Fig. 14. *Ronzotherium filholi* (Osborn, 1900), senior synonym of *R. kochi* Kretzoi, 1940, from Valea Popii, Cluj-Napoca (earliest Oligocene, Romania). Right maxilla MBT 1509 with P2–M3. **A**. Occlusal view. **B**. Drawing of P2–M3. **C**. Maxilla in lateral view. **D**. Maxilla in medial view. Scale bar: 2 cm.

side, the lunate and unciform facets are fused and form a unique L-shaped facet, occupying all the anterolateral part of the proximal apophysis. Distally, it contacts the distal facet for the McIII. This latter is very concave anteroposteriorly. The posterior tuberosity is very short and curved. In medial view, the distal McII facet and the medial facet for the trapezoid are almost in the same plane; they are only distinguished by a very low ridge, and there is no indentation separating them. The McII facet is flat. The trapezoid facet is large and widely connected to the proximal magnum facet.

Cuboid. The cuboid NMB-QE-362 is perfectly preserved (Fig. 13T–X). In proximal view, the posterior apophysis is almost not visible. The proximal articulation is oval-shaped, and the two surfaces for the astragalus and calcaneus are very poorly distinguished. It is very concave anteroposteriorly and very high at the posterior end. The proximal border of the anterior side is oblique, the distal one is slightly convex while the medial and lateral borders are irregular and are crossed by median grooves. The lateral one is much wider than the medial one and isolates the posterior apophysis. On the medial side, the anterodistal facet for the ectocuneiform is large and anteroposteriorly elongated. The postero-proximal facet for the navicular is very large, concave and bears a thin anterior extension below the proximal articulation. The small and rectangular posterior surface for the ectocuneiform is located almost perpendicular to the postero-distal border of this navicular surface. The distal articulation for the MtIV is a triangular-shaped lozenge and is deeper than wide.

Remark

Ronzotherium filholi is also known from other localities, notably in Villebramar and Bournoncle-Saint-Pierre, where specimens are rather well-preserved. It is found at several localities of South-Germany (e.g., Möhren, Burgmagerbein or Ronheim; Uhlig 1999a), but only by scarce remains. We also consider *R. kochi* from Cluj-Napoca (Fig. 14) as a junior synonym of *R. filholi*. All the material from Villebramar has already been fully described by Brunet (1979) so it will not be described again here. The locality of Villebramar provided by far the broadest sample for *R. filholi*, including a complete skull, several hemimandibles and numerous postcranial remains.

Ronzotherium romani Kretzoi, 1940
Figs 15–21

Ronzotherium romani Kretzoi, 1940: 91.
Hypsolophiodon csobánkanus Kretzoi, 1940: 94–95, fig. 6.
? *Praeaceratherium kerschneri* Spillmann, 1969: 241–253, figs 4 (bottom), 6, 13 (left), 15, pls XX–XXII.
Diaceratherium massiliae Ménouret & Guérin, 2009: 314–323, figs 10, 12a, 13a, b?, c–e, 14a?, 15a, 16a.

Acerotherium filholi – Roman 1910: 1559 (from La Ferté Aleps = La Ferté-Alais, La Comberatière and Marseille); 1912a: 55–56, fig. 17, pl. V–3.
Ronzotherium filholi – Bonis 1969: 1–8, pls 1–2. — Ginsburg 1969: 1267.
Ronzotherium velaunum – Heissig 1969: 20–36, figs 5, 6d, 7, 8d–g, 9c, 10c–d (from St-André, St-Henri, Marseille and Les Milles).
? *Ronzotherium filholi elongatum* – Heissig 1969: 47, 53, 82 (from Cournon).
Ronzotherium filholi romani – Heissig 1969: 55–90, figs 20–24, 26c–d, pls 1–3, 4(13).
Ronzotherium romani – Brunet 1979: 155, figs 7a, 9b, d, 10b, pls XVIb–n, XIXg–l, o–p (from Ferté-Alais, Etampes, Gaimersheim). — Brunet *et al*. 1981: 349. — Ginsburg & Hugueney 1987. — Ménouret & Guérin 2009: 306–314, figs 2, 7–9. — Mennecart *et al*. 2012: 166–169, fig. 3(3, 4?, 5–7, 8?, 9?) (partim). — Ménouret *et al*. 2015: 245–248, figs 4–5a–d.
Diaceratherium lamilloquense – Mennecart *et al*. 2012: 169, figs 3(10–11, 16), 4 (NMB-UM-2565) (partim).
Diaceratherium massiliae – Antoine & Becker 2013: 140. — Jame *et al*. 2019: 21.
"*Diaceratherium*" *massiliae* – Becker *et al*. 2018: 401.
"*Diaceratherium massiliae*" – Blanchon *et al*. 2018: 219.

Non *Ronzotherium filholi* – Lavocat 1951: 116, pl. 19 fig. 3, pl. 26 fig. 1 (from Vendèze).
Non *Ronzotherium romani* – Brunet 1979: 154, fig. 15, pls XVII–XVIII (from Vendèze).
Non *Ronzotherium romani* – Mennecart *et al*. 2012: fig. 4 (NMO-K3/13, NMOI10/103) (partim).

Historical diagnosis

Kretzoi (1940) did not provide any proper diagnosis when he named the species in a footnote. The only mentioned characters are that "the molars have higher crown and less forward inclined, more vertically-standing lophs" than *Ronzotherium filholi* (translated by the authors).

Emended diagnosis

The I1 is oval in cross-section and the crochet and crista are sometimes present on the upper molars. The lingual cingulum of the upper cheek teeth is usually absent. The protoloph of P2 is mostly interrupted and disconnected from the ectoloph. The posterior valley of d2 is usually open. The lingual cingulum of the lower premolars is usually absent. The radius and ulna are in contact or fused and there is a single distal contact facet. The gutter for the musculus extensor carpi is weak on the radius and the proximal ulna facets are not always separated. The trapezium facet is small on the scaphoid. The transverse diameter/height ratio of the astragalus is above 1.2 and the posterior stop on the cuboid facet is absent. The Cc1 facet of the astragalus is nearly flat. The proximal border of the anterior side of the MtIII is concave.

It differs from *R. velaunum* by the deep median constriction of the distal humeral articulation and from *R. filholi* by the absence of i1, the single-rooted d/p1, the reduced paraconid on p2 and the high posterior expansion of the scaphoid facet on the radius.

Type material

Lectotype (designated by Heissig 1969)
FRANCE • right lower i2; Essone, La Ferté-Alais; MNHN.F.OBP63.

Paralectotypes (designated by Brunet 1979)
FRANCE • 4 lower molars; same collection data as for lectotype; MNHN.F.OBP72, MNHN.F.OBP76, MNHN.F.OBP78, MNHN.F.OBP79.

Additional material
FRANCE – **La Ferté-Alais, Essone** • 1 P2; same collection data as for holotype; MNHN.F.OBP55 • 1 P4; same collection data as for holotype; MNHN.F.OBP56 • 1 lingual fragment of P4; same collection data as for holotype; MNH.F.OBP57 • 1 M1; same collection data as for holotype; MNHN.F.OBP59 • 3 M2; same collection data as for holotype; MNHN.F.OBP58, MNHN.F.OBP60, MNHN.F.OBP61 • 1 M3; same collection data as for holotype; MNHN.F.OBP62 • 1 d1; same collection data as for holotype; MNHN.F.OBP86 • 1 p2; same collection data as for holotype; MNHN.F.OBP65 • 2 p3; same collection data as for holotype; MNHN.F.OBP66, MNHN.F.OBP67 • 2 p4; same collection data as for holotype; MNHN.F.OBP68, MNHN.F.OBP69 • 6 additional lower molars excluding the paralectotypes; same collection data as for holotype; MNHN.F.OBP70, MNHN.F.OBP71, MNHN.F.OBP73, MNHN.F.OBP74, MNHN.F.OBP75, MNHN.F.OBP77. – **St-Henri/St-André/Les-Milles** • 1 complete maxilla P1-M2 (left) and P1-M3 (right) with subcomplete mandible with p2–m3 (left) and p3-m3 (right); FSL-8547 • 1 fragment of right maxilla with P1–3; FSL-520275 (not found in collection) • 1 left I1; FSL-8835 • 2 right I2 and 1 left I2, with the same inventory number; NMB-Mar-354a (not found in collection) • 1 left i2; FSL-9445 (not found in collection) • 2 right I2; FSL-9524 (not found in collection) and FSL-9448 • 1 right P1; FSL-9519 • 1 right D3; FSL-8557 • 1 left D4; FSL-9530 • 1 right P2; FSL-8834 • 1 left P2; FSL-8833 • 1 left P3; FSL-8832 • 1 right P4; NMB-Mar-844 • 2 left M3; FSL-8828, NMB-Mar-862 • 2 right M3; FSL-520290 (not found in collection), NMB-Mar-862 • 1 subcomplete mandible with p3–m3 (right) and p2–4 and m2–3 (left); FSL-8545 • 1 right hemimandible with p3–m3; NMB-Mar-843, NMB-Mar-861 • 3 i2; NMB-Mar-862 (right and left), FSL-9524 • 1 d1; FSL-9521 • 2 rows with d2–3; FSL-9520, FSL-9518 (right), FSL-9517, unnumbered specimen (possibly FSL-9519?) (left) • 1 left p3; FSL-8831 • 1 right P4; FSL-520277

(not found in collection) • 1 right m1/2; FSL-520277 (not found in collection) • 3 left m2; FSL-8827 (not found in collection), FSL-8829 (not found in collection), FSL-8830 • 1 right m2; FSL-520278 (not found in collection) • 1 right m3; NMB-Mar-1 • 1 left scapula; AIX.1979-2 • 1 distal humerus; FSL-9523 • 1 radius in two fragments; FSL-520279, FSL-520280 • 1 scaphoid; FSL-520285 • 2 trapezoids; FSL-9501, FSL-520283 • 2 unciforms; FSL-520289, FSL-520282 • 1 unciform; NMB-Mar-865 • 1 left McIII; UPM 13667 • 2 fragments of McIII; FSL-9505, FSL-520281 • 1 McIV; NMB-Mar-863 • 1 proximal fragment of McIV; NMB-Mar-864 • 1 McIV; FSL-520287 • 1 distal femur; NMB-Mar-828 • 1 navicular; NMB-Mar-847e • 1 cuboid; FSL-9528 • 1 cuboid; NMB-Mar-847d • 1 MtII, originally identified as a McII by Ménouret & Guérin (2009); NMB-Mar-847a • 1 MtIV; FSL-520286.

GERMANY – **Gaimersheim** • 1 axis and several fragments of vertebrae, 1 complete radius, 1 complete scaphoid and a fragmentary one, 1 partial magnum, 1 broken McIII in articulation with a well preserved McIV as well as an incomplete tibia, 1 almost complete astragalus, and all dental specimens already attributed to *R. romani* by Heissig (1969); BSPG (unnumbered) • 1 left MtIII; BSPG-1952-II.

SWITZERLAND – **Jura Canton, Poillat** • 1 fragment of squamosal; MJSN-POI-007-59 • 1 maxilla with P1–M3; MJSN-POI-007-3219 • 1 isolated I2; MJSN-POI-007-168 • 1 isolated P4; MJSN-POI-007-346 • 1 juvenile hemimandible with i2–p1–m1 and erupting m2; MJSN-POI-007-174 • 1 isolated i2; MJSN-POI-007-937 • 1 isolated p4; MJSN-POI-007-211 • 2 scapulae; MJSN-POI-007-306, MJSN-POI-007-222 • fragments of lumbar vertebra IV; MJSN-PRC-005-1 • 1 sacrum; MJSN-BEU-001-280 • 1 left femur; MJSN-POI-007-80. – **Zürich Canton, Rickenbach** • 1 D3/4; NMB-UM-971 • 1 P2; NMB-Ri-24 • 1 P4; NMO-H9-13 • 1 M1; NMB-UM-972 • 2 M1; NMO-K11/250, NMO-I12/13 • 1 M2; NMO-I12-24 • 1 M2; NMB-Ri27 • 1 maxilla fragment with P4–M1; NMB-UM-1840 • 1 maxilla fragment with M2–3 (unnumbered in SMNS collection); SMNS • 1 mandible with left and right p2–m3; NMB-UM-3832 • 1 p3; NMB-H.R.2 • 1 p4; NMO-L6/25 • 1 m1; NMB-UM-806 • 1 broken humerus; NMB-UM-973 • 1 scaphoid; NMO-I5-62 • 1 lunate; NMB-Ri-21 • 1 lunate; NMO-I7-115 • 1 pyramidal; NMO-I11-82 • 1 magnum; NMO-H10-110 • 1 McIV; NMO-I8-117 • 1 MtII; NMB-UM-2565.

The specimens from St-Henri/St-André/Les-Milles have previously been attributed to "*Diaceratherium*" *massiliae*.

Type horizon and locality

La Ferté-Alais (Essonne, France), MP24 (latest early Oligocene).

Stratigraphical distribution

?MP23 (early Oligocene) to MP30 (latest Oligocene).

Geographical distribution

France: Aubenas-les-Alpes, La Bénissons-Dieu, Brons, La Comberatière, Cournon, Étampes, Gannat?, Itteville, Pech Desse, Sainte-Quitterie, St-Henri/St-André/Les-Milles (= 'Marseille'), Vodable. Germany: Gaimersheim. Hungary: Csobánka. Switzerland: Poillat, Rickenbach, Rüfi bei Schänis.

Description

Material from the type locality

Part of this material was already described (Heissig 1969; Brunet 1979) but we provide here some short updated descriptions. Only isolated teeth are preserved from La Ferté-Alais.

Anterior dentition. The lectotype right lower i2 (MNHN.F.OBP63) is large and tusk-like (Fig. 15L–M). The root and the tip of the crown are broken, and the enamel is thin. The wear facet for the upper I1 is probably absent, either because of the absence of contact between these two teeth or because the tooth was not completely erupted if it belonged to a young individual. The transverse outline of the crown is drop-shaped, whereas the root is oval-shaped. There is a sharp mesial crest on the mesial border of the crown as well as a weaker crest on the lateral border. There is also a distomesial cingulum.

Upper cheek teeth. Seven isolated upper cheek teeth are preserved in La Ferté-Alais (Fig. 15A–E), but no upper incisors.

Upper premolars. Only P2 (MNHN.F.OBP55) and P4 (MNHN.F.OBP56) are preserved. A lingual fragment of P4 (MNH.F.OBP57) is also preserved but is not informative. The lingual cingulum is strong and continuous on upper premolars and is deeply rippled in lingual view. The labial cingulum is fainted between the paracone and metacone of P4 and completely absent on P2. Crochet and antecrochet are completely absent and there is no protocone constriction. On P2, the protocone and hypocone are separated, but they are united by a bridge at the base of the tooth. The protocone is as strong as the hypocone and the protoloph is separated from the ectoloph. The metaloph is transverse. The paracone and metacone folds are wide and strong, whereas the parastyle is rather weak. On P4, the protocone and hypocone are fused, there is no lingual groove separating them and the protoloph is L-shaped. It is only weakly connected to the ectoloph. The metaloph is weak, S-shaped, directed postero-lingually and does not join the protocone nor the metacone. It joins however the wide and shallow crista at the base of the paracone. The paracone and metacone folds are very strong and separated by a deep groove of the ectoloph. The parastyle is large and the metastyle short. The postfossette is long and narrow.

Upper molars. Five upper molars are preserved: one M1 (MNHN.F.OBP59), three M2 (MNHN.F.OBP58, MNHN.F.OBP60 and MNHN.F.OBP61) and one M3 (MNHN.F.OBP62). The upper molars have almost no lingual cingulum, except on one M2, where it is strong and continuous under the protocone. The labial cingulum is restricted to the posterior-most part of the ectoloph under the metacone. The antecrochet is strong on M1–2 but very weak on M3. There is a weak crochet on M1–2 that would disappear early with wear and the crista is always absent. There is no protocone constriction. The paracone fold is strong and the metacone fold and mesostyle are completely absent. The metaloph is long but the metastyle is quite short. There is a small hypostyle in the postfossette of M1, contiguous to the strong posterior cingulum. The posterior part of the ectoloph of M1–2 is very straight. The postfossette is deep, below the posterior cingulum. There is no lingual groove of the protocone. The ectoloph and metaloph of M3 are fused into an ectometaloph, and there is no posterior groove. It is quadrangular. The posterior cingulum is strong and continuous and the protocone is not constricted.

Lower cheek teeth. Sixteen lower cheek teeth are preserved in La Ferté-Alais, including six premolars and ten molars (Fig. 15F–K).

Lower premolars. Only one left d1 is known (MNHN.F.OBP86). It is very simple and has two cuspids: a very large protoconid and a small posterior cusp, possibly the hypoconid. There is a small paralophid, weakly constricted, but no anterior valley. The posterior valley is more developed. There is only a very short anterior cingulum but no lingual or labial one. The root is broken. A left p2 (MNHN.F.OBP65) and a left p3 (MNHN.F.OBP66) could have belonged to the same individual, whereas the right p3 (MNHN.F.OBP67) and the right p4 (MNHN.F.OBP68) could have belonged to another. Another left p4 (MNHN.F.OBP69) cannot be attributed to any individual. The p2 and p3 bear labial vertical rugosities whereas p4 only has discontinuous cingulum. The lingual cingulum is weak and only present at the opening of the valleys. The ectolophid groove is angular on p4, but less developed on p2–3, and it always disappears before the neck. The metaconid is very slightly constricted. The entoconid is either completely absent or very weak. The posterior valley is wide and U-shaped on p4 but narrower on p2–3. The paralophid of p2 is not constricted and the anterior valley is absent. The paraconid is reduced. The posterior valley is narrowly open. The anterior branch of the paralophid is long on p3–4.

Lower molars. The isolated lower molars are difficult to differentiate from one another, so they will be discussed globally. The ectolophid groove is developed until the neck. The trigonid is angular, in right dihedron, while the talonid is rounded. The entoconid and metaconid are very slightly constricted. Lingual cingulum is only present in the posterior valley of one specimen, otherwise it is completely absent. However, the anterolingual cingulum is present in the opening of the anterior valley, though it is weak. The labial cingulum is usually present, anteriorly, labially and in the ectolophid groove, but it is always discontinuous and rather weak. The hypolophid and protolophid are slightly oblique. There is no lingual groove of the entoconid. The anterior branch of the paralophid is high and long. The opening

of the anterior valley is higher than the posterior one. The posterior cingulum is always present, strong and continuous.

Material from other localities

Maxilla and mandible from Poillat. A complete upper tooth row (MJSN-POI-007-3219) and a very well-preserved juvenile mandible (MJSN-POI-007-174) are preserved (Fig. 16) from the recently discovered locality of Poillat, near Delémont (Jura Canton, Switzerland), which also yielded a well-preserved skull of *Epiaceratherium delemontense* Becker & Antoine, 2013, another rhinocerotid (Becker *et al.* 2013). The upper teeth are very worn, indicating a very old individual, but some characters can nonetheless be observed. The P1 is quite large, with a well-developed parastyle, and a single large lingual cusp. The ectoloph is convex. The paracone and metacone folds are strong on P2–4. There is almost no labial cingulum, but the lingual is subcomplete (it slightly faints below the protocone) and waved. The protocone and hypocone of P2 are connected by a lingual bridge. The protoloph is very short and does not connect to the ectoloph while the metaloph is oblique and connects to the paracone. The protocone and hypocone of P3–4 were either fused or connected. The molars have neither lingual nor labial cingulum, except below the metacone and at the opening of the median valley of M3. There is a posterior groove on the ectometaloph of M3.

The juvenile mandible is subcomplete. The symphysis is slightly upraised compared with the corpus mandibulae and its posterior border was just in front of d1. The foramen mentale is below p1 and there is no lingual groove for the sulcus mylohyoideus. The base of the corpus is completely straight, and the ramus is vertical. The coronoid apophysis is large and well-developed. The foramen mandibulare was below the teeth neck.

The i2 is partly unerupted. The d1 is single rooted and very simple. The posterior valley is very small. Lingual and labial cingulum are completely absent on d1–4 and m1 and there are no vertical rugosities on the ectolophid. The protoconid fold is present and the metaconid is slightly constricted on d3–4, but not the entoconid. The paralophid of d2–3 is double and the ectolophid folds are absent. The anterior groove of the ectolophid is present on d2 and its posterior valley is open lingually.

Postcranial remains

Until now, the postcranial skeleton of *R. romani* was almost completely unknown. No remains are preserved in the type locality of La Ferté-Alais and only a few bones were described from St-Henri/St-André/Les-Milles (Ménouret & Guérin 2009) and Rickenbach (Mennecart *et al.* 2012): a scapula, a distal femur, a cuboid and an ectocuneiform from the former locality, and a distal humerus, two astragali and various metapods from the latter. However, after re-examination of the material from Gaimersheim, several postcranial remains can be assigned to *R. romani*: a complete radius, a complete scaphoid, a partial magnum, a broken McIII articulated with a well-preserved McIV as well as an almost complete astragalus and a MtIII. These specimens are of drastic importance because they can be confidently attributed to *Ronzotherium*, contrary to specimens from other localities such as Rickenbach

Fig. 15 (next page). *Ronzotherium romani* Kretzoi, 1940 from La Ferté-Alais (late early Oligocene, France). – **A**. Left P2 MNHN.F.OBP55. **A1**. Occlusal view. **A2**. Lingual view. **A3**. Labial view. – **B**. Left P4 MNHN.F.OBP56. **B1**. Occlusal view. **B2**. Lingual view. **B3**. Labial view. – **C**. Left M1 MNHN.F.OBP59. **C1**. Occlusal view**. C2**. Lingual view. **C3**. Labial view. – **D**. Left M2 MNHN.F.OBP60. **D1**. Occlusal view. **D2**. Lingual view. **D3**. Labial view. – **E**. Right M3 MNHN.F.OBP62. **E1**. Occlusal view. **E2**. Lingual view. **E3**. Labial view. – **F**. Left p2 MNHN.F.OBP65. **F1**. Occlusal view. **F2**. Labial view. **F3**. Lingual view. – **G**. Left p3 MNHN.F.OBP66. **G1**. Occlusal view. **G2**. Labial view. **G3**. Lingual view. – **H**. Left p4 MNHN.F.OBP69. **H1**. Occlusal view. **H2**. Labial view. **H3**. Lingual view. – **I**. Right m1? MNHN.F.OBP71. **I1**. Occlusal view. **I2**. Labial view. **I3**. Lingual view. – **J**. Paralectotype right m3? MNHN.F.OBP72. **J1**. Occlusal view. **J2**. Labial view. **J3**. Lingual view. – **K**. Paralectotype right m3? MNHN.F.OBP79. **K1**. Occlusal view. **K2**. Labial view. **K3**. Lingual view. – **L–M**. Lectotype right i2 MNHN.F.OBP63. **L**. Medial view. **M**. Anterior view. (Labial view towards the top). Scale bars: 2 cm.


A1
B1
C1
D1
E1
A2
B2
C2
D2
E2
A3
B3
C3
D3
E3
F1
G1
H1
I1
J1
K1
F2
G2
H2
I2
J2
K2
H3
G3
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I3
J3
K3
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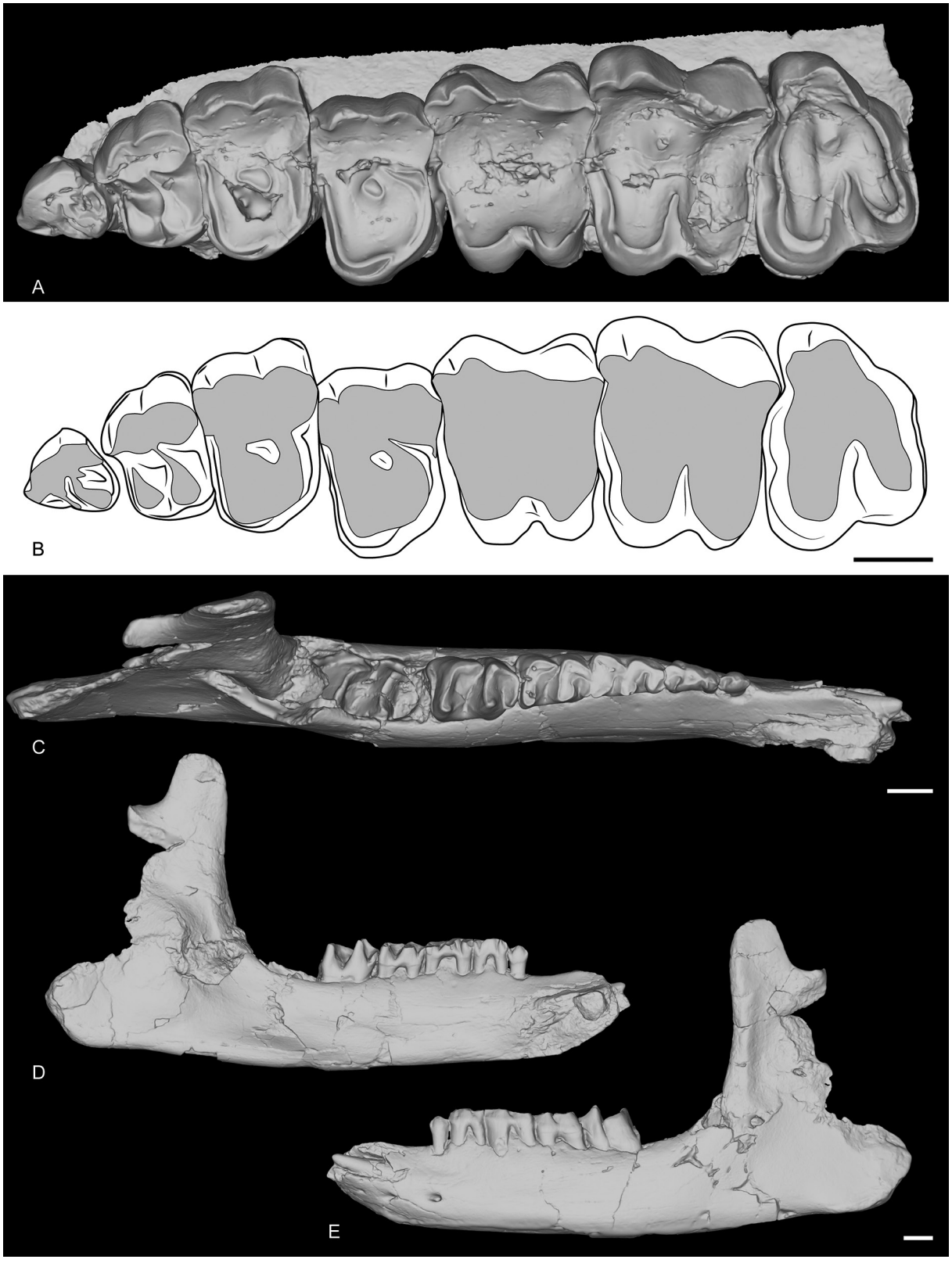

Fig. 16. *Ronzotherium romani* Kretzoi, 1940 from Poillat, near Delémont (late early Oligocene, Switzerland). – **A–B**. Left maxilla MJSN-POI-007-3219 with P1–M3. **A**. Occlusal view. **B**. Drawing of P1–M3. – **C–E**. Right juvenile hemimandible MJSN-POI-007-174 with erupting i2, d1–4, m1 and erupting m2. **C**. Occlusal view. **D**. Medial view. **E**. Lateral view. Scale bars: 2 cm.

or 'Marseille', that were previously partly referred to as the co-occurring *Diaceratherium*, mostly because of their dimensions. Yet, based on fine anatomical comparisons, we now refer most of the specimens from 'Marseille' (Figs 17–18), originally assigned to "*Diaceratherium*" *massiliae* (including the holotype McIV) by Ménouret & Guérin (2009), as well as new specimens from Poillat, Gaimersheim (Figs 19–20) and Rickenbach (Fig. 21), to *R. romani*. Furthermore, the two astragali previously identified as *R. romani* from Rickenbach (Mennecart *et al.* 2012) should in fact be referred to as *Diaceratherium*, while the metatarsals, also identified as *R. romani*, should be referred to as *Mesaceratherium* (Tissier *et al*. 2021). These new attributions show that *R. romani* had a larger size than previously thought and that it was less cursorial than other species of the genus. Throughout the description, comparisons will be made with other ronzothere species as well as with *Diaceratherium*, and in particular *D. tomerdingense*, the type species of the genus, to validate the synonymy of *R. romani* and "*D*." *massiliae*.

Scapula. Two scapulae are preserved from Poillat (MJSN-POI-007-306 and MJSN-POI-007-222), and one from 'Marseille' (AIX.1979-2). The two scapulae from Poillat are complete, whereas the one from 'Marseille' is not. It is very wide, compared to its height (= spatula-shaped, sensu Antoine 2002). In distal view, the medial border of the articulation is straight. The posterior border of the scapula and the glenoid cavity are very concave.

Comparison. The scapula of *R. velaunum* is unknown but it is preserved in Villebramar for *R. filholi* (Brunet 1979) and it shares with *R. romani* the very concave posterior border of the scapula and glenoid cavity. The scapula of *Diaceratherium aginense* (Répelin, 1917) from Laugnac (Répelin 1917) widely differs by its reduced width compared to the height (being elongated, sensu Antoine 2002) and its slightly less concave distal border.

Humerus. It is known from 'Marseille' and Rickenbach (Fig. 17G–H). The distal fragment of humerus FSL-9523 from 'Marseille' is large-sized and incomplete. The fossa olecrani is low and wide in posterior view and the distal articulation is hourglass-shaped (or 'diabolo-shaped') in anterior view: there is a deep proximal incision between the two lips of the trochlea. However, there is no scar on the trochlea. The epicondylar crest is wide and laterally expanded. In anterior view, the articulation is oblique compared to the shaft of the humerus. The humerus NMB-UM-973 from Rickenbach is the most complete one but is very poorly preserved. The trochiter and the deltoid tuberosity are not preserved. The distal articulation is similar to that of other humeri from 'Marseille' in every aspect.

Comparison. The humerus of *R. velaunum* (PUY.2004.6.262.RON) differs by a smaller size and a higher fossa olecrani, as well as a distal articulation not medially constricted in anterior view. It further differs from the humerus from Rickenbach by a less developed lateral epicondyle. The largest humeri of *R. filholi* from Villebramar are more similar in size, in particular compared to the one from Rickenbach (NMB.UM-973). However, Ménouret & Guérin (2009) had referred the humerus from 'Marseille' FSL-9523 to *Diaceratherium massiliae* based on the size difference with *R. filholi*, as well as morphological differences, such as the wide coronoid and olecranon fossae. Yet, the humerus Vil.1970-225 of *R. filholi* from Villebramar (Brunet 1979: pl. XXI, fig. a) is very similar to FSL-9523: the two fossae are wide and the epicondylar crest and lateral epicondyle are equally developed. It only differs by less constricted condyles in anterior view. Furthermore, we believe that another very large humerus from 'Marseille' (FSL-8546; but see Ménouret & Guérin 2009: fig. 10a–b, which is indeed FSL-8546 and not FSL-9523, contrary to the legend of the figure) attributed to *D. massiliae* by Ménouret & Guérin (2009) could in fact come from another locality, based on its very different preservation. Finally, the humeri of *D. tomerdingense* (type species of the genus; SMNS-16154), *D. lamilloquense* Michel, 1987 (NMB-L.M.429) and even *D. aginense* (Répelin 1917: pl.VIII, fig. 1) all have a rather high fossa olecrani in posterior view, and unconstricted condyles in anterior view.

Fig. 17. *Ronzotherium romani* Kretzoi, 1940 from St-Henri/St-André/Les-Milles, near Marseille (late Oligocene, France). – **A–B**. Maxilla FSL-8547. **A**. Occlusal view. **B**. With left P1–M2 in lingual view. – **C, E–F**. Mandible FSL-8547 from the same individual. **C**. Occlusal view. **E**. With left p2–m3 in labial view. **F**. Right p3–m3 in lingual view. – **D**. Left i2 NMB-Mar-862, lingual view. – **G–H**. Left humerus FSL-9523. **G**. Anterior view. **H**. Posterior view. – **I–J**. Right radius FSL-520279+520280. **I**. Anterior view. **J**. Posterior view. Scale bar: 2 cm.

Radius. It is preserved from 'Marseille' and Gaimersheim. The radius from 'Marseille' FSL-520279+ 520280 (Fig. 17I–J) is subcomplete, but the distal articulation is poorly preserved. In proximal view, the anterior border of the articulation is straight. The proximal facets for the ulna are separated in posterior view. The lateral one is large and concave. The medial border of the diaphysis is straight in anterior view. In anterior view, the insertion for the m. biceps brachii is marked and deep. The gutter for the m. extensor carpi is very shallow on the distal articulation. The radius from Gaimersheim (BSPG collection, Fig. 19A–D) is complete and very well preserved. It shows that the radius was connected to the ulna over three quarters of the diaphyseal length. In proximal view, the medial articulation facet for the humerus is much larger than the lateral one and they are both concave. The medial articulation for the ulna is a thin lateromedially elongated band, whereas the lateral articulation is large and triangular. Distally, there are two poorly distinguished articulations: a large, medial one for the scaphoid and a smaller one, lateral, triangular and concave anteroposteriorly for the lunate. In posterior view, the extension of the distal articulation for the scaphoid is large and well developed, but wider than high. The distolateral contact area for the ulna is large.

Comparison. The radius of *R. velaunum* is unknown. The proximal facets for the ulna from the radii of *R. filholi* are like those of *R. romani*. The radius of *R. filholi* mostly differs from *R. romani* by its deep and wide gutter for the m. extensor carpi on the anterior side of the distal extremity, which is very shallow on the radii from 'Marseille' and Gaimersheim. This deep gutter is also present on a radius from Espenhain (BSPG-2008-I-44), also attributed to *R. filholi*, although the total length of the bone is much smaller than in Villebramar (around 30 cm versus 38 to 41 cm in Villebramar). However, a very deep gutter is also present on the radius of *Diaceratherium tomerdingense* (SMNS-16154), whereas it is shallow on a hand of *D. lemanense* (Pomel, 1853) from Gannat (MNHN-LIM-598). Therefore, there seems to be variation within this character, even among species of a same genus. Finally, Ménouret & Guérin (2009) referred the radius from 'Marseille' to *Diaceratherium massiliae* because they considered that in "*R. filholi* it is the external humeral facet that is the most developed (Brunet 1979: pl. 21)" [translated by the authors], which is actually incorrect. Brunet (1979: 138) in fact states in the description of the material from Villebramar that "[the proximal articulation surface] is composed of two glenoid cavities (a large internal one, long, weakly concave; a smaller external one, thinner and more concave, pl XXIc)" [translated by the authors], which is also the case in the radii described here. The radius of *D. lamilloquense* from Castelmaurou (UM CAM-22) differs by the very concave posterior border of the proximo-medial articulation surface in proximal view, whereas it is straight in *Ronzotherium*.

Scaphoid. It is preserved in 'Marseille' (FSL-520285, Fig. 18A), Gaimersheim (BSPG collection, Fig. 19E–H) and Rickenbach (NMO-I5-62, Fig. 21G). All three specimens are very well preserved and almost identical. The proximal articulation for the radius is triangular, and concave anteroposteriorly. Posterodistal to the proximal articulation, there is a large lateromedially elongated tuberosity on which occurs an articulation for the lunate (the postero-proximal articulation for the lunate sensu Antoine (2002). This articulation for the lunate is fused with the anteroproximal facet for the lunate on the scaphoids from Gaimersheim and Rickenbach, but they are partly separated by a shallow groove on the specimen from 'Marseille'. The anteroproximal articulation for the lunate is band-shaped and separated from the anterodistal articulation for the lunate by a large and deep groove for ligaments, extending anteroposteriorly, below the proximal tuberosity. On the lateral side, the anterodistal articulation for the lunate is anteroposteriorly elongated, band-shaped and almost fused with the distal magnum facet. The distal articulations for the magnum (anteriorly) and the trapezoid (median) are concave and almost equal-sized. Posterior to these two facets, there is a small articulation facet for the trapezium on the specimens from 'Marseille' and Gaimersheim, that seems to be absent or fused with the trapezoid facet on the specimen from Rickenbach. The anterior and posterior heights of the scaphoid are equal. In medial view, the trapezoid facet is prominent and high, whereas the other facets are not visible.