Diamantochloris mandible from the Ypresian/Lutetian of Namibia

Martin PICKFORD

Sorbonne Universités – CR2P, MNHN, CNRS, UPMC – Paris VI, 8 rue Buffon, 75005, Paris
(martin.pickford@mnhn.fr)

Abstract: The Black Crow limestone has yielded a fragment of lower jaw of the primitive chrysochlorid, *Diamantochloris inconcessus*, containing four teeth. The mandibular ramus shows a suite of morphological features that link it with tenrecids but it possesses some derived characters of the mandible and teeth which indicate that it belongs to Chrysochloridae (golden moles), thereby indicating a close phylogenetic relationship between these two groups of afrotheres. A damaged maxilla is attributed to this species. A lower molar from Black Crow, similar in morphology to the holotype m/3 but of considerably smaller dimensions, probably represents a second genus of chrysochlorid.

Key words: Chrysochloridae; Afrotheria; Ypresian/Lutetian; Namibia; Mandible; Maxilla; Audition; Vocalisation.

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Introduction

The freshwater limestone at Black Crow is a rich source of information about Eocene mammals of Africa. Although fossils tend to be scattered and rather rare, some of them are remarkably complete and thus throw a great deal of light on the groups to which they belong. A taxon hitherto poorly represented at the site is *Diamantochloris inconcessus*, a primitive chrysochlorid in which the lower molars possess large talonids which suggest affinities with tenrecoids. The limestone recently yielded a partial mandible with four teeth which reveals that the ramus of this species shares some features with tenrecoids but already shows modifications of the dento-gnathic complex of the kind found in chrysochlorids related to the presence of a hyoid-dentary articulation and as such appears to be derived in the direction of later chrysochlorids. The rear of the right mandible from Black Crow is bent medially and twisted slightly clockwise, unlike the straight almost vertical ramus that occurs in tenrecoids, but similar to that of Late Eocene *Namachloris* and Miocene to Quaternary and extant chrysochlorids. In addition the trigonids of the lower molars are mesio-distally compressed like those of Late Eocene, Miocene and extant chrysochlorids and when the jaws are closed, they slot into the spaces between the upper molar protocones. Some maxillary fragments and isolated upper molars from Black Crow are provisionally attributed to the species.

There is an isolated lower molar from Black Crow which belongs to a much smaller chrysochlorid, probably representing an undescribed genus, meaning that by the Ypresian/Lutetian, there was already an unsuspected high diversity of chrysochlorids in southwestern Africa.

Material and Methods

Limestone blocks from Black Crow were dissolved in 7% formic acid without buffer, as explained by Pickford (2018a). The mandible was photographed with a Sony Cybershot Camera with its eyepiece placed over the lenses of a stereo microscope. Surface scans were performed on some of the specimens. Measurements were taken with sliding calipers and calculated from figures in which the scale was superposed on the specimen. Fossils are curated at the National Earth Science Museum at the Geological Survey of Namibia.

Geological and faunal context

The geological context of the Black Crow Carbonate has been described on several occasions (Pickford 2015a, 2018a; Pickford *et al*. 2008a, 2008b). The presence of a primitive paramyid-like rodent (Mein & Pickford 2018) and two species of zegdoumyids (Pickford 2018a) allied to the apparent absence of phiomyids and ctenohystricans in the deposits indicates an age earlier than any of the Fayum (Egypt) deposits. The primitive morphology of the arsinoithere from Black Crow (*Namatherium*) and the hyracoid *Namahyrax*, trend in the same sense. Mein & Pickford (2018) suggested a correlation close to the Ypresian/Lutetian boundary (ca 47 +/- 1 Ma (Late Ypresian to Early Lutetian) (Ogg *et al*. 2016).

A primitive adapoid from Black Crow (Godinot *et al*. submitted) shows morphology which is close to that of adapids from the localities of Egerkingen (MP 14, Middle Eocene) Germany and Shanghuang, (Middle Eocene) China, inviting correlation.

Abbreviations:

BC - Black Crow (Sperrgebiet, Namibia)
CGM - Cairo Geological Museum, Egypt
DPC - Duke Primate Centre, Durham, Carolina
GSN - Geological Survey of Namibia, Windhoek

Systematic Palaeontology

Order Chrysochloridea Broom 1915

Family Chrysochloridae Gray 1825

Genus and species *Diamantochloris inconcessus* Pickford 2015a

Holotype: GSN BC 17’08, right m/3 (Fig. 2).

Additional material:

GSN BC Di 1’17, right mandible with p/3-m/2 (Fig. 1).

GSN BC Di 1’16, unworn, rootless left lower molar (Figs 2, 3).

Provisional attributions:

GSN BC Di 2’16, left maxilla with P4/-M1/ (Fig. 4).
GSN BC Di 3’16, right P3/ in maxilla fragment (Fig. 4).

GSN BC Di 4’16, right M2/ (Fig. 5).
GSN BD Di 5’16, right M1/ (Fig. 5).

Description

GSN BC Di 1’17 is a right mandibular ramus containing four teeth (Fig. 1). The buccal surface of the jaw shows two prominent mental foramina in its lower third as in tenrecoids in general and as in *Namachloris arenatans* from the Bartonian of Eocliff, Namibia, and other chrysochlorids. On the basis of the position of these foramina it is deduced that the teeth in the Black Crow specimen are the p/3 to m/2. The jaw is broken across the canine alveolus, behind which is the alveolus for the p/2. None of the symphyseal surface of the jaw is preserved. In buccal view, it is noted that there is a distinct change in level of the alveolar margin from low under the premolars, to higher under the molars. In occlusal view, a slight lingual bend in the jaw is evident beneath the molars with the crowns of the molars aligned such that their distal parts are more lingually positioned than their anterior ends. This bending is partly due to an offset in the positions of the alveoli, and partly due to a slight difference in angulation between the anterior and posterior roots with the posterior root being more lingually oriented than the anterior root.

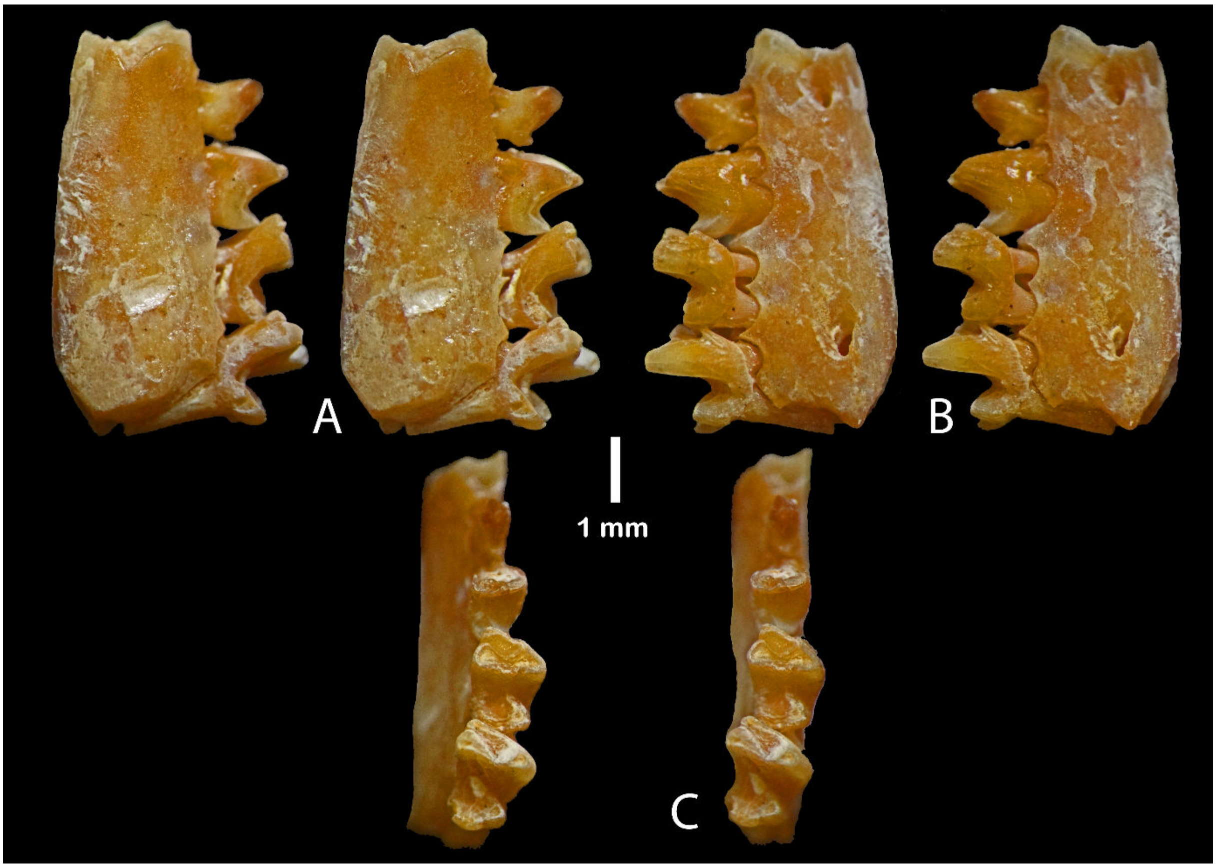

Figure 1. Stereo images of GSN BC Di 1'17, right mandibular ramus with p/3-m/2 of *Diamantochloris inconcessus* from Black Crow, Namibia. A) lingual, B) buccal, C) occlusal views (scale : 1 mm).

The p/3 has two roots, a prominent distal one, and a diminutive mesial one which slants anteriorly. The crown shows a prominent main cusp supported largely by the posterior root but leaning mesially such that its apex is above the small mesial root. There is a low, pointed posterior cusplet in the mid-line of the crown, projecting beyond the posterior root.

The p/4 is appreciably bigger than the p/3 and is supported by two large roots, the distal one somewhat larger than the mesial one. The mesial part of the crown is damaged, but the posterior part shows a tall transverse crest comprised of the protoconid and metaconid, the paraconid having sheared off. Behind the trigonid there is a low talonid, comprised of a centrally positioned hypoconid with no sign of an entoconid or hypoconulid.

The m/1 and m/2 are basically similar to each other in morphology, the m/2 being slightly larger than the m/1. The trigonid is tall, the paraconid is closely applied to the metaconid with its apex slightly below that of the metaconid. In front of the trigonid there is a sloping mesial cingulid that is lower than the talonid. The protoconid is slightly taller than the metaconid and is strongly joined to it by the post-protocristid, forming a tall transverse wall with a v-shaped profile in distal view. The pre-protocristid extends lingually towards the paraconid. The trigonid basin so enclosed is mesio-distally compressed but bucco-lingually spans about two-thirds of the breadth of the crown.

The talonid of the lower molars is well formed, but much lower than the trigonid. It is comprised of two main cusplets, a small hypoconid and a larger hypoconulid which together enclose the talonid basin. The entoconid is subtle, represented by a bulge in the pre-hypoconulid cristid. The pre-hypocristid (cristid obliquid) extends from the apex of the hypoconid towards the midline of the tooth, terminating at the base of the distal wall of the trigonid, thereby forming a distinct buccal sinusid (hypoflexid) between it and the posterior surface of the trigonid. The pre-entocristid runs mesio-lingually but stops short of the trigonid, leaving the lingual spout of the talonid basin wide open. Distally, there is a low incision between the hypoconid and hypoconulid slightly to the buccal side of the midline of the tooth and there is a narrowing of the pre-hypoconulid cristid in front of which is the subtle entoconid.

The radicular system in this jaw warrants close examination. The teeth each have two roots with sub-circular sections. In the premolars the roots are almost directly beneath the cusps and slant slightly anteriorly, but in the molars the roots are displaced slightly lingually and come to underlie the paraconid, and they curve gently lingually and slightly distally, more so in the m/2 than in the m/1. The isolated m/3 shows the distal root slanting lingually, distally and slightly curved as well. Not only do the molar roots slant lingually, but the crowns also curve lingually in the tooth row. This curvature of the posterior molars is not due to mal-positioning of the teeth in their alveoli, but is due to a convergence of the posterior parts of the left and right rami relative to the anterior part which contains the premolars. A similar bend in the mandible at the rear of p/4 occurs in *Namachloris arenatans* from the Bartonian limestones at Eocliff and functionally it appears to be linked with the ventral bending of the ramus and angle of the jaw, which thereby brings the angle of the jaw close to the bullae of the skull as well as to the hyoid apparatus. In *Diamantochloris*, however, the posterior and lingual bending of the ramus beneath the molars is in a relatively nascent phase, not as markedly developed as it is in Eocene *Namachloris* (Pickford 2015b) or Pliocene to extant *Chrysochloris* (Asher & Avery 2010).

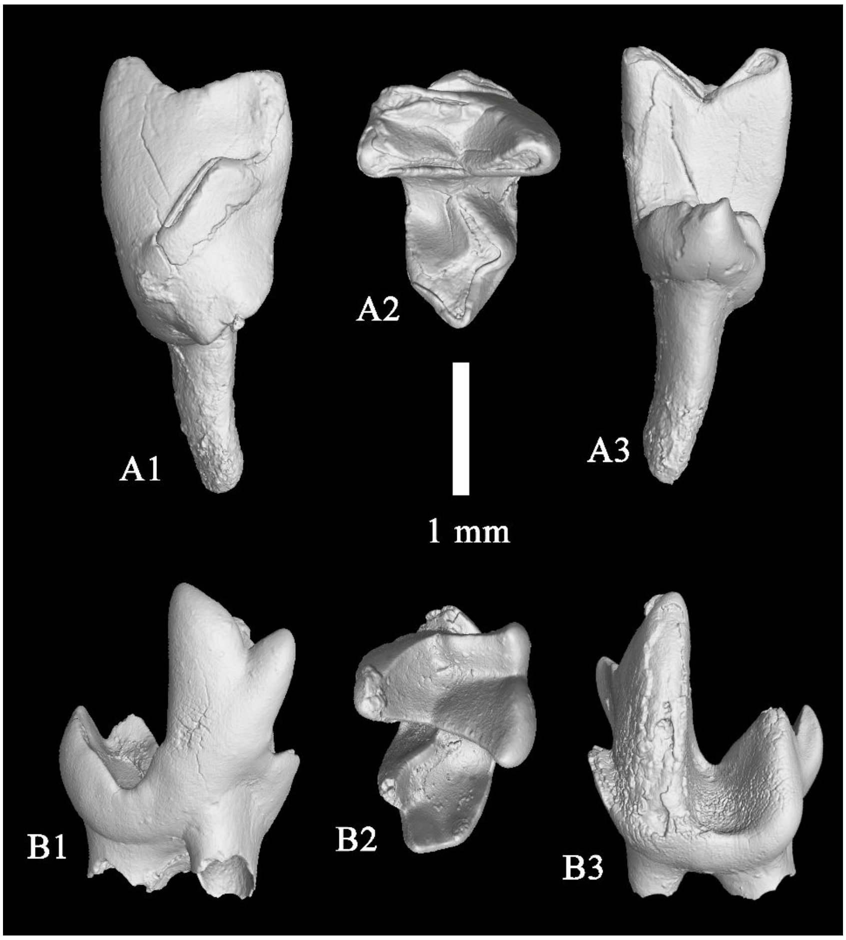

Figure 2. Digital surface images of lower molars of *Diamantochloris inconcessus* from Black Crow, Namibia. A) GSN BC 17’08, holotype right m/3 (A1 - mesial, A2 - occlusal and A3 - distal views); B) GSN BC Di 1’16, unerupted left lower molar (B1 - lingual, B2 - occlusal, B3 - buccal views). Note the offset between the mesial and distal root bases in B1 (scale : 1 mm).

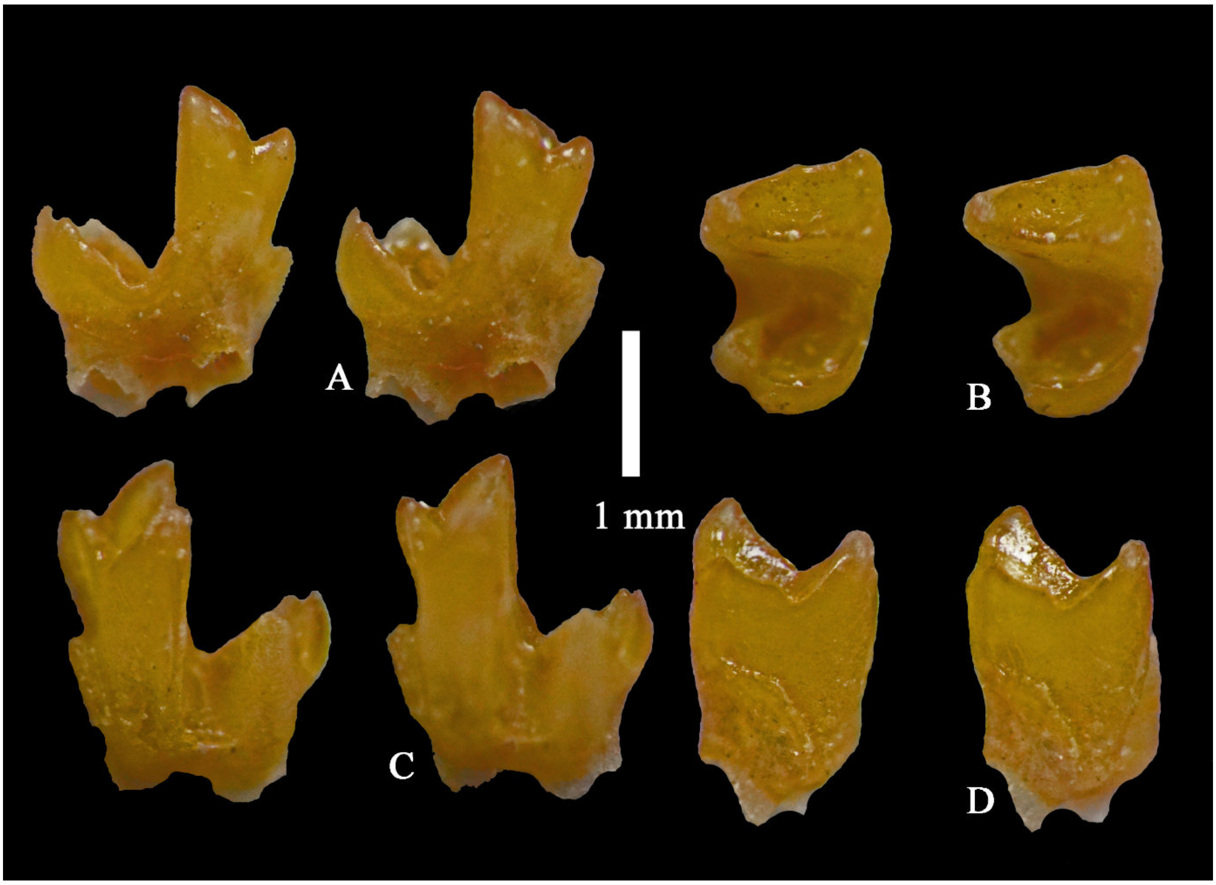

Figure 3. GSN BC Di 1’16, unworn left lower molar of *Diamantochloris inconcessus* from Black Crow, Namibia. Stereo views, A) lingual, B) occlusal, C) buccal, D) mesial (scale : 1 mm).

Table 1. Measurements (in mm) of the teeth of *Diamantochloris inconcessus* and other chrysochlorid specimens from Black Crow, Namibia.

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
GSN BC Di 1’16	p/3 right	0.94	0.46
GSN BC Di 1’16	p/4 right	1.42	0.91
GSN BC Di 1’16	m/1 right	1.67	1.14
GSN BC Di 1’16	m/2 right	1.81	1.29
GSN BC 17’08	m/3 right	2.09	1.39
GSN BC Di 2’17	m/2 left	1.00	0.67
GSN BC Di 2’16	P4/ left	1.21	1.22
GSN BC Di 2’16	M1/ left	--	1.46
GSN BC Di 3’16	P3/ right	1.22	1.08

GSN BC Di 2’16 is a fragment of left maxilla containing the P4/ and a damaged M1/. GSN BC Di 2’16 is a fragment of right maxilla containing P3/. These specimens are provisionally attributed to *Diamantochloris inconcessus* on the basis of their dimensions and dental morphology, but until associated remains are found, there will persist some doubt about their identification. However, the basic layout of the cusps in the P3/ and P4/ recalls that of *Namachloris arenatans*, but the latter species is smaller and has the cusps more mesio-distally compressed and with sharper crests than in *Diamantochloris*.

The P3/ has a dune-shaped protocone, with prominent pre- and post-cristae extending lingually to the base of the paracone. It is supported on a strong root. The paracone is twice as tall as the protocone and has a weak to absent pre-crista but a well-formed post-crista which curls buccally towards the mesostyle, from which it is separated by a shallow depression. The parastyle is low but reasonably large and anteriorly pointed, and its cervix is lower than the cervix beneath the paracone and mesostyle. There is a low but sharp buccal cingular ridge extending between the mesostyle and the base of the paracone, which borders a shallow buccal depression behind the paracone.

The P4/ has a pointed protocone with a somewhat swollen pre-crista with a bulge running lingually towards the anterior base of the paracone. There is a small hypocone separated from the base of the protocone by a depression. The low hypocone has short cristae running lingually and buccally but stopping short of the paracone. The paracone is twice as tall as the protocone, and it has a curved blade-like post-crista but no pre-crista. There is a prominent parastyle with a pointed apex which has two cristae, a long one extending distally towards a style at the base of the paracone, and thence onwards to the mesostyle, and onwards towards the point where the post-paracrista joins the post-parastyle crest, and a short one that reaches disto-lingually to join the pre-protocrista at the antero-lingual base of the paracone, forming an open oblique angle of ca 110°. The blade-like posterior half of the paracone forms an open angle with the protocone-hypocone complex which is about half the mesio-distal length of the buccal part of the crown.

The M1/ is damaged, but it shows a mesio-distally compressed protocone which is narrower than that in the P4/. The pre-protocrista has a bulge at the base of the protocone, and it then extends almost straight buccally as far as the parastyle which curves a small amount mesially. The post-hypocrista has a bulge to the bucco-distal side of the protocone, resembling a hypocone, but not detached from the protocone as it is in the P4/. Between the pre-protocrista and the post-hypocrista, there is a dune-shaped basin, bordered buccally by the base of the paracone. The pre-paracrista is well-developed and reaches the parastyle, forming a short parastylar hook. The metacone and style of the M1/ have sheared off, but part of the supporting root is preserved which indicates that the metacone was probably a well-formed cusp.

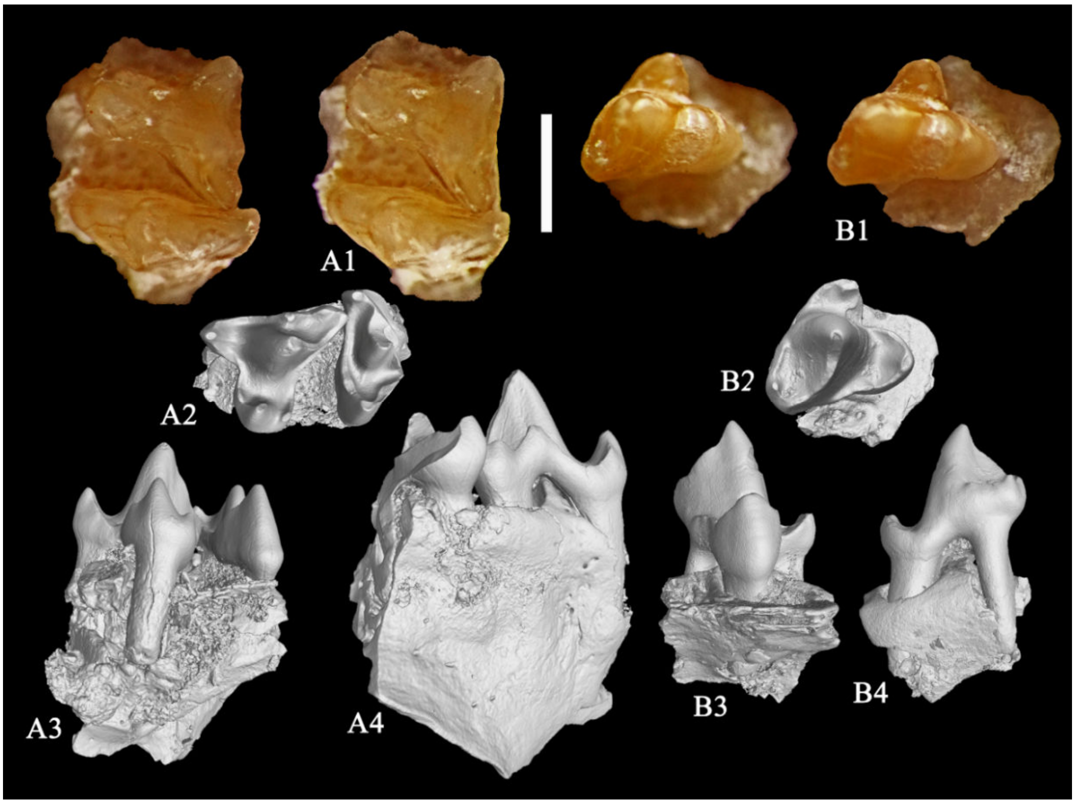

Figure 4. Maxillary specimens from the Ypresian/Lutetian limestone at Black Crow, Namibia, tentatively attributed to *Diamantochloris inconcessus*. A) GSN BC Di 2'16, left maxilla with P4/ and M1/ (A1 - stereo occlusal view, A2 - occlusal view (mesial to left), A3 - lingual view, A4 - buccal view) ; B) GSN BC Di 3'16, right maxilla fragment containing P3/ (B1 - stereo occlusal view, B2 - occlusal view, B3 - lingual view, B4 - buccal view) (scale : 1 mm).

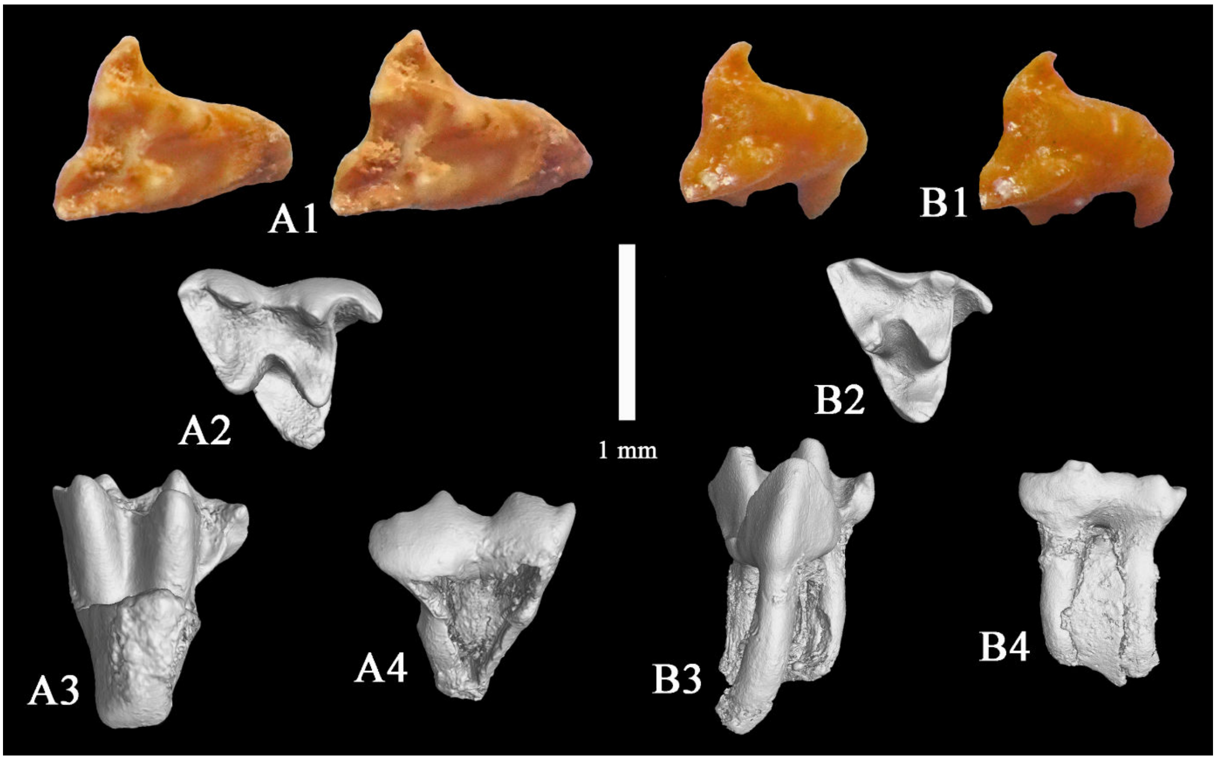

Figure 5. Upper molars from the Ypresian/Lutetian limestone at Black Crow, Namibia, tentatively attributed to *Diamantochloris inconcessus*. A) GSN BC Di 4'16, right M2/ (A1 - stereo occlusal view, A2 - oblique bucco-occlusal view (mesial to right), A3 - oblique lingual view, A4 - oblique buccal view) ; B) GSN BC Di 5'16, right M1/ (B1 - stereo occlusal view, B2 – oblique bucco-occlusal view (mesial to right), B3 - lingual view, B4 - buccal view) (scale : 1 mm).

Two isolated upper molars from Black Crow are tentatively attributed to *Diamantochloris inconcessus* on the basis of their dimensions, their moderately mesio-distally compressed protocones which are supported by a relatively robust root and by the fact that they were dissolved from the same blocks of limestone as other fossils of the species.

The teeth have a prominent parastylar hook as in the younger, Bartonian, species *Namachloris arenatans*. The pre-protocrista extends along the mesial edge of the tooth forming a cingulum which reaches the base of the parastylar hook. The parastyle is separated from the parastylar hook by a thinning of the buccal cingulum, but it is joined to the paracone by a blade-like pre-paracrista. The metastyle is distinct, and there is a small, low post-metastyle crista. The paracone and metacone are large and are well-separated from each other. The metacone is smaller than the paracone, but it is not as reduced as it is in *Namachloris*.

The overall morphology of these upper molars from Black Crow is tenrecoid, but the slight compression of the protocones indicates that there would have been a large space between neighbouring protocones into which would slot the mesio-distally compressed trigonids of the lower molars. As such, the molars are compatible with a primitive chrysochlorid, but confidence in this inference requires the discovery of associated mandibles and maxillae.

Genus and species indeterminate

Material : GSN BC Di 2'17, left m/2 (Fig. 6).

Description and comments

An isolated lower molar with both roots, GSN BC Di 2'17, shows light wear at the apices of the trigonid and the talonid. The roots slant at a steep angle lingually but the posterior one does not slant markedly distally, on which basis the tooth is considered to be an m/2 rather than an m/3 or m/1.

The basic morphology of the crown is similar to that of *Diamantochloris inconcessus*, the only obvious difference from this species being the presence of a relatively broader talonid comprised of three cusplets instead of two. In this tooth, the entoconid is clearly differentiated from the hypoconulid whereas in *Diamantochloris* it is subtle, being barely more than a bulge in the pre-hypoconulid cristid. The trigonid morphology of this small tooth is similar to that of *Diamantochloris* but with the cristids that extend between the protoconid and paraconid forming a deeper v-shaped profile. The mesial cingulum slants steeply from its base on the mesio-buccal part of the cervix upwards towards the paraconid before bending downwards again at half the height of the crown, as in *Diamantochloris*.

It is concluded that this tooth represents a second, smaller taxon of Chrysochloridae at Black Crow, the dimensions of which would have been in the ratio of ca 1.8-1.0 with *Diamantochloris*, based on linear measurements of the m/2. The differences in talonid morphology and the form of the v-shaped profile on the posterior wall of the trigonid suggest that the tooth represents a genus distinct from *Diamantochloris*, but we refrain from naming one in the hope of discovering more substantial fossils.

An alternative possibility for this molar is that it might represent a deciduous tooth, but the strength of the roots indicates that this is unlikely to be the case. More probable is the hypothesis that there are two genera of chrysochlorids at Black Crow.

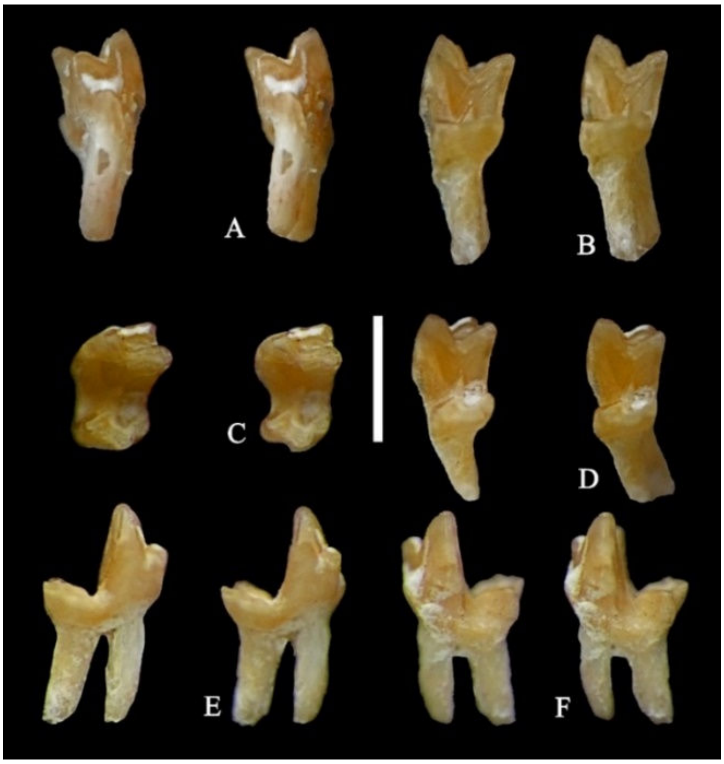

Figure 6. Stereo images of GSN BC Di 2’17, left lower molar of a small species of chrysochlorid, different from *Diamantochloris inconcessus*. A) mesial, B) distal, C) occlusal, D) oblique distal, E) lingual, and F) buccal views (scale : 1 mm).

Discussion

The holotype of *Diamantochloris inconcessus* was tentatively thought to be a lower third molar by Pickford (2015a) but, being an isolated tooth, there was some doubt about its meristic position. The new mandible from Black Crow resolves the issue, because it is clear that in lateral view, the root beneath the talonid is almost vertical in m/1 and m/2, whereas the posterior root in the holotype tooth slants distinctly distally, indicating that it is the last tooth in the tooth row.

The new mandible is slightly bent at the junction between the premolars and molars, and there is an offset in the level of the alveolar margin on the buccal side of the jaw, with the premolar alveoli being lower than that of the molars (Fig. 7).

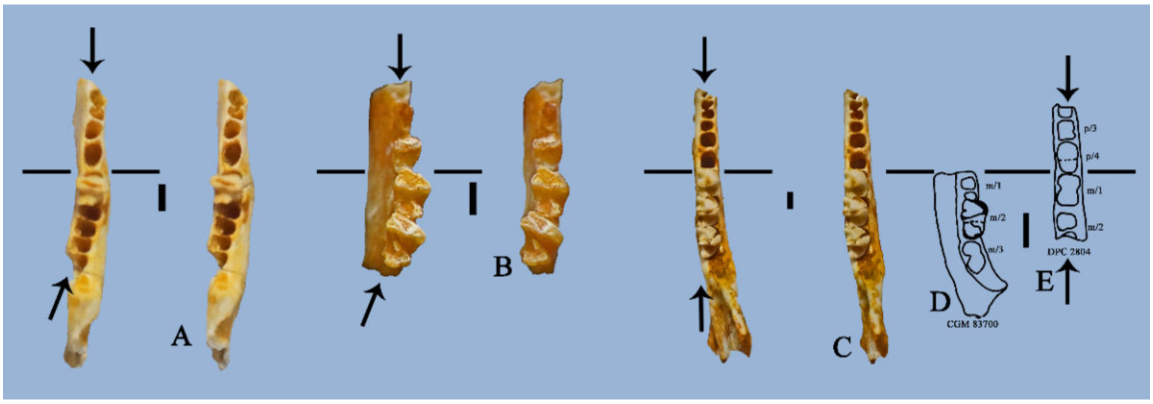

Figure 7. Comparison of right mandibles of primitive chrysochlorids and tenrecoids (A - GSN EC Na 5.2, *Namachloris arenatans* Pickford 2015b, left mandible (reversed); B - GSN BC Di 1'17, *Diamantochloris inconcessus*; C - GSN Ng 13, *Namagale grandis* Pickford, 2015c ; D - CGM 83700, *Eochrysochloris tribosphenus* Seiffert *et al*. 2007, left mandible (reversed); E - DPC 2804, *Eochrysochloris tribosphenus* with tooth positions as interpreted by Seiffert *et al*. 2007). Arrows indicate the bend in the mandible at the level of m/1 (horizontal lines) in chrysochlorids and the straight mandible in tenrecoids (D and E drawn from images in Seiffert *et al*. 2007) (scales : 1 mm).

The combination of the bend in the mandible and the lingual positioning of the molar roots means that in occlusal view the molar crowns appear to be twisted in the jaw.

Examination of the mandible and roots as a funtional ensemble, rather than visualising them as separate disconnected elements, suggests that the rear of the jaw in *Diamantochloris* has undergone reorganisation that implicates not just the mandible but also the teeth. Although the mandible from Black Crow is broken behind the m/2, it appears that the reorganisation of the dento-gnathic system would bring the angle of the jaw closer to the bullae in the skull and to the hyoid apparatus in the neck than would be the case had there been no mandibular bending or longitudinal twisting. The fact not only that the jaw is bent, but also that the dental roots have been reoriented, suggests that *Diamantochloris* had evolved a longitudinally twisted lower jaw which brings the angular process of the jaw close to the bullae and the hyoid, much as in extant chrysochlorids.

The somewhat younger genus *Namachloris* from the Bartonian of Eocliff, Namibia, possesses a similarly twisted posterior part of the mandible as well as a posteriorly elongated angular process with a thickened ventral margin, from which it was concluded that, like extant golden moles (Bronner *et al*. 1990) this genus had articulation between the hyoid and the mandible (Figs 7, 9). Although the evidence for *Diamantochloris* is slender, what little that is available suggests that it too may have possessed a hyoid-dentary articulation.

The mesio-distally compressed trigonid in the lower molars of *Diamantochloris* permits the trigonids to slot neatly between the gaps between the protocones of the upper molars, again as in extant chrysochlorids and *Namachloris* from the Bartonian of Namibia.

Apart from these derived modifications, the available remains of *Diamantochloris inconcessus* reveal that it is remarkably primitive within a chrysochlorid context, exhibiting a significant quantity of tenrecoid-like aspects such as well-developed bicuspid talonids in the lower molars, dilambdodont upper molars and two prominent mental foramina in the mandible. Other chrysochlorids tend to diminish the posterior mental foramen (the one associated with the m/1) (still present but small in Bartonian *Namachloris*), or even to suppress it as in some extant golden moles (Asher & Avery 2010).

Finally, it is noted that the genus *Eochrysochloris* from the Fayum, Egypt (Seiffert *et al*. 2007, fig. 5, CGM 83700, holotype left mandible with m/2; DPC 2804, right mandible with one tooth and the stub of a second) has a straight mandible (Fig. 7) as in tenrecs, and not a bent and twisted one as in chrysochlorids. Indeed, in the holotype of the species *Eochrysochloris tribosphenus*, the roots of the m/3 are slightly buccally positioned. Furthermore, the paraconid of the lower molar trigonid is not reduced and is well-separated from the metaconid, as in tenrecs, unlike the reduced paraconid and mesio-distally compressed trigonid that is characteristic of chrysochlorids. From this it is concluded that *Eochrysochloris* is not a chrysochlorid but is more likely to be a tenrecid, as already discussed by Pickford (2015b, 2015c).

If this so, then it is possible that the tooth in DPC 2804, identified as the p/4 by Seiffert *et al*. (2007) is in reality the m/1, because in the three genera of tenrecoids from the Bartonian of Eocliff described by Pickford (2015c) (*Namagale*, *Arenagale*, *Sperrgale*) the posterior mental foramen is located beneath the middle of the m/1, as it is in the Fayum genus *Dilambdogale gheerbranti* Seiffert (2010) and the much younger Early Miocene *Promicrogale* from Elisabethfeld, Namibia (Pickford 2018b) *Protenrec tricuspis* Butler & Hopwood (1957) from East Africa and *Protenrec butleri* Mein & Pickford (2008) from Arrisdrift, Namibia, as well as the older primitive chrysochlorids *Diamantochloris* and *Namachloris*. The position of the distal mental foramen beneath the m/1 presumably represents a primitive condition shared by tenrecs and golden moles. Extant tenrecs (eg *Tenrec ecaudatus*, *Microgale thomasi*, *Microgale brevicaudata*, *Microgale cowani* and others) also have the posterior mental foramen beneath the m/1 (Asher & Lehman 2008; MacPhee 1987; Tabuce *et al*. 2008).

A final possibility that needs consideration is that, if the tooth in DPC 2804 really is the p/4, then *Eochrysochloris* is probably neither a tenrecid nor a chrysochlorid but possibly represents another order of mammals.

Cranial Architecture in Golden Moles

Chrysochloridae are peculiar among mammals in a number of cranial features (Bronner *et al*. 1990; Broom 1915, 1916). As concerns the mandible, there are several peculiarities, especially in the parts posterior to the premolar row (Asher & Avery 2010; Bronner *et al*. 1990; Pickford 2015b). The scale of these cranial peculiarities prompted Broom (1915) to classify the golden moles in their own order Chrysochloridea.

Whilst many of the morphological details of the cranium have been described in depth, there has been relatively little written about the functional aspects of such a specialised cranial architecture, except to link it generally to a subterranean lifestyle which requires whole-head movements during burrowing, or to the development of a specialised way of processing food items such as worms and termites, accenting tongue movements with strong musculature linked to the hyoid (Bronner *et al*. 1990). However, even though the scenario of a strong hyoid-tongue link has some merits, it does not explain why the mandible and hyoid would have developed an articular relationship, which is unique among mammals (Figs 8, 9).

The uniqueness of the morphological cranio-dental complex of chrysochlorids indicates that palaeontologists need to search for an unsuspected, alternative explanation of the selection pressures that led to all aspects of its evolution, outside the usual suite of scenarios concerning audition, mastication, locomotion, communication with conspecifics and detection of prey, all of which have been proposed in the past, but none of which account for the unique morphology as an ensemble.

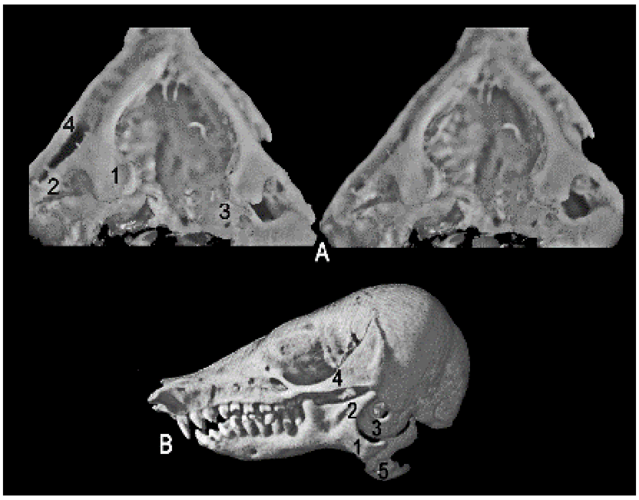

Figure 8. Oblique stereo basicranial and left lateral views of the skull of extant *Chrysochloris* highlighting aspects of the architecture of the angular process of the mandible and its spatial relationships with the bullae and hyoids (1 - angular process of the mandible, 2 - condylar process of the mandible, 3 - bulla, 4 - zygomatic arch, 5 - hyoid apparatus). Note how the angular process of the mandible twists medially and comes into proximity with the bulla, almost hiding it in basal view, whereas the condylar process of the mandible is located in an extremely lateral position. Note the hyoid apparatus beneath the bulla close to the angular process of the mandible.

The observation that the mandibular architecture in *Chrysochloris* brings the posteriorly elongated angular process close to the bullae and the hyoid apparatus invites a correlation with hearing and vocalisation, perhaps some element of bone-conduction of sounds transmitted via the jaws and teeth towards the bulla, although this explanation was rejected by Bronner *et al*. (1990).

There could be other explanations for this architectural relationship which have little or nothing to do with audition. The condylar process of the mandible is in a very lateral position, mainly because the temporo-mandibular joint is itself in a lateral position due to posterior broadening of the neurocranium, meaning that the twisting of the rear half of the mandible, which is necessary to place the condylar process in a lateral conformation, would automatically result in a medial position of the angular process.

But this explanation does not account for the posterior elongation of the angular process of the mandible nor of the thickening of its ventral margin, nor of its articulation with the hyoid. Thus in chrysochlorids, there seem to be two structuro-functional components which have modified the rear half of the mandible : a first one twisting the ramus such that the condylar process lies in a very lateral position, combined with a second component comprising elongation of the angular process and the thickening of its ventral margin. It is the latter modification that results in the development of a hyoid-dentary articulation, chrysochlorids being the only mammals known to possess such a condition.

From this it is inferred that the bend in the mandible of *Diamantochloris* at the junction between the premolar and molar rows, indicates that this genus may have been endowed with a hyoid-mandible articulation. However, more completely preserved fossils are required to confirm or falsify this inference.

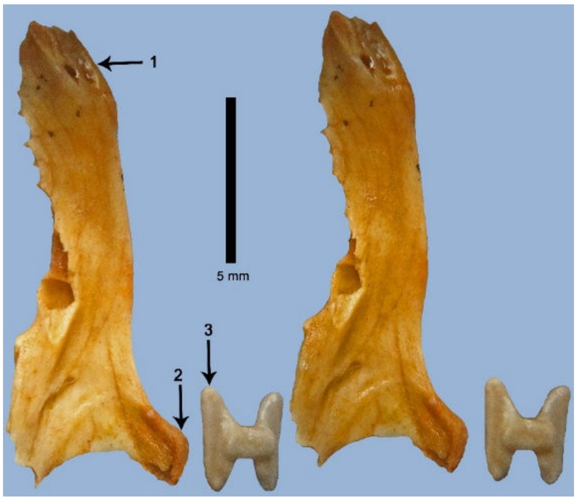

Figure 9. *Namachloris arenatans* from the Bartonian of Eocliff, Namibia. Stereo views of GSN Na 101, edentulous left mandible and an « H »-shaped bone presumed to be the hyoid (1 - unfused symphyseal area of the mandible, 2 - posteriorly elongated angular process of the mandible with a thickened margin for articulation with the hyoid, 3 - stylohyal bone fused to its opposite number in the midline, with a well-developed 'sliding' articulation surface (arrowed)). Note the longitudinal twist in the mandible which starts at the level of the rear of p/4 (scale : 5 mm).

The development of a sliding articulation between the angular process of the mandible and the hyoid could be related to fore-and-aft movements of the base of the tongue during maceration of food, as proposed by Bronner *et al*. (1990) (Fig. 10). For such a system to be as efficient as possible, the mandibular component would need to be stable, forming a relatively immobile base along which the hyoid moves back and forth with little if any lateral, medial or rotational component of movement. One way of achieving this stability would be for the upper and lower molars to slot between each other when the jaws are closed thereby preventing or limiting fore-and-aft movements of the jaw - the tall trigonids of the lower molars slot into the gaps between successive protocones of the upper molars rendering the ensemble immobile to fore-and-aft movements. Such a conformation of the tooth rows is present in a nascent form in *Diamantochloris*, is in an advanced stage of development in *Namachloris*, and is taken to extremes in extant chrysochlorids. If this is so, then it is probable that *Diamantochloris* used its tongue to macerate its food, or most of its food.

A further possible explanation for the presence of a hyoid-dentary articulation relates to the proximity between the hyoid and the larynx. To my knowledge, no-one has proposed that the hyoid-dentary articulation could be related to the transmission of sound. The whole head can be imagined as a system for amplifying sound produced in the larynx and transmitted to the head via a series of more or less solid elements linking it to the larynx. Communicating underground presents peculiar challenges, and chrysochlorids have developed a unique apparatus for detecting sound and determining the direction from which it is coming (Mason 2003; Narins *et al*. 1997; Willi *et al*. 2006) so it is not beyond the realms of possibility that they also evolved a unique system for transmitting sound. Further research is necessary but it is reported that chrysochlorid vocalizations during courtship involves chirruping, head-bobbing and foot stamping by the male, and rasping and squealing by the female (Kuyper 1985). It would be interesting to investigate how the females make rasping sounds and whether sound production involves the teeth.

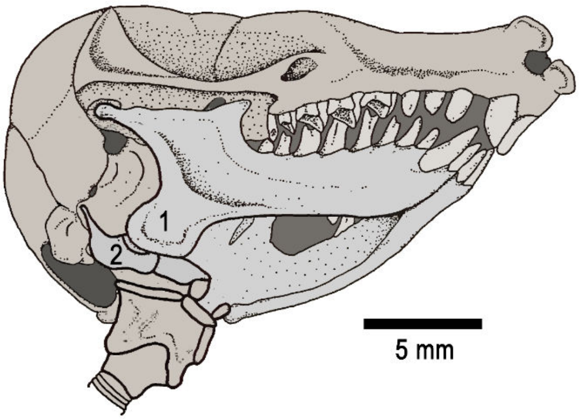

Figure 10. Oblique latero-ventral view of the head and neck of *Amblysomus julianae* Meester 1972, showing the posteriorly elongated angular process of the mandible (1) and the stylohyoid (2) with which it articulates (drawing modified from Bronner *et al*. 1990). Note the proximity between the larynx and the hyoid, and the bony links between it and the skull.

Conclusions

The chrysochlorid from Black Crow, Namibia, *Diamantochloris inconcessus*, shows several primitive traits in the dento-gnathic system which indicate close phylogenetic links with the tenrecoids. However, it possesses several characters that reveal that it is already differentiated enough from other tenrecoids for it to be classified among Chrysochloridea rather than Tenrecoidea.

Among the characters that differentiate *Diamantochloris* from tenrecoids is the reduced paraconid in the lower molars, which is closely applied to the metaconid, a combination which has reduced the mesio-distal dimensions of the trigonid basin to a marked degree, as in fully derived chrysochlorids such as *Namachloris* from the Bartonian of Namibia (Pickford 2015b) and later forms. Another feature is the presence of a bend in the mandible at the level of the p/4-m/1 which carries the molar row into a lingual position relative to the premolar row while a longitudinal twist shifts the condyle laterally and the angular process medially, a reorganisation of the lower jaw typical of chrysochlorids in which a hyoid-mandible articulation is present, and markedly different from tenrecoids which have straight mandibular rami which are almost vertical throughout their post-canine extent.

Namachloris from the Bartonian of Eocliff possessed a posteriorly elongated angular process of the mandible with a thickened ventral margin (Fig. 9) implying articulation with the hyoid (Pickford 2015b) and it possessed a fully developed seismic sensing apparatus (Mason *et al*. 2017).

The evidence from the mandible of *Diamantochloris* indicates that by the Ypresian/Lutetian, some 10 million years earlier than Eocliff, primitive chrysochlorids were probably already engaged in sensing seismic vibrations via modified dental, mandibular, hyoidal, tympanic and inner ear apparati.

Finally, the possible presence of a second genus of chrysochlorid at Black Crow suggests that the dichotomy between chrysochlorids and tenrecoids may have occurred during the Ypresian, if not earlier.

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