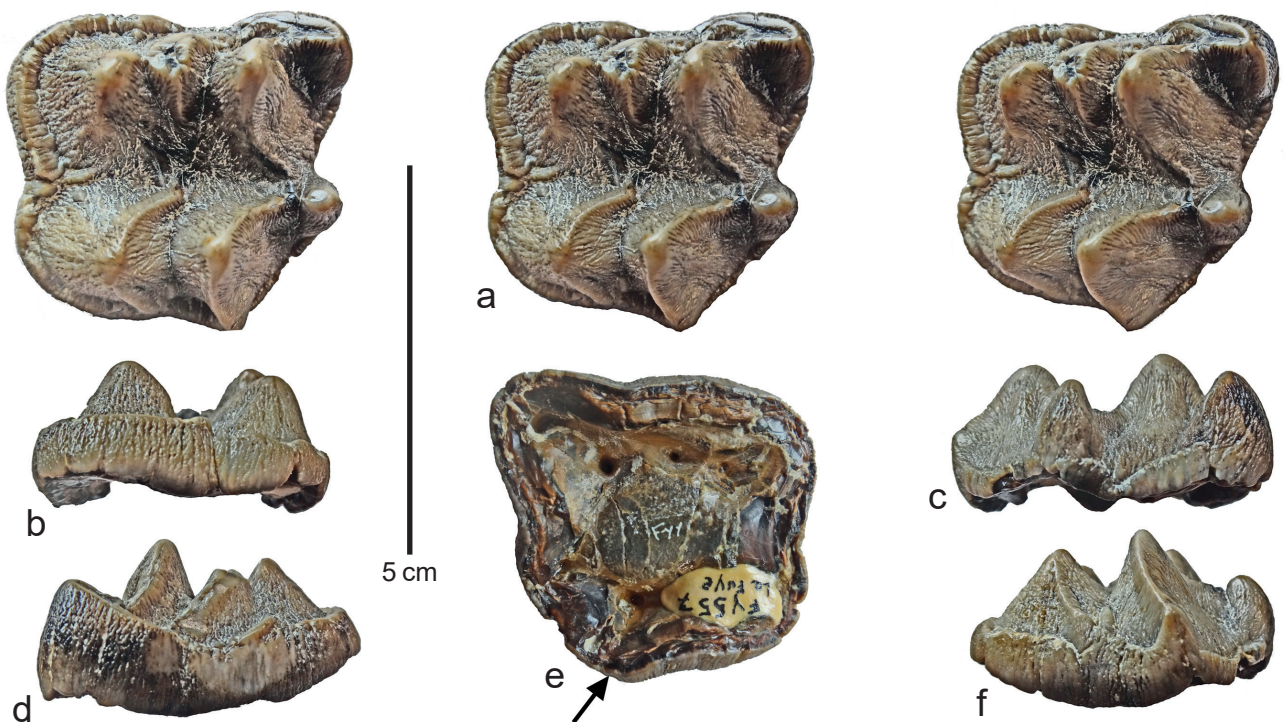
In individuals of *Brachyodus* with normally developed mandibles (Text-fig. 19) the lingual surface of the dorsal half of the jaw immediately beneath the m/3 is flattened to the extent that it is in line with, or slightly overhung by the lingual margin of the tooth, while the lower half of the ramus is concave where the sublingual fossa is present (Text-fig. 19b, d). An m/3 with a much enlarged and lingually



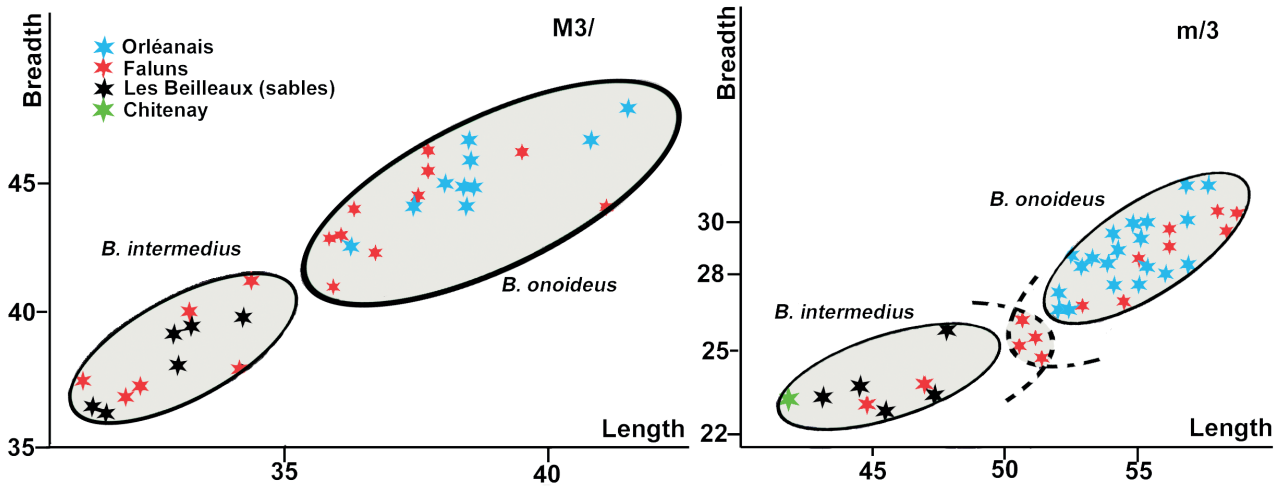
Text-fig. 11. P4/s of *Brachyodus* from La Fuye. a: Musée du Savignéen 51, b: Musée du Savignéen 98-1, 50 Levé, I81, c: Musée du Savignéen sans #. 1 – stereo occlusal views, 2 – mesial views, 3 – buccal views, 4 – lingual views, 5 – distal views. Arrows point to the metaconule. Scale bare = 10 mm.



Text-fig. 12. Coll. Sinturet FY 3106, left maxilla fragment of *Brachyodus onoideus* with M2/ and anterior half of M3/. a: stereo occlusal views, b: lingual view, c: mesial view of M2/, d: buccal view. Scale bar = 5 cm.



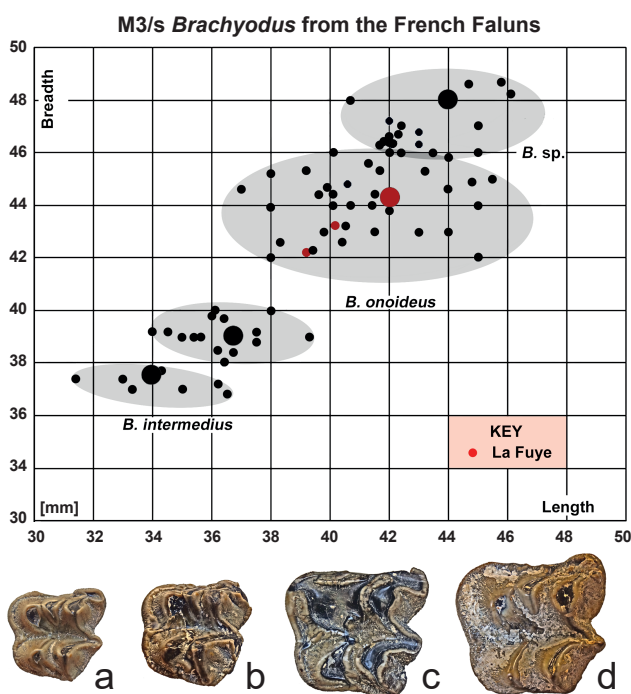
Text-fig. 13. Coll. Chevrier 557, left M3/ of *Brachyodus onoideus* from La Fuye. a: stereo occlusal views, b: lingual view, c: buccal view, d: mesial view, e: radicular view to show the distal extension of the root that supports the metastyle (arrow), f: distal view. Scale bar = 5 cm.



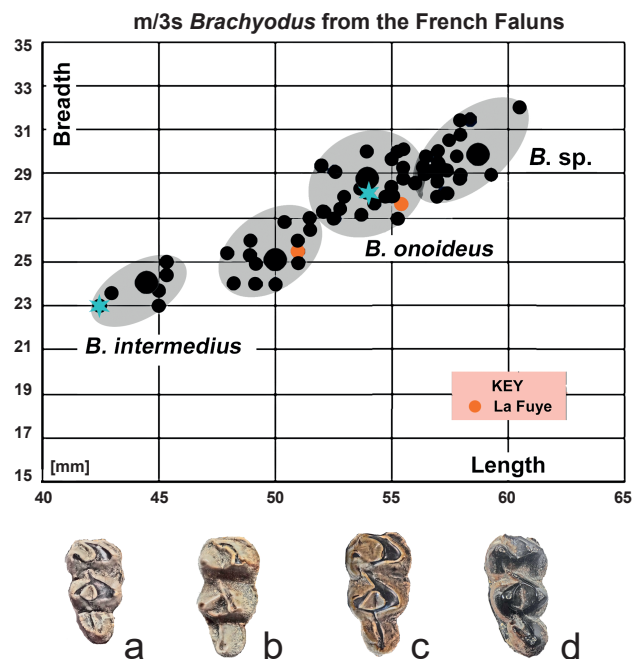
Text-fig. 14. Metric variation in upper and lower third molars of *Brachyodus* from the French Faluns. Bivariate plots modified from Dineur and Ginsburg (1986: fig. 2). Note the four lower third molars that form a separate group intermediate in dimensions between *B. onoides* and *B. intermedius*.

displaced root beneath the entoconid, such as occurs in FY 3416 would, if it erupted parallel to and in line with the other molars, modify this profile by producing a swelling in its lingual surface. If it erupted at an angle to, or out of line with the other cheek teeth (maleruption), however, it might not have altered the profile of the lingual surface of the ramus. In the latter scenario, the occlusal wear pattern would likely have been abnormal, which appears to be the

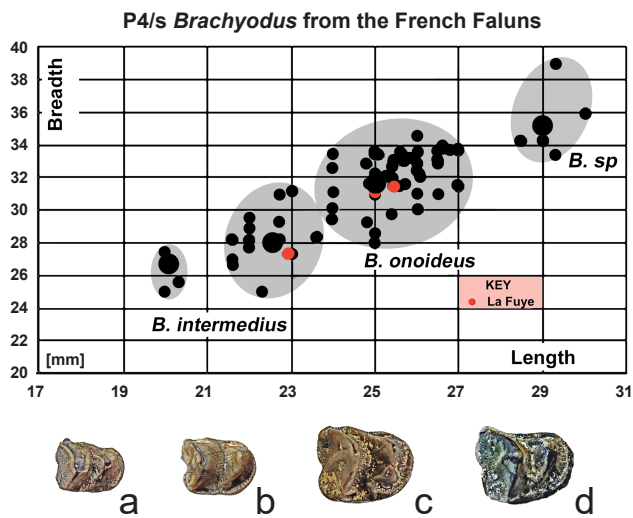
case with this specimen, the wear facets of the second lophid (Text-fig. 2a1) suggesting that the tooth was twisted about 20° anticlockwise with respect to the rest of the tooth row but was probably in line with it as show by the orientation of the interstitial contact facet between the m/2 and the m/3 (dotted lines in Text-fig. 2a1).



Text-fig. 15. Bivariate (buccal length-mesial breadth) plots of upper third molars of *Brachyodus* from the French Faluns. The three specimens from La Fuye plot within the range of variation of *Brachyodus onoides*. The large dots correspond to the illustrated samples in the right column. a: Coll. Gain 9c from La Guimardière, b: Coll. Gain 9a from La Guimardière, c: Musée du Savignéen 93 from La Fuye, d: Musée du Pressigny 03, Faluns sensu lato.



Text-fig. 16. Bivariate (length-breadth) plots of lower third molars of *Brachyodus* from the French Faluns. One of the specimens from La Fuye plots within the range of variation of *Brachyodus onoides*, the other plots into a smaller size group intermediate between *B. onoides* and *B. intermedius*. Blue stars are the holotypes of *B. onoides* and *B. intermedius*. Note the possibility of four metric groups in the sample. The large dots correspond to the illustrated samples in the right column. a: Coll. Guével 42 from Pont Boutard, b: MNHN FS 27 from Pontigné (reversed), c: Coll. Sinturet 52 from La Fontaine, d: MNHN FS 1702 from the Faluns sensu lato.



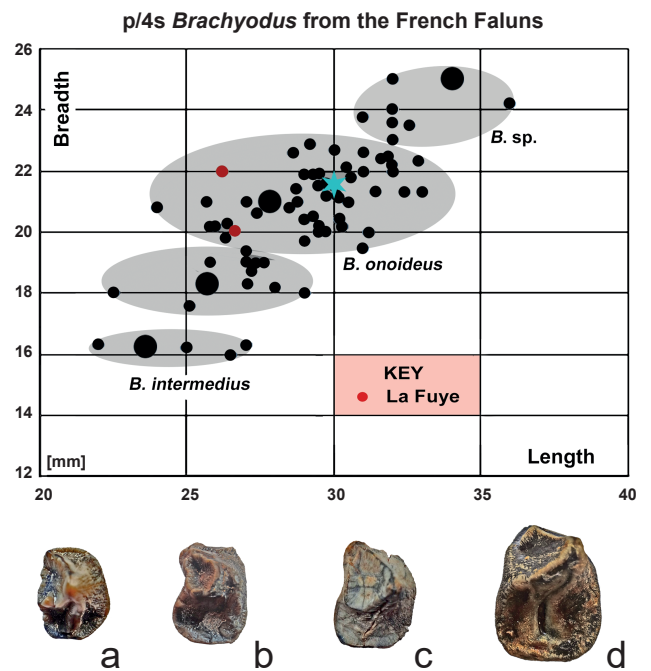
Text-fig. 17. Bivariate (length-breadth) plots of upper fourth premolars of *Brachyodus* from the French Faluns. Two of the specimens from La Fuye plot within the range of variation of *Brachyodus onoideus* whereas the third specimen plots within a size group intermediate between *B. onoideus* and *B. intermedius*. Note the presence of four metric groups of *Brachyodus* in the French Faluns. The large dots correspond to the illustrated samples in the right column. a: Coll. Gain 9o from La Guimardière (reversed), b: Coll. Sinturet 10 from the Faluns sensu lato, c: Musée d'Angers 12 from Meigné le Vicomte, d: Coll. Albert 71 from Breil.

The dental anomaly in the La Fuye tooth is unlikely to have resulted from genetic modifications due to inbreeding, even though *Brachyodus* was on its way to extinction following the arrival of gomphotheres in Europe (Antunes and Ginsburg, 2003). As the overall population of *Brachyodus onoideus* declined, there may have been isolated groups here and there that survived in favourable places, but with heightened occurrence of endogamy.

It is plausible that the M3/ with anomalous wear (Musée du Savignéen 98-2, 37; Text-fig. 4a) may have belonged to the same individual as the aberrant m/3 described above, but from the opposite side of the jaw. If so, then the dental anomaly in the m/3 may have been bilateral which would favour the hypothesis of a genetic underlying cause of the anomaly. However, there is no definitive evidence of this, unlike the case of the Thai anthracotheres described by Ducrocq et al. (1995) in which endogamy was the most likely cause of the dental anomalies that they observed.

Conclusion

A lower third molar (FY 3416) of *Brachyodus onoideus* from La Fuye (Early Miocene, France), provides a rare example of anomalous dental development in which the posthypocristid and entoconid were greatly enlarged in contrast to the normal dimensions and proportions of the other cusps in the tooth. The fact that the anomalous structures in the tooth affected only the posthypocristid and entoconid (and the associated root) suggests that there occurred a localised modification of the odontoblast and ameloblast complexes in the region of the posthypocristid and entoconid, leaving the



Text-fig. 18. Bivariate (length-breadth) plots of lower fourth premolars of *Brachyodus* from the French Faluns. Both of the specimens from La Fuye plot within the range of variation of *Brachyodus onoideus*. Note the possible presence of four size groups of *Brachyodus* in the French Faluns. The blue star is the holotype of *B. onoideus*. The large dots correspond to the illustrated samples in the right column. a: Musée du Savignéen 17 from Pelmer (reversed), b: Coll. Hautefort 12 from the Faluns sensu lato (reversed), c: MNHN FS 29 from the Faluns sensu lato, d: Coll. Gain 7d from La Guimardière.

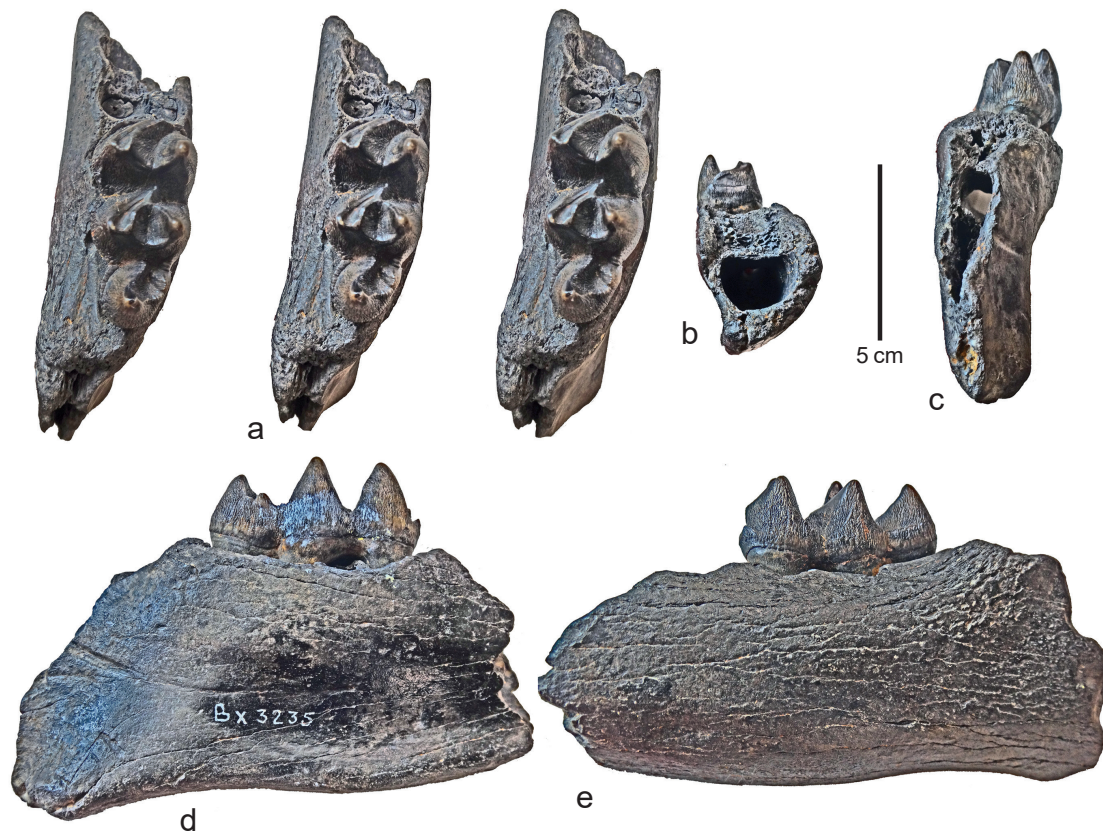
odontoblast and ameloblast complexes of the rest of the tooth unaltered. The observation that the other cusps in the tooth are of normal morphology, suggests that the anomalous tooth from La Fuye is unlikely to represent a case of inbreeding, but was probably a case of individual variation, possibly related to some event that took place during the juvenile phase of growth, and which affected only a restricted part of the odontoblast and amelogenetic system.

There is however, an upper third molar (Musée du Savignéen 98-2, 37) from La Fuye from the opposite upper jaw, which displays anomalous wear of the crown. If this tooth is from the same individual as the anomalous lower third molar then it would suggest that the dental anomaly may have been bilateral, in which case a genetic underlying cause (teratogeny) would provide a more likely explanation than a pathogenic or accidental cause.

Whatever the case, despite the dental anomaly, the associated effects of which persisted into adulthood (enlarged and lingually displaced root beneath the entoconid), the individual survived well into adulthood as shown by the moderate wear stage of the third molar.

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Text-fig. 19. Coll. Sinturet Bx 3235, left mandible fragment containing m/3 of a young adult *Brachyodus onoideus* from Les Billeaux. a: stereo occlusal views, b: anterior view to show the large mandibular canal, c: posterior view, d: lingual view, e: buccal view. Scale bar = 5 cm.

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