



General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

Tragoportax cf. *rugosifrons* (Schlosser, 1904) from the late Miocene of Cessaniti (Southern Italy)



Tragoportax cf. *rugosifrons* (Schlosser, 1904) du Miocène supérieur de Cessaniti (Italie méridionale)

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ABSTRACT

This paper describes remains attributable to *Tragoportax* cf. *rugosifrons* (Schlosser, 1904) found in the late Miocene site of Cessaniti (Vibo Valentia, Calabria) and the surrounding area. The studied specimens come from the *Clypeaster* sandstones, included in a marine/fluvial succession dated between 8 and 7.2 Ma. At Cessaniti, *Tragoportax* is associated with *Stegotrabelodon syrticus* Petrocchi, 1941; *Samotherium* cf. *boissieri* Forsyth-Major, 1888; *Bohlinia* cf. *attica* Matthew, 1929; and an undetermined Rhinocerotid still under study. The genus *Tragoportax* was common in Eurasia and Africa during the late Miocene. The occurrence of *Tragoportax* cf. *rugosifrons* at Cessaniti confirms the peculiarity of the assemblage, with its association of species of North African and Pliocene (Greco-Iranian bioprovince) affinities.

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RÉSUMÉ

Cet article décrit les restes attribuables à *Tragoportax* cf. *rugosifrons* (Schlosser, 1904) trouvés dans le site du Miocène tardif de Cessaniti (Vibo Valentia, Calabria) et dans les environs. Les spécimens étudiés proviennent des grès à *Clypeaster*, inclus dans une succession fluvio-marine datée entre 8 et 7,2 Ma. À Cessaniti, *Tragoportax* est associé à *Stegotrabelodon syrticus* Petrocchi, 1941 ; *Samotherium* cf. *boissieri* Forsyth-Major, 1888 ; *Bohlinia* cf. *attica* Matthew, 1929 ; et un Rhinocérotyde encore à l'étude. Le genre *Tragoportax* était commun en Eurasie et en Afrique à la fin du Miocène. La présence de *Tragoportax* cf. *rugosifrons* à Cessaniti confirme la particularité de l'assemblage, où sont associées des espèces d'affinités nord-africaines et pliocènes (bioprovince gréco-iranienne).

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1. Introduction

In the last fifteen years, a consistent record of terrestrial mammals has been recovered in the late Miocene succession of Cessaniti (Calabria, southern Italy; Ferretti et al., 2003, 2017; Marra et al., 2011, 2017), a site previously known for the occurrence of marine mammals and invertebrates (Carone and Domning, 2007; Carone et al., 2013; Checchia Rispoli, 1925). The succession of Cessaniti (Fig. 1) is well exposed in the Gentile's Quarry ("Cava Gentile"), the most representative site of the area. The mammalian assemblage comes from the *Clypeaster* sandstones ("Arenarie a *Clypeaster*", sensu Ogniben, 1973), and includes *Stegotetrabelodon syrticus* Petrocchi, 1941; *Samotherium* cf. *boissieri* Forsyth-Major, 1888; *Bohlinia* cf. *attica* Matthew, 1929; and an undetermined Rhinocerotid still under study (Marra et al., 2011, 2017). Marine mammals are represented by abundant remains of *Metaxytherium serresii* (Carone and Domning, 2007; Carone et al., 2013) and scanty fossils of Cetaceans (Carone and Marra, 2013; Marra et al., 2016). The Cessaniti assemblage represents a novelty among the late Miocene

bioprovinces of the central Mediterranean, as it includes species associated with both North African and Pikermian (Greek-Iranian bioprovince) affinities.

In this scenario, the Bovid remains of Cessaniti are of noticeable interest. Fossils belonging to Bovids of two different size classes have been found at Cava Gentile (Cessaniti, Vibo Valentia) and in a neighbouring site at Papaglioni (Fig. 1). The specimens of larger size are here attributed to *Tragoportax* cf. *rugosifrons*, whereas the smaller ones are still indeterminable because of the scarcity of the remains.

2. Geological setting

The Capo Vaticano–Monte Poro sedimentary basin is located in the southwestern sector of the Calabria–Peloritani Arc. The basin overlies a crystalline substratum, Palaeozoic in age, and is characterised by a stratigraphic succession, attributable to the late Miocene, that outcrops with different thickness and facies throughout the area (Nicotera, 1959).



Fig. 1. Geographic position of the sites quoted in the text.
Fig. 1. Position géographique des sites cités dans le texte.

The succession consists of the following four informal units, from bottom to top:

- “dark argillaceous sands with *Ostrea* and *Cerithium*”, alternating with coarse sandstones, attributed to lagoonal deposition (Neri et al., 2005);
- “*Clypeaster* sandstones” (“Arenarie a *Clypeaster*”, sensu Ogniben, 1973), attributed to shallow marine water deposition;
- “*Heterostegina* yellow sandstones” (Papazzoni and Sirotti, 1999), deposited in clearly marine conditions;
- “*Orbulina* marls” (“Marne a *Orbulina*”, Rao et al., 2007), deposited in a hemipelagic environment.

The succession is covered by Messinian and Plio-Pleistocene deposits. At the Cessaniti site (Fig. 1), quarry works have exposed the stratigraphic sequence and have released a rich paleontological record. At the Gentile's Quarry, the outcrop of the late Miocene succession is complete and at a maximum thickness (Fig. 2). The succession has been interpreted as a single transgressive event (Carone and Domning, 2007; Gramigna et al., 2008; Neri et al., 2005), until recent research that has suggested a more complex evolution of the basin (Marra et al., 2017). In particular, the recognition of soils and fluvial deposits in the “*Clypeaster* sandstones” (FL1 to 3 in Fig. 2) has allowed reinterpretation of the unit as having been affected by temporary falls in sea level within the general transgressive trend, probably under control of tectonics (Marra et al., 2017). The most relevant fall of the relative sea level is documented by the thick fluvial deposit FL1, which sharply cuts the lagoonal deposit LG (Fig. 2). The shoreface deposit SH1 represents a subsequent marine ingressions, marked by a ravinement surface (RS in Fig. 2) overlying FL1. Two minor fluvial phases (FL2 and FL3) are interlaid on the shoreface deposits SH1–SH3, marked at the bottom by ravinement surfaces (RS, Fig. 2). The shoreface sandstones SH4 (“*Heterostegina* yellow sandstones”) indicate a definitive setting of frankly marine conditions, with a subsequent increasing of depth documented by the overlying marls OT (Offshore Transition; “*Orbulina* marls”). The maximum age range of the Cessaniti succession, from the lagoonal deposits to the top of “*Heterostegina* yellow sandstones”, ranges between 8.1 Ma (by the attribution of LG to the Chron C4n; Marra et al., 2017) and 7.2 Ma (by the attribution of the “*Orbulina* marls” to the nannoplankton zone CNM17; Marra et al., 2017).

At Cava Gentile, mammalian remains arise mainly from the “*Clypeaster* sandstones” (Fig. 2) and are attributed to *Metaxytherium serresii* (Carone and Domning, 2007; Carone et al., 2013), *Bohlinia* cf. *attica* (Marra et al., 2011), Cetaceans (Carone and Marra, 2014; Marra et al., 2016), Rhinocerotidae indet., Anthacotheridae indet. and Bovidae indet. (Marra et al., 2011, 2017). *Stegotrabelodon syrticus* is recorded in the brackish mud deposits LG, as well as in the “*Clypeaster* sandstones” (Fig. 2; Ferretti et al., 2003, 2017). Giraffidae fossils, attributable to *Samotherium* cf. *boissieri*, have been recovered in the “*Clypeaster* sandstones” that form outcrops at Zungri, near Cessaniti (Fig. 1; Marra et al., 2011).

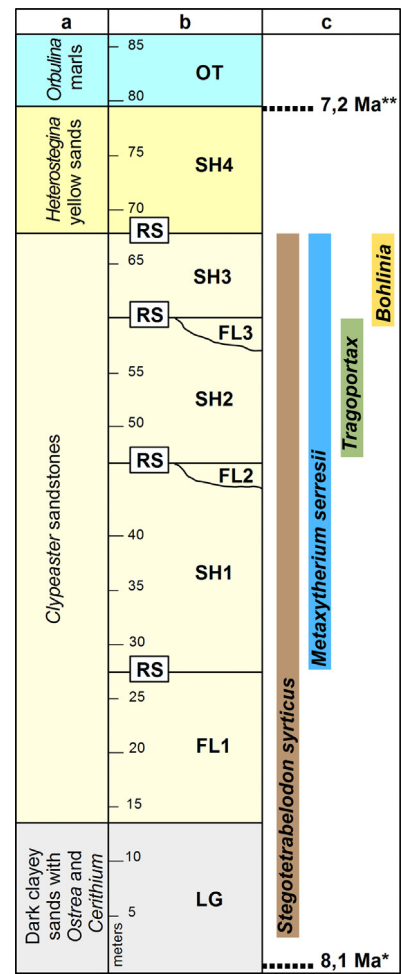


Fig. 2. Simplified stratigraphy of Cava Gentile (Cessaniti) with large mammalian occurrences: a) informal stratigraphy (according to Neri et al., 2005; Nicotera, 1959; Ogniben, 1973; Rao et al., 2007); b) stratigraphy according to Marra et al. (2017) (LG: Lagoonal deposits, FL: fluvial deposits, SH: shoreface deposits, OT offshore transition, see text for explanations); c) occurrences of mammalian taxa; *) dating by the attribution of LG to the Chron C4n (Marra et al., 2017); **) dating by the attribution of OT to the nannoplankton zone CNM17 (Marra et al., 2017).

Fig. 2. Stratigraphie simplifiée de Cava Gentile (Cessaniti) avec les occurrences de grands mammifères : a) stratigraphie informelle selon Nicotera, 1959 ; Ogniben, 1973 ; Neri et al., 2005 ; Rao et al., 2007 ; b) stratigraphie selon Marra et al., 2017 (LG : dépôts lagunaires, FL : dépôts fluviaux, SH : dépôts riverains, OT : transition vers l'offshore, voir texte pour explications) ; c) occurrences de taxons de mammifères ; *) datation par l'attribution de LG au Chron C4n (Marra et al., 2017) ; **) datation par l'attribution de OT à la zone de nannoplancton CNM17 (Marra et al., 2017).

The hemimandible attributed to *Tragoportax* cf. *rugosifrons* in this paper, and the tentatively referred radius, astragalus and anterior phalanx, have been recovered at Cava Gentile and come from sandstones SH2–FL3 (Figs. 1 and 2). Other post-cranial bones, tentatively referred to *Tragoportax* cf. *rugosifrons*, come from Papaglionti (Fig. 1), a village near Cessaniti, where the succession thickness is reduced compared to the thickness at Cessaniti. The succession outcropping near the village of Papaglionti is located on the “Serre” hill, whose

northeastern side released the studied materials. The succession, from bottom to top, consists of:

- grain-coarse sandstones, correlatable to FL1 of Cava Gentile;
- *Clypeaster* sandstones, correlatable to SH1–SH3 of Cava Gentile;
- *Heterostegina* yellow sands, correlatable to SH4 of Cava Gentile.

The thickness of the outcrop is lower than that at Cessaniti, and the sandstones do not show evidence of fluvial phases. The remains, tentatively attributable to *Tragoportax*, have been recovered in the uppermost layers of the *Clypeaster* sandstones.

3. Systematic palaeontology

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Subfamily Bovinae Gray, 1821

Tribe Boselaphini Knottnerus-Meyer, 1907

Genus *Tragoportax* Pilgrim, 1937

***Tragoportax* cf. *rugosifrons* (Schlosser, 1904)**

HOLOTYPE. — Skull (Schlosser, 1904: pl. 12, fig. 6).

TYPE LOCALITY. — Samos

Referred material: hemimandible (Inventory Number: 4 (CES)vc6);

Tentatively referred material: radius (Inventory Number: 13 (CES)vc6); humerus (Inventory Number: 26 (PAP)vc2); anterior phalanx (Inventory number: 123 (CES)vc7); metatarsal (Inventory Number: 119 (PAP)vc2); posterior phalanx (Inventory number: 124 (PAP)vc2); astragalus (Inventory Number: 120 (CES)vc7).

Repository: Civico Museo di Paleontologia di Ricadi (MURI), via Strada Provinciale, 89866 Santa Domenica di Ricadi (VV) Italy.

3.1. Preservation and stratigraphic position of the specimens

The specimens from Cava Gentile (Cessaniti) are well preserved, with some secondary fragmentations mainly due to the quarry works. The specimens come from layers SH2–FL3 of the *Clypeaster* sandstones (fig. 2), where phosphatic remains are usually well preserved (Guido et al., 2012).

The hemimandible (Inventory Number: 4 (CES)vc6; Fig. 3A–C) is well preserved, with only the part anterior to p2 lacking. The tooth row is preserved from p3 to m3, with the alveolus of p2 present.

The radius (Inventory Number: 13 (CES)vc6; Fig. 3D–F) is almost complete, with restored parts. The proximal end is badly preserved.

A strongly abraded astragalus also comes from Cessaniti (Inventory number: 120 (CES)vc7).

An anterior phalanx (123 (CES)vc7; Fig. 3L–M) has been found at the Gentile's Quarry, in layers SH2–FL3.

The specimens from NE Serre (Papaglionti) are slightly abraded. Their stratigraphic position is correlatable to layers SH2–FL3 of the *Clypeaster* sandstone outcropping at Cessaniti (Fig. 2).

The humerus (Inventory Number: 26 (PAP)vc2; Fig. 3G–H) is preserved only at the distal end and is strongly damaged on the posterior side.

The left metatarsal (Inventory Number: 119 (PAP)vc2; Fig. 3I–K) is represented by the proximal end and a part of the shaft. It is partly covered by encrusted sediment and is very slightly abraded.

The posterior phalanx (Inventory number 124 (PAP)vc2; Fig. 3N–O) recovered at Papaglionti is complete and shows a slight abrasion.

3.2. Description and measurements

Hemimandible (Inventory Number: 4 (CES)vc6; Fig. 3A–C). The left hemimandible is slender. The horizontal ramus is straight, and its height gently decreases anteriorly to m1. The ascending ramus is backwards directed, with a slight curve, forming a slightly obtuse angle with the horizontal ramus. The mandibular angle is robust, with a well-marked border and evident wrinkling on the lingual side. The mandibular incisor is well outlined, and its deepness does not exceed the basis of the condylar process. The condyle is short in height and laterally elongated towards the lingual side.

Teeth

p3 The anterior styloid is well developed. The anterior conid is small. The anterior valley is wide. The mesolingual conid (metaconid) is pronounced, and its lingual border points backwards. The posterior valley is deep and narrow. The posterolingual conid is wide.

p4 The anterior styloid is well pronounced. The anterior conid has a curved lingual margin. The anterior valley is wide and deep. The mesolingual conid is wide, and its rounded border is slightly enlarged on the lingual margin. The posterior valley is deep and very narrow. The posterolingual conid is wide and squared.

m1 The first molar is extensively worn. The metaconid and the protoconid preserve only the lingual and labial margins, respectively. The external postprotocristid is observable as two small enamel folders. The ectostyloid is worn; it is wide and elongated toward the labial side.

m2 The protoconid is wide. Its labial margin forms a curve, with a smoothed point directed posteriorly. The ectostyloid is unworn; it is evident and rounded. The metaconid is wide; its lingual border is almost straight. The hypoconid is smaller than the protoconid; its labial margin forms a curve with a pronounced point that is oriented backwards. The entoconid is small, with an almost straight lingual border.

m3 The protoconid forms a curve on the labial side, with a weak point slightly oriented towards the posterior side. The metaconid is wide, with an almost straight lingual margin. The ectostyloid is unworn and weak. The hypoconid is rounded and forms a narrow curve that is slightly directed backwards. The entoconid is small, with an almost straight lingual border.

Measurements are given in Table 1.



Fig. 3. Fossils attributable to *Tragoportax* cf. *rugosifrons*: left hemimandible (Inventory Number: 4 (CES)vc6) in occlusal (A), labial (B) and lingual (C) views; right humerus (Inventory Number: 26 (PAP)vc2) in anterior (D) and posterior (E) views; left radius (Inventory Number: 13 (CES)vc6) in proximal (F), anterior (G) and posterior (H) views; left metatarsal bone (Inventory Number: 119 (PAP)vc2) in proximal (I), anterior (J) and posterior (K) views; right anterior phalanx (Inventory Number: 123 (CES)vc7) in anterior (L) and posterior (M) views; right posterior phalanx (Inventory Number: 124 (PAP)vc2) in anterior (N) and posterior (O) views.

Fig. 3. Fossiles attribuables à *Tragoportax* cf. *rugosifrons*: hémimandibule gauche (numéro d'inventaire : 4 (CES)vc6) en vues occlusale (A), labiale (B) et linguale (C) ; humérus droit (numéro d'inventaire : 26 (PAP)vc2) en vues antérieure (D) et postérieure (E) ; radius gauche (numéro d'inventaire : 13 (CES)vc6) en vues proximale (F), antérieure (G) et postérieure (H) ; os métatarsien gauche (numéro d'inventaire : 119 (PAP)vc2) en vues proximale (I), antérieure (J) et postérieure (K), phalange antérieure droite (numéro d'inventaire : 123 (CES)vc7) en vues antérieure (L) et postérieure (M), phalange postérieure droite (numéro d'inventaire : 124 (PAP)vc2) en vues antérieure (N) et postérieure (O).

Table 1

Measurements (in mm) of the hemimandible (Inventory Number: 4 (CES)vc6); * measurements at the alveolus.

Tableau 1

Mesures (en mm) de l'hémimandibule (numéro d'inventaire : 4 (CES)vc6); * mesures à l'alvéole.

Measurements of hemimandible 4 (CES)VC6	
Length p2–m3*	113.8
Length p2–p4*	45.5
Length m1–m3*	68.3
p/m index	0.66
Length p3	15.7
Breadth p3	9.1
Length p4	16.9
Breadth p4	9.4
Length m1	17.9
Breadth m1	12.2
Length m2	20.5
Breadth m2	13.6
Length m3	28.8
Breadth m3	12.5
Height behind m3	43.1
Height in front of m1	34.2
Height in front of p2	24.3
Height gonion – condyle	98.1
Length gonion – m3 alveolus aboral border	83.7

Humerus (Inventory Number: 26 (PAP)vc2; Fig. 3D–E). The right humerus has a wide trochlea. The dorsal margin of the medial condyle is smoothed and uniform. The groove of the trochlea is shallow. The medial epicondyle is small, albeit well pronounced.

Measurements. Breadth of the distal end: 44.0 mm; breadth of the trochlea: 42.5 mm.

Radius (Inventory Number: 13 (CES)vc6; Fig. 3F–H). The left radius shows a straight shaft with a tube shape, antero-posteriorly compressed, for the whole length. A large groove is present on the interosseous margin. On the distal end, the scaphoid facet is concave and almost circular; it is slightly elongated laterally. The lunar facet is squared and fairly flat. The dorsal tubercle is not particularly prominent. The margin of the radioulnar joint is straight.

Measurements. Greatest length (approximated): 273.5 mm; physiological length: 264 mm; breadth of the proximal end: 51.1; breadth of the humeral articular surface: 47.7 mm; smallest breadth of the diaphysis: 32.2 mm; smallest circumference of the diaphysis: 85.0 mm.

Patella (Inventory Number: 125 (PAP)vc2). A left patella is tentatively attributable to *Tragoportax*. Measurements: greatest breadth: 31.1 mm; greatest length: 45.2 mm.

Metatarsal bone (Inventory Number: 119 (PAP)vc2; Fig. 3I–K). The left metatarsal bone is slender and laterally compressed. The proximal articulation is partly covered by consolidated sediment, but some observations can be documented. The articular facets are flat. The medial facet seems to have a quadrangular shape. The antero-lateral facet has a wide triangular profile – a sort of “bean” shape. The posterior facet is triangular. A small facet, triangular in shape, is present in the postero-medial position.

Measurements: proximal breadth: 35.4 mm; proximal depth (antero-posterior diameter): 36.6 mm; smallest breadth of the diaphysis: 20 mm.

Astragalus (Inventory Number: 120 (CES)vc7). The abrasion does not allow measurements. The specimen is tentatively attributed to *Tragoportax* based on its overall morphology and size.

Phalanges (Inventory Number: Anterior 123 (CES)vc7, Fig. 3L–M; Posterior: 124 (PAP)vc2, Fig. 3N–O). Two right phalanges, one anterior (123 (CES)vc7) and one posterior (124 (PAP)vc2), are tentatively attributed to *Tragoportax*. The anterior phalanx measurements: greatest length: 52.3 mm; breadth of the proximal end: 19.5 mm; smallest breadth of the diaphysis: 16.0 mm; breadth of the distal end: 16.8 mm. The posterior phalanx measures: greatest length: 53.1 mm; breadth of the proximal end: 19.9 mm; smallest breadth of the diaphysis: 16.3 mm; breadth of the distal end: 17.3 mm.

4. Comparisons

The main criticism in Boselaphini taxonomy lies in features of the *Tragoportax*–*Miotragocerus* complex, represented by two genera instituted after the invalidation of the genus *Tragocerus* and included in the Tribe *Tragoportacini* (Bibi et al., 2009). The distinction between the two genera is not often definite: new genera have been erected in recent times and species have been moved among them (Bibi, 2011; Bibi et al., 2009; Gentry, 2010). At the present state of the art, the genus *Tragoportax* includes species signalled in the late Miocene–Pliocene of Eurasia and Africa, with an opened debate on the generic attribution and on possible synonymies. Diagnostic characters for the determination of the species are derived mainly from the horn-cores; however, some data on the lower teeth can be considered for taxonomic attributions of the Boselaphine from Cessaniti.

Spassov and Geraads (2004) indicated morphological and biometrical differences between the genera *Tragoportax* and *Miotragocerus* using the sample from Hadjidimovo (Bulgaria; 8.1–7.1 Ma), and they referred to the species *T. rugosifrons* and *M. (Pikermicrus) gaudryi*. Although the main differences are in the body size (larger in *Tragoportax*) and in the morphologies of the horn-cores, the authors indicated distinctive characters in teeth and post-cranial bones as well.

As observed in *T. rugosifrons* from Hadjidimovo (Spassov and Geraads, 2004), the specimen from Cessaniti has a premolar row that is shorter than the molar row; the metaconids of p3 and p4 are large but less enlarged lingually; the anterior valleys of the premolars are open and well developed; and the premolar row is short compared to the molar row. These characters are distinctive for the genus *Tragoportax sensu Spassov and Geraads (2004)*. Furthermore, tooth dimensions and proportions clearly separate the two genera (Fig. 2 in Kostopoulos, 2009).

The tooth measurements and proportions of the specimen from Cessaniti lie within the variability described for the genus *Tragoportax*. The premolar/molar (p/m) index of the specimen from Cessaniti is 0.67, which is comparable with the values for *Tragoportax rugosifrons* from Hadjidimovo (0.65, 0.64% and 0.58; Spassov and Geraads, 2004), but differs from the values for *Miotragocerus (Pikermicrus) gaudryi* from the same site (0.68 to 0.78; Spassov and Geraads, 2004).

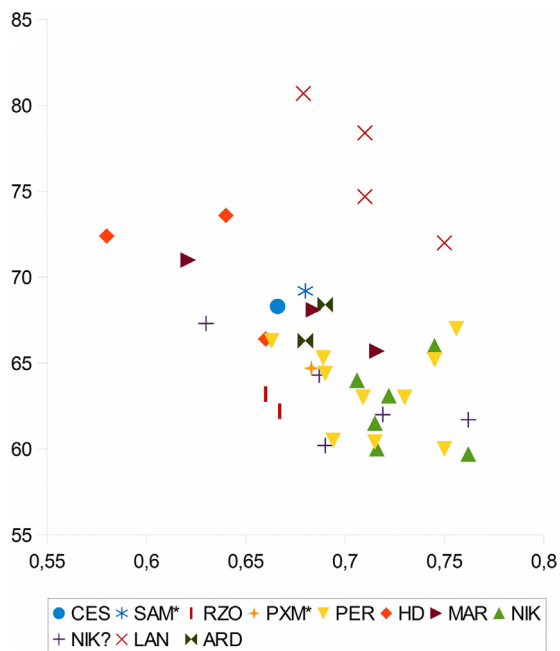


Fig. 4. Plot of the lower premolar/molar index (X axis) against the lower molar row length (Y axis). CES: *Tragoportax* from Cessaniti, this paper; SAM* *T. rugosifrons* from Samos, Greece, mean values (Solounias, 1981); RZO *T. rugosifrons* from Ravine des Zouaves 5, Greece (Bouvrain, 1994); PXM* *T. rugosifrons* from Prochoma, Greece, mean values (Bouvrain, 1994); PER: *T. rugosifrons*, Perivolaki, Greece (Kostopoulos, 2006); HD: *T. rugosifrons*, Hadjidimovo, Bulgaria (Spassov and Geraads, 2004); MAR: *T. cf. amalthea*, Maragheh, Iran (Bernor and Kostopoulos, 2011); NIK: *T. amalthea*, Nikiti-2, Greece (Kostopoulos, 2009); NIK?: *Miotragocerus*, Nikiti-2, Greece (Kostopoulos, 2016); LAN *T. acrae* from Langebaanweg, South Africa (Gentry, 1974, 1980); ARD: *T. abyssinicus*, Ardi Kadabba, Ethiopia (Haile-Selassie et al., 2009).

Fig. 4. Graphique de l'indice pré-molaire/molaire inférieur (axe X) par rapport à la longueur de la rangée de molaires inférieure (axe Y). CES : *Tragoportax* de Cessaniti, cet article ; SAM* *T. rugosifrons*, Samos, Grèce, moyenne des mesures (Solounias, 1981) ; RZO *T. rugosifrons*, Ravines des Zouaves 5, Grèce (Bouvrain, 1994) ; PXM* *T. rugosifrons*, Prochoma, Grèce, moyenne des mesures (Bouvrain, 1994) ; PER : *T. rugosifrons*, Perivolaki, Grèce (Kostopoulos, 2006) ; HD : *T. rugosifrons*, Hadjidimovo, Bulgarie (Spassov and Geraads, 2004) ; MAR : *T. cf. amalthea*, Maragheh, Iran (Bernor et Kostopoulos, 2011) ; NIK : *T. amalthea*, Nikiti-2, Grèce (Kostopoulos, 2009) ; NIK?: *Miotragocerus*, Nikiti-2, Grèce (Kostopoulos, 2009) ; LAN : *T. acrae*, Langebaanweg, Afrique du Sud (Gentry, 1974 et 1980) ; ARD : *T. abyssinicus*, Ardi Kadabba, Éthiopie (Haile-Selassie et al., 2009).

The distinction of the species belonging to the genus *Tragoportax* is highly debated and further complicated by the moving of some *Tragoportacini* species from one genus to another, as well as by erecting new species based on scanty materials. Given the characters of the Cessaniti assemblage, comparisons have mainly addressed the *Tragoportax* species of the Greco-Iranian bioprovince and of Africa.

The tooth dimensions and proportions of the Cessaniti specimen fall within the morphological and biometrical variability of *Tragoportax rugosifrons* from Hadjidimovo (Spassov and Geraads, 2004; Fig. 4), and are similar to those of *T. rugosifrons* from Samos (Greece; Solounias, 1981; Fig. 4) and from Perivolaki (Greece, 8.1–7.1 Ma; Kostopoulos, 2006; Fig. 4). However, the tooth measurements and proportions of *Tragoportax rugosifrons*

from Perivolaki are very close to those of *T. amalthea* (Kostopoulos, 2006; Fig. 4). An interesting observation is that Kostopoulos (2006) noticed more advanced features for the sample from Perivolaki, where 8 of the 13 specimens showed a molarised p4 in addition to an elongated p2 and a decrease of the paraconid in p3. These observations could explain why the premolar row was slightly more elongated than in *T. rugosifrons* from Hadjidimovo and *Tragoportax* from Cessaniti, where these characters are not reported, as well as providing a reason for the partial overlap with the p/m indexes vs. molar length of *T. amalthea* from Nikiti-2 (Greece, 8.7–8.0 Ma; Kostopoulos, 2016), a species characterised by proportionally longer premolars (Fig. 4).

The occurrence of a second Boselaphine tentatively referred to the genus *Miotragocerus* at Perivolaki and at Nikiti introduces an intriguing hypothesis (Kostopoulos, 2006, 2016). According to Kostopoulos (2006), some cranial materials from Perivolaki are determined to belong to *Miotragocerus* sp.; however, the possibility that some females of *Tragoportax* also had horns leaves the taxonomic attribution open. In addition, some horn-core features considered useful for the distinction between *T. rugosifrons* and *T. amalthea* may also be due more to ontogenetic variability than to interspecific differences (Kostopoulos, 2006, 2009, 2016). Specimens from Nikiti, which were dubitatively attributed to *Miotragocerus* sp., show features that are not decisive for their attribution to this genus (Kostopoulos, 2016). These specimens show a frequently molarised p4, and their dental measurements and proportions fall within the variability of *T. amalthea* from the same site (Kostopoulos, 2016) and of *T. rugosifrons* from Perivolaki (Fig. 4). Therefore, open questions remain due to the uncertain taxonomic position of these specimens, together with the suspicion of a significant incidence of sexual dimorphism and ontogenetic stages for the characters of *Tragoportacini* that are presently considered taxonomically distinctive.

Compared to *Tragoportax amalthea* from Maragheh, Iran (*T. cf. amalthea* in Kostopoulos and Bernor, 2011, *T. amalthea* in Kostopoulos, 2016), the p4 of the specimen from Cessaniti seems less advanced, as it shows a protruding, but slightly antero-posteriorly extended, metaconid and an open anterior valley. The dental sample from Maragheh, Iran (Age: 8.16–7.68 Ma) is considered more advanced than those of *T. amalthea* from Pikermi and *T. rugosifrons* from Hadjidimovo, while it is comparable to *T. rugosifrons* from Perivolaki (Kostopoulos and Bernor, 2011; Fig. 4). The marked T or Y shape of the p/4 metaconid, as well as the close anterior valley, as observed in the sample from Maragheh, are not present in the specimen from Cessaniti.

The specimen from Cessaniti is comparable to *Tragoportax rugosifrons* from the Macedonian sites of Ravine des Zouaves 5 (about 8.2 Ma; Koufos, 2006; Sen et al., 2000), Vathylakkos 2 and Prochoma (the latter are dated back to about 7.5 Ma, Koufos, 2006; Sen et al., 2000) (Bouvrain, 1994). The horizontal ramus of the mandible is higher under the molars than under premolars in the Cessaniti and the Macedonian specimens (Bouvrain, 1994). The lower molars from Ravine des Zouaves 5, Vathylakkos 2 and Prochoma, and Cessaniti show the presence of strong ectostylids. The metastylid of m3, absent in the specimen

from Cessaniti, is also often absent in specimens from the three Macedonian sites (Bouvrain, 1994). The wear stage of the specimen from Cessaniti does not allow verification of the presence of a strong mesostylid or of a feeble goat fold, as these characters are not observable in the inferior 3/4 of the crown (according to Bouvrain, 1994). Bouvrain (1994) reports a certain variability in the premolar characters. The fourth premolar from Cessaniti has a paraconid that is more developed than the parastylid, as in 64% of the specimens from Ravine des Zouaves (n. 41 specimens) and in 54% of the specimens from Prochoma (n. 11 specimens; Bouvrain, 1994). The third lower premolar from Cessaniti shows a paraconid that is more developed than the parastylid, whereas in the samples from Macedonian sites, this morphology is present in 42% (Ravine des Zouaves, n. 27 specimens) and 22% (Prochoma, n. 2 specimens; Bouvrain, 1994). The tooth dimensions and proportions of the specimen from Cessaniti are within the variability of the Macedonian samples (Bouvrain, 1994; Fig. 4).

T. cyrenaicus (formerly *Miotragocerus cyrenaicus*) has been found at Sahabi (Libya, 6.7 Ma; Bernor and Rook, 2008; Lehmann and Thomas; Thomas, 1979). Lehmann and Thomas (1987) pointed out that this species is larger than *T. rugosifrons* and shows marked differences in its lower dentition. However, the differences indicated by Lehmann and Thomas (1987) (paraconid and parastylid distinct from parastylid on premolars and not sub-equal in size, open valley between paraconid and metaconid, metaconid and entoconid not fused) are among the characters emphasised by Spassov and Geraads (2004) for distinguishing the genus *Tragoportax*, and they are present in *T. rugosifrons*. The metaconid is T-shaped, whereas the metaconid in the specimen from Cessaniti is moderately laterally expanded. In both, the anterior valley is open and the metaconid and entoconid are not fused. The teeth are larger in *T. cyrenaicus* than in *T.* from Cessaniti. *T. cyrenaicus* falls within the variability of *T. rugosifrons*–*T. amalthea* (Bouvrain, 1994; Kostopoulos, 2009, 2016; Lehmann and Thomas, 1987; Solounias, 1981; Spassov and Geraads, 2004; Thomas, 1979). The mandibular horizontal ramus is higher in the specimen from Cessaniti than in *T. cyrenaicus*.

T. abyssinicus is a species recently proposed by Haile-Selassie et al. (2009) on the basis of the Mio-Pliocene materials from the Middle Awash (approx. 5.6 my; Ethiopia). The metrics of its teeth fall within the variability of *T. rugosifrons*–*T. amalthea* (Fig. 4). The tooth morphology has similarities with that from *T. rugosifrons* from Hadjidimovo and from the specimen from Cessaniti: the metaconid of the premolars points backwards; the metaconid is well separated from the entoconid in the premolars; small basal pillars are present in the molars; and deep valleys are separated by cusps. The molars differ by the presence of developed flanges but not so much as to represent a true “goat fold”. In *T. rugosifrons*, the flanges are very weak.

The spread of *Tragoportacini* to sub-Saharan Africa probably occurred later than the spread to Eurasia and North Africa (Bibi, 2011). *T. acrae* (previously *Mesembriportax acrae* and *Miotragocerus acrae*; Gentry, 1974, 1980) from Langebaanweg, South Africa (dated about 4.5 Ma), shows more advanced features in its lower dentition: a small

goat fold on the lower molars, long premolar rows, and the hypoconid of p/4 sometimes projecting. The teeth are measurably larger than those of other *Tragoportax* species (Fig. 4).

Post-cranial bones allow few comparisons due to the scanty available data. The characters of the right humerus from Cessaniti differs from that from Alcelaphini (see Gentry, 1974): the dorsal margin of the medial condyle is smoothed and uniform, without interdigitations; the trochlea has a shallow groove.

The radius from Cessaniti differs from that of *T. acrae* (Gentry, 1974) in terms of the overall shape of the proximal articulation and the lack of a central fossa in its central part. The distal end is abraded, but the distal facet for the cuneiform seems to be reduced, as in *T. rugosifrons* (Bouvrain, 1994), rather than wide like in *T. acrae* (Gentry, 1974). The distal end of the radius from Cessaniti shows flat facets. The measurements of the metatarsals are within the variability of *T. rugosifrons* of Hadjidimovo (Spassov et al., 2004).

5. Discussion and conclusions

The specific attribution of the *Tragoportax* specimens from Cessaniti is difficult because of the limited taxonomic significance of teeth. Moreover, some species have been moved and/or synonymised into the genus *Tragoportax*, adding to the complexity of the picture and often based on scanty materials.

The lower dentition of the Cessaniti mandible is quite comparable to that of the specimens of *T. rugosifrons* from Hadjidimovo, Bulgaria (Spassov and Geraads, 2004), and from some Macedonian sites (Ravine des Zouaves 5, Vathy-lakkos 2 and Prochoma; Bouvrain, 1994), whereas it differs from that of *Tragoportax amalthea* from Nikiti 2, Greece (Kostopoulos, 2016) by having a shorter premolar row. However, a trend towards the molarisation of p/4 and an elongation of the premolar row has been detected in *T. rugosifrons* from Perivolaki, Greece (Kostopoulos, 2006). For this reason, the variability in the lower dentition of *T. rugosifrons* shifts into the variability of *T. amalthea*, which is characterised by longer premolar rows (Fig. 4). Molarised p4 are present in some of the specimens from Nikiti that are dubitatively attributed to *Miotragocerus* sp. (Kostopoulos, 2016). The tooth proportions of the specimens of *Miotragocerus* sp. from Nikiti overlap those of *T. rugosifrons* from Perivolaki (Kostopoulos, 2016; Fig. 4) and *T. amalthea* from Nikiti (Kostopoulos, 2016; Fig. 4), in contrast to the marked separation of tooth proportions and dimensions usually observed between the two *Tragoportacini* genera (Kostopoulos, 2009). The complex picture of morphometric variability and the taxonomic assessment of the species *T. rugosifrons* and *T. amalthea* remain unclear. *T. cyrenaicus* also falls into this wide variability, as does *T. abyssinicus*, whereas the more derived species, *T. acrae* from South Africa, shows a clear trend toward larger size.

As noted above, tooth morphology is not particularly conclusive. The comparisons of morphological characters and biometrical data, however, suggest that the specimen from Cessaniti can be assigned to the genus *Tragoportax*, while its specific attribution to *T. rugosifrons* remains provisional. The specimen from Cessaniti is, by and

large, comparable to the less derived forms of *Tragoportax rugosifrons*, while it differs from *T. amalthea*. By contrast, comparisons with *T. cyrenaicus* can only be based on scarce materials and are unreliable; albeit, the tooth measurements are larger in *T. cyrenaicus* than in the specimen from Cessaniti. For these reasons, the specimen from Cessaniti can be considered *conformis* to *T. rugosifrons*.

The genus *Tragoportax* was common in Eurasia and Africa during the late Miocene (Bibi, 2011; Kostopoulos, 2009), so the occurrence of *T. cf. rugosifrons* at Cessaniti confirms that the assemblage from Cessaniti represents a peculiar bioprovince in the late Miocene of the central Mediterranean, including North African species associated with Pikermian (Greco-Iranian bioprovince) ones. Cessaniti probably records the westernmost occurrence of some taxa belonging to the Pikermian biome. The extent of the emerged lands of Cessaniti and their possible connection to North Africa are still not fully elucidated by geological studies.

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