

The upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): Another brick for a latest Miocene bridge across the Mediterranean

Simone Colombero, Chiara Angelone, Edmondo Bonelli, Giorgio Carnevale, Oreste Cavallo, Massimo Delfino, Piero Giuntelli, Paul Mazza, Giulio Pavia, Marco Pavia, and Giovanni Repetto

With 12 figures and 3 tables

Abstract: A considerable amount of vertebrate remains have been found in the upper Messinian Cassano Spinola Conglomerates Formation, which crops out along the Tanaro River near Verduno (Piedmont). The fossil-bearing deposits were deposited during the third stage of the Messinian Salinity Crisis (5.55–5.33 Ma) in connection with the ‘Lago-Mare’ event. Sedimentological evidence indicates that the deposition of this Formation originated in a variety of fresh- and brackish-water environments. This is the most diverse Late Miocene faunal community found in NW Italy up to now, and includes remains of fish (cyprinodontiforms and putative lophiiforms), amphibians (bufonids, ranids), reptiles (testudinids, geoemydids, lacertids, anguils, varanids, agamids, amphisbaenians, scolecophidians, colubrids), birds (galliforms, accipitriforms and strigiforms) and mammals (proboscideans, perissodactyls, artiodactyls, carnivores, insectivores, rodents and lagomorphs). The tetrapod assemblages are consistent with the late Turolian age inferred based on sedimentological evidence and indicative of an open, semi-arid woodland savanna with at least modest, sparse fresh and brackish water bodies. The Verduno fossil assemblages share faunal similarities with coeval ones of southwest, central, and eastern Europe, as well as of peninsular Italy. Located at the crossroads between the two sides of the Mediterranean, northwestern Italy witnessed faunal exchanges between the different corners of the European continent. It was also on the access pathway to the Italian peninsula. The Verduno assemblage made it possible to track the migration of several taxa during latest Miocene across the whole southern Europe.

Key words: vertebrates, faunal interchanges/migrations, palaeoenvironment, Messinian, late Turolian, northwestern Italy.

1. Introduction

Messinian fossil remains of terrestrial vertebrates are relatively rare in Italy, despite numerous Italian sedimentary successions of this time-span have been extensively investigated for the study of the events related to the Messinian Salinity Crisis (MSC) (e.g., SELLI 1973; ROVERI & MANZI 2006; Fig. 1). Until the last few decades, Italian Late Miocene vertebrate-bearing continental fossiliferous localities were largely repre-

sented by strongly endemized mammal assemblages. The most outstanding of these communities are those from the Tusco-Sardinian palaeobioprovince [i.e., Monte Bamboli, Baccinello (Tuscany), with its three fossiliferous levels V0, V1, V2, and Fiume Santo (Sardinia) (*Oreopithecus* Zone faunas, see BERNOR et al. 2001; ROOK et al. 2006, 2011; ABBAZZI et al. 2008a)], as well as from the Apulian Platform [i.e., Scontrone (Abruzzo) and the numerous karst fissures of Gargano (Apulia) (*Mikrotia* fauna, see FREUDENTHAL

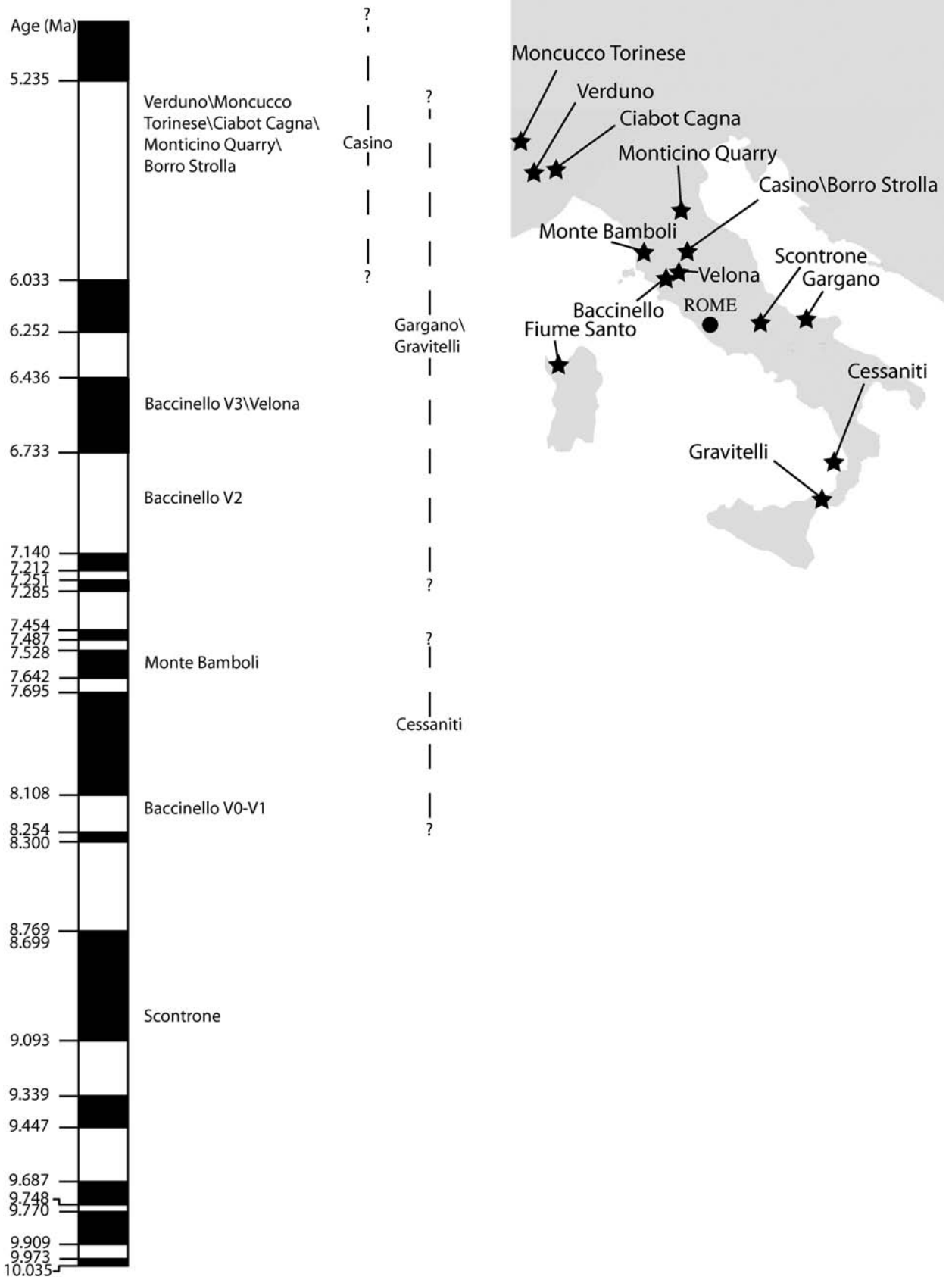


Fig. 1.

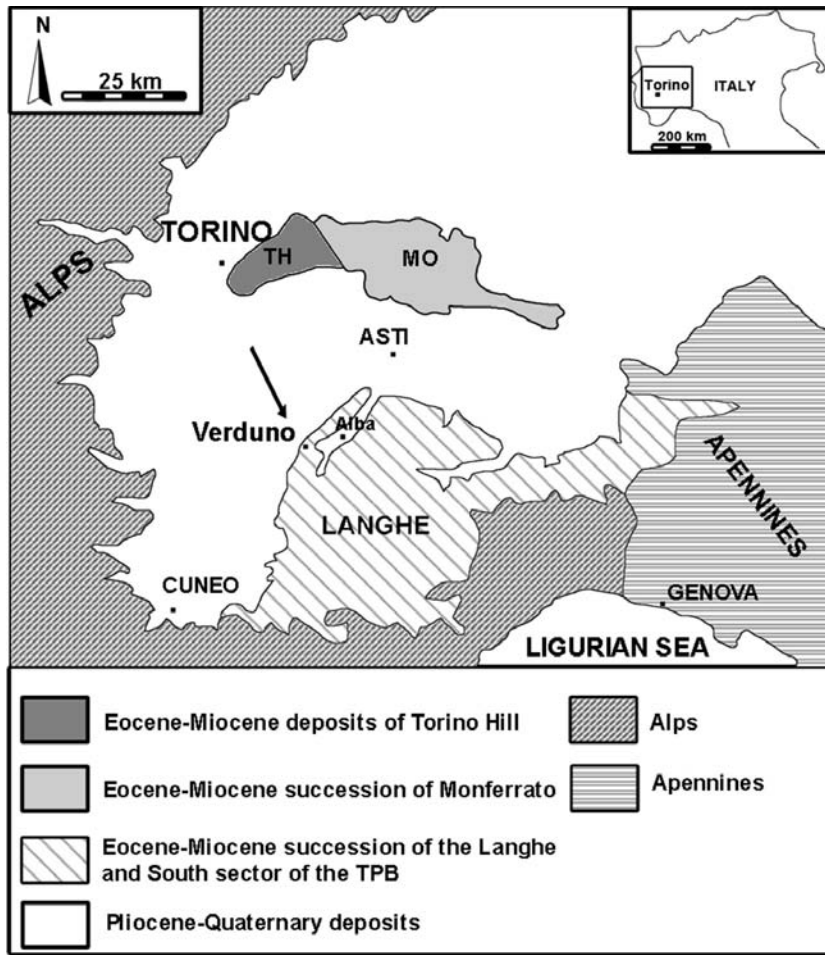


Fig. 2. Geographical and stratigraphical setting of the Tertiary Piedmont Basin (TPB). The arrow indicate the position of Verduno. TH: Torino Hill; MO: Monferrato (modified from COLOMBO & PAVIA 2013).

1971; MASINI et al. 2010, 2013; MAZZA 2013; VILLIER & CARNEVALE 2013)]. Recent studies have highlighted the association of these endemic mammal communities with crocodylians of probable African origin, at Baccinello (DELFINO & ROOK 2008), Scontrone (DELFINO & ROSSI 2013), and Gargano (DELFINO et al. 2007). These reptiles had never before been found in Late Miocene European assemblages. Baccinello V1-V3 include also chelonians that survived the mammal turnover that signed the end of the so-called *Oreop-*

ithecus Zone Fauna of the Tusco-Sardinian palaeobio-province (CHESI et al. 2009). Baccinello's uppermost fossiliferous level (V3) yields, within a "non-insular" mammal assemblage, a few mammal taxa endemic to southern Tuscany, and yet none survived from the older V0-V2 endemic assemblages (BERNOR et al. 2001; ROOK et al. 2006, 2011; ABBAZZI et al. 2008a). They developed, in contrast, from new continental incomers (ANGELONE & ROOK 2011, and references therein). Non-endemized Italian Miocene mammals are much

Fig. 1. Location of the major Italian late Miocene sites and their correlation to the geomagnetic polarity time scale (BOSSIO et al. 2001; HILGENS et al. 2003; LOURENS et al. 2004; EVANS et al. 2007; ABBAZZI et al. 2008b; MARRA 2009; MARRA et al. 2011; ROOK et al. 2011; PATACCA et al. 2013).

less frequent. This category comprises the assemblages from Gravitelli (Sicily, southern Italy), which were discovered in the earliest XX century (SEGUENZA 1902, 1907; ROOK et al. 2006), and Cessaniti (Calabria, see ROOK et al. 2006; MARRA et al. 2011), which includes taxa of African origin. The latter confirm the existence of an eastward-migrating Calabro-Peloritan Arc that was momentarily connected with North Africa at least between late Tortonian and early Messinian. New non-endemic late Turolian faunal communities have also been recognized in central and northern Italy. All show close affinities with coeval European fossil assemblages. In central Italy the most prominent are those from Velona (Tuscany, GHETTI et al. 2002), Casino and Borro Strolla (Tuscany, see ABBAZZI et al. 2008b). In northern Italy, outstanding Late Miocene vertebrate assemblages are those from Monticino Quarry (Brisighella, Romagna: see MARABINI & VAI 1988; DE GIULI 1989; MASINI & THOMAS 1989; GALLAI & ROOK 2011), and Piedmont (NW Italy). Messinian deposits crop out in the northern and southern part of the episutural Tertiary Piedmont Basin (TPB), which includes Eocene-to-Messinian sediments piled-up over the Alpine-Apennine juncture. Large-scale surveys, started by Carlo Sturani in the 1970s, (STURANI 1973, 1976) led to the discovery of continental deposits capping the TPB's Messinian succession. Terrestrial vertebrate remains were first discovered at Ciabòt Cagna, near Corneliano d'Alba (CAVALLO & REPETTO 1988; CAVALLO et al. 1993; ANGELONE & CAVALLO 2010). Two newly discovered sites are Moncucco Torinese (in the province of Asti) and Verduno (near Alba, in the province of Cuneo), in the northern and southern part of the TPB, respectively (Fig. 2). ANGELONE et al. (2011) preliminarily analysed the rich and varied fossil assemblage from Moncucco Torinese, and the rodent assemblages were recently described by COLOMBERO et al. (in press) and COLOMBERO & PAVIA (2013). Analyzing the primate remains from Moncucco Torinese, ALBA et al. (2014) have found the outstanding association of *Mesopithecus pentelicus* and cf. *Macaca* sp. This noteworthy co-occurrence proves the dispersal of African taxa into Europe at the end of the Miocene.

The present study focuses on the vertebrates from Verduno. The bone-bearing layers of this locality crop out along the Tanaro River in the upper portion of a very thick Messinian succession, known in the literature as the "Pollenzo section" (BERNARDI et al. 2010; DELA PIERRE et al. 2011). This stratigraphic sequence was recently studied to investigate the sedimentary processes that occurred during the MSC at the bound-

ary between marginal and basinal areas of the TPB. The Verduno fossil remains have been the subject of a preliminary unpublished bachelor thesis by DAMIANI (2009), and SARDELLA (2008) had classified carnivore remains, erratically collected near the site, to *Hyaenictitherium* sp. and *Eucyon monticinensis*. COLOMBERO et al. (2013) have recently examined rodents from Verduno. Throughout the latest Miocene, Moncucco Torinese and Verduno were at a crossroads between the Western and Eastern Mediterranean, but also at the junction between central Italy and the north-eastern margin of the rising northern Apennine chain. This confers great palaeobiogeographical significance to the two localities.

2. Stratigraphic setting

The Messinian (late Turolian) vertebrates from Verduno were collected from the fresh- and brackish-water deposits of the Cassano Spinola Conglomerates Formation, which are exposed along the Tanaro River and represent the uppermost term of the so-called "Pollenzo section" (coordinates: 44°41'9"N, 7°55'53"E; BERNARDI et al. 2010; DELA PIERRE et al. 2011; Fig. 3).

The stratigraphic study of the Messinian succession that crops out along the Tanaro River provided relevant information about the development of the Messinian Salinity Crisis (BERTINI & MARTINETTO 2011; DELA PIERRE et al. 2011). The basal part of the succession consists of the pre-evaporitic marine deposits of the Marne di S. Agata Fossili Formation (M.S.A.). The chronostratigraphic and palaeoecologic characteristics of the Messinian portion of this formation have been analyzed in detail by DELA PIERRE et al. (2011). The M.S.A. is overlain by the Primary Lower Gypsum Unit (ROVERI et al. 2008; LUGLI et al. 2010; DELA PIERRE et al. 2011, 2012), an evaporitic member of the Vena del Gesso Formation (ROVERI & MANZI 2007; ROVERI et al. 2008; LUGLI et al. 2010), which is characterized by a cyclic alternation of euxinic shales and primary shallow water gypsum deposits accumulated during the first stage of the Messinian Salinity Crisis (5.97–5.6 Ma; DELA PIERRE et al. 2011; MANZI et al. 2013). The Primary Lower Gypsum Unit is in turn overlain by the post-evaporitic deposits of the Valle Versa Chaotic Complex (DELA PIERRE et al. 2007, and references therein), which consist of slumped mudstones containing dislodged, meter-sized blocks of gypsum derived from the Primary Lower Gypsum unit. These deposits are overlain by the Cassano Spinola Conglomerates Formation, which accumulated during the Messin-

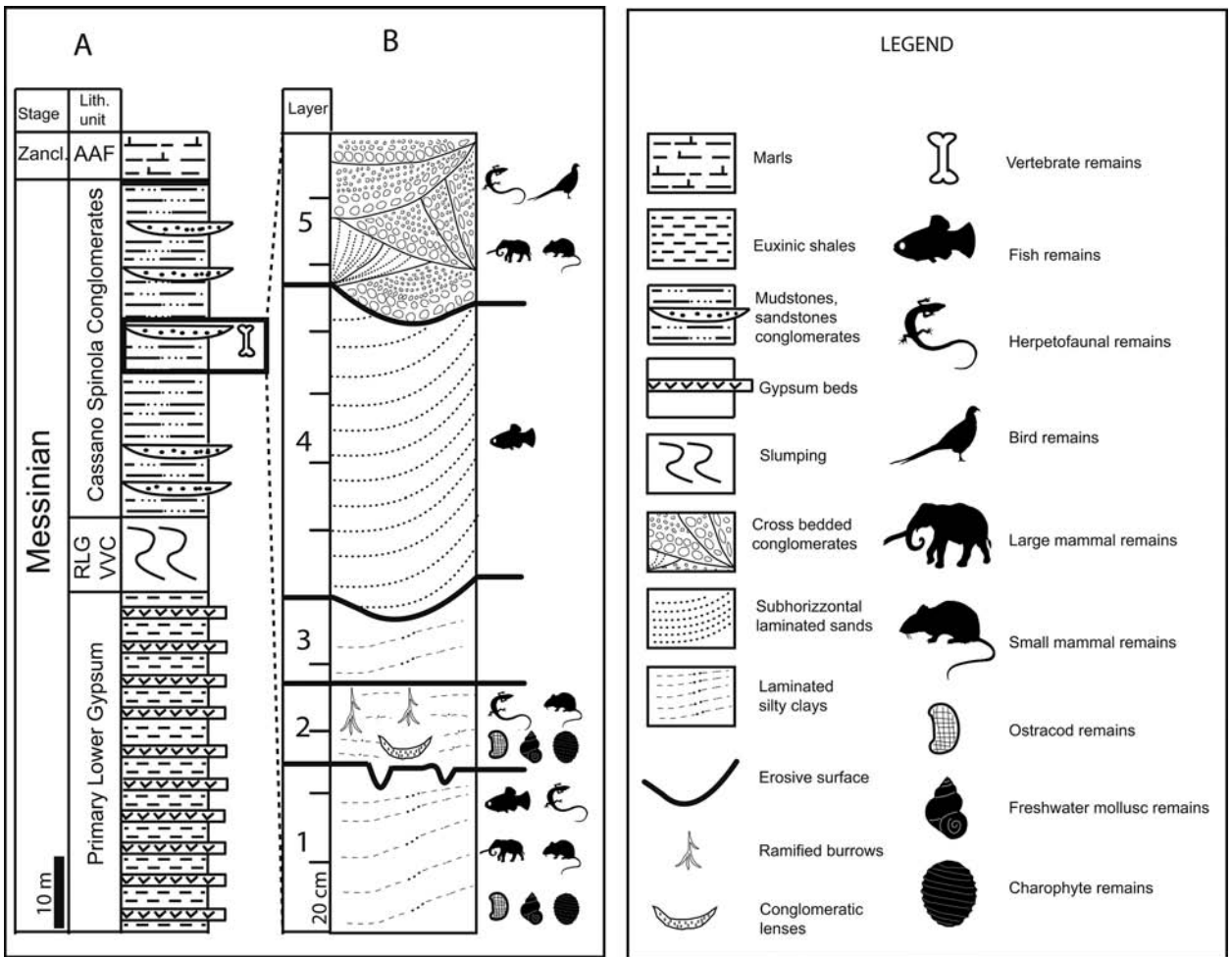


Fig. 3. The Pollenzo section with the stratigraphic position of the studied vertebrate remains described in the text. The box indicates the stratigraphic position of the excavation area. Lith. unit: lithostratigraphic unit; Zanclean: Zanclean; AAF: Argille Azzurre Formation; VVC: Valle Versa Chaotic Complex; RLG: Resedimented Lower Gypsum (modified after DELA PIERRE et al. 2011).

ian Salinity Crisis, approximately within the 5.55 to 5.33 Ma time span (DELA PIERRE et al. 2011). In the Pollenzo section, the Cassano Spinola Conglomerates Formation consists of 45 m of fresh- and brackish water terrigenous sediments (clays, marls and conglomerates). These are followed, upwards, by 30-40 cm of dark clays strongly bioturbated, and subsequently by the grey marls of the Argille Azzurre Formation. The latter contains the nannofossil *Reticulofenestra zancleana* and was thus referred to the lower Zanclean MNN12a calcareous nannofossils subzone (BERNARDI et al. 2010).

The vertebrate-bearing layers of the Cassano Spinola Conglomerates Formation (see COLOMERO et

al. 2013) lie about 20 m below the transition to Argille Azzurre Formation, which marks the Miocene-Pliocene boundary, and nearly 25 m above the Valle Versa Chaotic Complex. The vertebrate-bearing layers of the Cassano Spinola Conglomerates Formation include five distinct lithofacies, numbered 1 to 5 from the base upwards (Fig. 3). Lithofacies 1 consists of some 50 cm of grey to greenish silty clays, with parallel to oblique laminae. These deposits could be interpreted as overbank or waning flood deposits in a fluvial environment (EINSELE 1992). However, further detailed analyses are necessary to confirm this hypothesis. Skeletal remains of both large and small mammals, some of which partially articulated, were found about



Fig. 4. SEM photographs of charophyte gyrogonites and ostracods from lithofacies 1 of the vertebrate-bearing deposits of Verduno. **1-2** – *Lychnothamnus cf. barbatus*: 1: lateral view, 2: star-like basal opening. **3-4** – *Cyprideis* sp.: 3: female carapace, external lateral view, 4: male carapace, external lateral view. Scale bars equal 1 mm.

10 cm from the passage to lithofacies 2, which lies over the deposits of lithofacies 1 separated by an erosional surface associated with small sandy conglomerate lenses. The richly fossiliferous lithofacies 2 is composed of 10-15 cm of dark-brownish to black clays characterized, in the upper part, by abundant bioturbations, in the form of ramified burrows; the fossil content consists of abundant remains of small mammal remains. These vertebrate-rich deposits (lithofacies 1 and 2) also include gyrogonites of the charophyte *Lychnothamnus cf. barbatus* (1 and 2 in Fig. 4), opercula of *Bithynia*, as well as ostracod valves of the genus *Cyprideis* (Fig. 4.3-4.4). Lithofacies 3 is barren of fossil remains; it is lithologically similar to lithofacies 1, consisting of 10-15 cm of grey to greenish clays with subhorizontal to slightly oblique, irregularly laminated silty clays. The overlying lithofacies 4 exclusively includes disarticulated fish skeletal remains and consists of 50-90 cm of sub-horizontally- to obliquely-laminated greenish-greyish sands, with conglomerates at the base. Locally, the deposits of this lithofacies are

covered by the sediments of the present-day Tanaro River. An erosional surface marks the transition to the following lithofacies 5, which yielded remains of small mammals; this lithofacies consists of 20-50 cm of cross-bedded conglomerates with subcentimetric pebbles, mostly of reworked gypsum. The possibility that the fossil remains of small mammals from lithofacies 5 may be reworked cannot be ruled out. Some bones from this lithofacies were found still articulated (e.g., MCEA P00991), which indicates that bone burial must have been particularly rapid. Moreover, all the fossil remains from this lithofacies are uniformly dark brown to black-coloured and show no or low degree of abrasion. This evidence argues against reworking of the specimens. Lithofacies 1, 2 and 3 show a relatively high degree of lateral continuity. In contrast, lithofacies 4 and 5 are typical laterally-discontinuous fluvio-lagoonal deposits (EINSELE 1992) over erosive surfaces. These lithofacies have neither been observed in the type locality of the Cassano Spinola Conglomerates Formation, nor in any other places in Piedmont



Fig. 5. Fish remains from Verduno. **1-4** – *Aphanius crassicaudus*: 1-3: Abdominal vertebrae (MGPT-PU 130331), lateral view, 4: Scale. **5** – Lophiiformes indet., saccular otolith (MGPT-PU 130333), medial view. Scale bars equal 1 mm.

where the Formation crops out. This prevents any possible attempt to correlate them with other exposures.

3. Material and methods

The present material is stored both in the Museo Civico “Federico Eusebio” of Alba (Cuneo, North-western Italy), and in the Museo di Geologia e Paleontologia of the University of Torino, under the abbreviations MCEA and MGPT-PU, respectively. The morphometric measurements of the mammalian remains were taken with a digital calliper using standard measuring points. Morphometrical terminology for large mammalian specimens is in part that used by VON DEN DRIESCH (1976) with several additions. The osteometrics of birds are given in Table 1, those of large mammals in Table 2, and the odontometrics of insectivores in Table 3. Anatomical nomenclature follows SANCHIZ (1998) for anurans, SZYNDLAR (1984) for snakes, and AZANZA et al. (2013) for the pedicle morphology of Muntjacinae species. Dental nomenclature and measurement follow ANGELONE & SESÉ (2009) for lagomorphs. Capital letters are used for upper teeth (D, P, M) and lower case letters for lower teeth (d, p, m).

4. Systematic palaeontology

4.1. Fishes

Teleostei *sensu* PATTERSON & ROSEN, 1977
 Cyprinodontiformes *sensu* PARENTI, 1981
 Cyprinodontidae GILL, 1865
Aphanius NARDO, 1827
Aphanius crassicaudus (AGASSIZ, 1832)
 Fig. 5.1.-5.4

The fish skeletal material consists of about 250 well-preserved, hyperostotic elements of the axial skeleton, as well as of a few scales clearly belonging to the cyprinodontid

Aphanius crassicaudus. The material analyzed was largely collected from lithofacies 4, just a few specimens come from lithofacies 1. Abdominal vertebrae are by far the most abundant among the skeletal elements of the assemblage (Fig. 5.1-5.3), followed by caudal vertebrae, epineurals and scales; a fragmentary hypural fan (see PARENTI 1981) was also recognized.

The vertebral centra are strongly thickened and nearly rectangular in outline, longer than high. The abdominal centra bear prominent rounded to ovoid parapophyses along their lateral surface and variously developed neural spines, ranging from very large and spatulate to conical and postero-dorsally oriented (Fig. 5.1-5.3); small dorsal prezygapophyses can be recognized at the base of the anterior margin of the neural spine. The centra of the caudal vertebrae are roughly quadrangular in outline of the exhibiting an extreme degree of hyperostosis; the neural and haemal spines are posteriorly oriented with an angle measuring about 45°. Epineural bones are remarkably thickened, nearly fusiform in outline. The cycloid scales are very thick, characterized by 11 to 14 circuli and six to eight radii on the posterior field (Fig. 5.4).

All the identified fish skeletal elements were collected from lithofacies 1 and 4 are consistent with those of the cyprinodontid *Aphanius crassicaudus* (see GAUDANT 1979), a species widespread in the Mediterranean basin throughout the Messinian (see CARNEVALE et al. 2006b; CAPUTO et al. 2009; REICHENBACHER & KOWALKE 2009).

Lophiiformes GARMAN 1899
 ?Lophiiformes indet.
 Fig. 5.5

The single available saccular otolith is thick and nearly triangular in outline (MGPT-PU 130333; Fig. 5.5). Both the inner and outer surfaces are gently convex. The sulcus is rather wide, obliquely oriented; its posterior end is poorly distinguishable. The ostium appears to be narrow. The cauda is almost ovoid, characterized by a well developed roughly rounded colliculum.

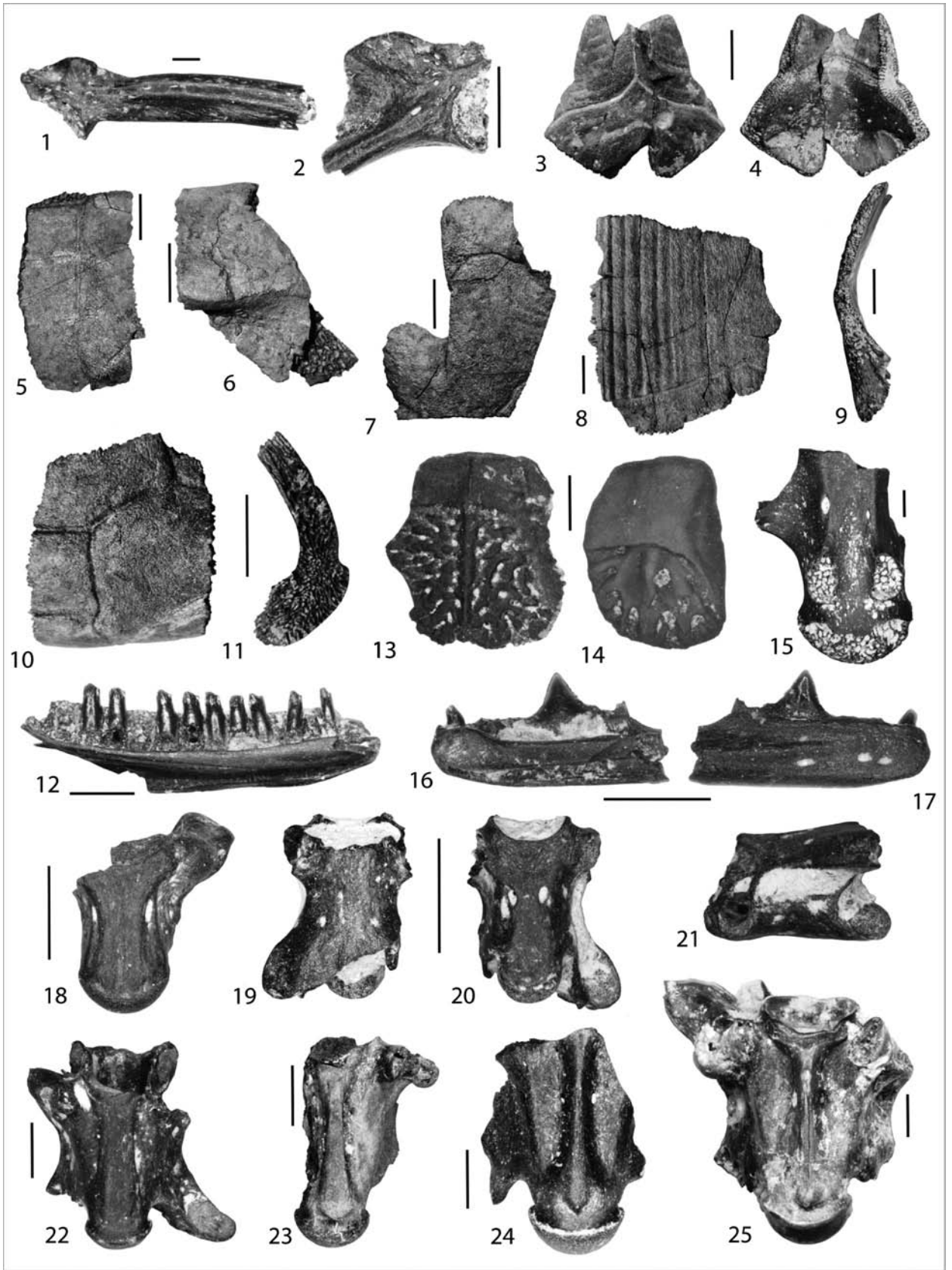


Fig. 6.

The taxonomic placement of the single otolith collected from lithofacies 1 is rather problematic. Several teleostean groups, including congroids, bythitidioids, lophiiforms, brachoidids and uranoscopids are characterized by a similar otolith morphology (e.g., NOLF 1985, 2013), probably resulted from convergent evolution. Abundant material consistent with the single specimen documented herein from Verduno was reported by CARNEVALE et al. (2006b, 2008) from upper Messinian deposits of Tuscany, central Italy, and tentatively referred to an indeterminate taxon of Lophiiformes.

4.2. Amphibians

Anura FISCHER VON WALDHEIM, 1813

Bufonidae GRAY, 1825

Bufo GARSALT, 1764

Bufo s.l.

Fig. 6.1

A small, fragmentary right ilium (MGPT-PU 132060; Fig. 6.1) has the typical traits of a bufonid anuran: pars cylindri-formis flattened mediolaterally but without crista dorsalis; tuber superior relatively massive, well-defined, and located in the anterior sector of the acetabulum; absence of a sulcus between the tuber and the base of the pars cylindri-formis; presence of the pars descendens (almost completely broken off). Although the preacetabular region is not preserved, a hardly visible depression could be identified as the fossa preacetabularis.

The poor state of preservation of this single remain, plus the complex, still unsettled systematics of European bufonids (e.g., FROST et al. 2006; SPEYBROEK et al. 2010), prevents from referring this fossil remain to any known genus. Based on the likely presence of a preacetabular fossa, as well as on the absence of an evident “calamita ridge” the specimen is possibly referable to the group of *Bufo viridis*.

Ranidae RAFINESQUE-SCHMALTZ, 1814

Rana LINNAEUS, 1758

Rana s.l.

Fig. 6.2

Two very small, fragmentary left ilia show a high crista dorsalis. Only the smallest of the two (MGPT-PU 132061; Fig. 6.2) preserves the tuber superior. The latter structure, prominent and flattened mediolaterally, is suggestive of juvenile individuals of *Pelophylax* and *Rana*. MGPT-PU 132061 is therefore classified generically as *Rana* s.l.

Anura indet.

A few fragmentary and highly damaged humeri, radioulnae, ilia, vertebrae, and urostyles do not preserve characters diagnostic of any given taxon.

4.3. Reptils

Testudines BATSCH, 1788

Testudo LINNAEUS, 1758

Testudo sp.

Fig. 6.3-6.8

The sample includes 1 nuchal (MGPT-PU 132062), 1 right first costal (MGPT-PU 132063), 2 undetermined costals (MGPT-PU 132064-5), 1 left third peripheral (MGPT-PU 132066), 2 undetermined peripherals (MGPT-PU 132067-8), 1 right epiplastron (MGPT-PU 132069), 1 right hyoplastron (MGPT-PU 132070), and 1 left hypoplastron (MGPT-PU 132071). The nuchal (Fig. 6.3-6.4) is characterized by a very narrow anterior edge, which is distinctly convex in anterior view and notched in dorsal view. The cervical scute

Fig. 6. Amphibians (1-2) and reptiles (3-25) from Verduno. **1** – *Bufo* s.l. right ilium (MGPT-PU 132060) in lateral view. **2** – *Rana* s.l., left ilium (MGPT-PU 132061) in lateral view. **3-6** – *Testudo* sp. **3-4**: nuchal (MGPT-PU 132062) in dorsal and ventral view; **5**: undetermined peripheral (MGPT-PU 132067) in external view; **6**: right epiplastron (MGPT-PU 132069) in dorsal view; **7** – right hyoplastron (MGPT-PU 132070) in ventral view; **8** – left hypoplastron (MGPT-PU 132071) in ventral view. **9-11** – Geoemydidae indet. **9**: left fifth costal (MGPT-PU 132072) in anterior view; **10-11**: undetermined peripheral from the bridge (MGPT-PU 132073) in external and anterior or posterior view. **12** – Lacertidae indet. left dentary (MGPT-PU 132075) in medial view. **13-14** – Anguinae indet. osteoderms (MGPT-PU 132079) in external view. **15** – *Varanus* sp. caudal vertebra in ventral view (MGPT-PU 132080). **16-17** – Agamidae indet. right dentary (MGPT-PU 132081) in medial and lateral view. **18** – *Amphisbaenia* indet. precloacal vertebra (MGPT-PU 132082) in ventral view. **19-21** – Scolecophidia indet. precloacal vertebra (MGPT-PU 132083) in dorsal, ventral and left lateral view. **22-25** – “Colubrinae” indet. precloacal vertebrae in ventral view (from left to right MGPT-PU 132084-7). Scale bars equal 1 mm (**1, 2, 12-25**) or 10 mm (**3-11**). Specimens **1-2** and **9-25** come from lithofacies 2, **3-8** from lithofacies 1.

is absent (also on the inner surface). On both sides, the first pleural scute slightly overlaps the nuchal somewhat in front of its lateral tip. The costals are trapezoidal in shape. The peripherals are elongated; the pleuro-marginal sulcus does not cross the peripherals, it rather corresponds approximately to the costo-peripheral suture (Fig. 6.5). The scar for the plastral buttress reaches at least the mid height of the inner surface of the third peripheral. The epiplastron is characterized by the anteroposterior length of the pad, which is slightly overhanging medially, producing a modest gular pocket (Fig. 6.6). The position of the gulo-humeral sulcus indicates that the gular scutes deeply entered the entoplastron. Despite the fragmentary state of the hyoplastron (Fig. 6.7), the axillary scute was manifestly absent, and the humero-pectoral sulcus reached the lateral edge of the hyoplastron quite far from the axilla, probably crossing the entoplastron (unfortunately, the hyo-entoplastron suture is not preserved). On the hypoplastron (Fig. 6.8), the abdomino-femoral sulcus is entirely placed far from the hypo-xiphoplastral suture and the latter was a real suture and not the surface of a hinge. Marked growth marks are visible on each shell bone, and especially on the costals and hypoplastron. All these elements, except the nuchal and right first costal, likely belong to a single specimen.

The morphology trapezoidal costals, as well as the position of the pleuro-marginal sulcus are suggestive of *Testudo*. The absence of the cervical scute distinguishes the Verduno tortoise from any of the extant members of *Testudo* and approximates it to *Testudo csakvarnensis* SZALAI, 1934, from the Late Miocene of Hungary, to *Testudo kalksburgensis* TOULA, 1896, from the Middle Miocene of Austria (see also BACHMAYER & MLYNARSKI 1981, fig. 1, for an epiplastral pad similar to that of MGPT-PU 132069), as well as to *Testudo pyrenaica* DEPÉRET & DONNEZAN, 1890, from the Pliocene (MN15) of France. *T. kalksburgensis* and *T. csakvarnensis*, however, have a cervical scute present on the inner surface of the nuchal; moreover, the nuchal is not notched, at least in *T. csakvarnensis* (MLYNARSKI 1976; LAPPARENT et al. 2006a, b). LAPPARENT et al. (2006a, b) have reported a certain degree of variability and homoplasy in the cervical scute of testudinids. Possible relationships of the Verduno tortoise with *T. pyrenaica* would need to be tested on a larger amount of fossil material. Detailed comparisons with the type of *Testudo craverii* PORTIS, 1880, from the Late Miocene of Santa Vittoria d'Alba (CN), are not possible because the latter consists only of the cast of the visceral surface of the shell (PORTIS 1880). CHESI (2009) recently considered *T. craverii* as an undetermined testudinid.

Geoemydidae THEOBALD, 1868

Geoemydidae gen. et sp. indet.

Fig. 6.9-6.11

A left fifth costal (MGPT-PU 132072; Fig. 6.9) is curved and maintains a constant anteroposterior width. The external surface shows a weak "ridge" approximately at mid height (as in extant *Mauremys*), together with the intervertebral and vertebro-pleural sulci. On a thickened projection close to the posterior edge of the visceral surface, it shows

the scar for the suture with the plastral buttress.

The left (?) peripheral from the bridge (MGPT-PU 132073; Fig. 6.10-6.11) is complete and entirely delimited by sutures; it is markedly bent but forms only a very weak external keel. The external surface of the peripheral hosts the pleuro-marginal and intermarginal sulci; the former is located far from the costo-peripheral suture. A short tract of the intercostal sulcus is also present, together with the sulcus between the marginals and an unknown plastral (pectoral or abdominal) scute. There is no scar for the plastral buttress on the visceral surface.

This set of characters is typical of geoemydids and of *Mauremys* in particular, a taxon that was present in the Late Miocene of Italy and that locally persisted until the Pleistocene (CHESI et al. 2007, 2009). Nonetheless, the scarcity of the fossil material does not allow an unambiguous taxonomic identification beyond the family level.

Lepidosauria HAECKEL, 1866

Squamata OPPEL, 1811

Lacertidae BONAPARTE, 1831

Lacertidae gen. et sp. indet.

Fig. 6.12

Lacertids are represented by 1 maxilla and 4 dentaries (MGPT-PU 132074-8; Fig. 6.12). A few fragmentary tooth-bearing bones share sets of elongated, slender, cylindrical, pleurodont, and bicuspid teeth. The posterior cusp is much larger than the anterior one. A longitudinal groove marks the lingual surface between the two cusps. There are no evident ornamentations on the main cusp. The sulcus Meckeli of the dentaries is entirely open. The teeth are tightly spaced and are visible in lateral view for about half their height.

Based on these characters, these specimens can be ascribed to a lacertid lizard approximately the size of a small *Podarcis*. Lacertid lizards are common in the Neogene fossil record of the European squamates, but their taxonomy is still unsettled because of the imperfectly known osteology of their living counterparts, and the apparently uniform skeletal morphology (see ROČEK 1984; BARAHONA & BARBADILLO 1997; ARNOLD et al. 2007, among others). The tooth-bearing bones MGPT-PU 132074-8 cannot be reliably classified at the genus level.

Anguinae GRAY, 1825

Anguinae GRAY, 1825

Anguinae gen. et sp. indet.

Fig. 6.13-6.14

About 20 relatively well-preserved osteoderms and numerous other osteoderm fragments (MGPT-PU 132079; Fig. 6.13-6.14) are referred to anguine lizards. Most of these elements, which are approximately rectangular in shape, are highly fragmentary. Externally and cranially, or both cranially and laterally, they show a smooth, overlapping-gliding surface. The rest of the external surface of the osteoderm,

often most of it, is streaked by a range of irregular grooves separated by ridges. A main, sagittal keel divides this part of the outer surface in two halves. Most of the best preserved osteoderms are slightly convex externally and concave internally. The internal surface is regularly smooth, but often pierced by at least two foramina.

Because osteoderms lack sufficient diagnostic characters to permit reliable systematic identification at the generic level, in a site they are usually classified generically based on the cranial remains they are associated with. It is agreed that when cranial remains reveal the presence of two taxa, osteoderms should not be ascribed to any known genus (AUGÉ & RAGE 2000). Nevertheless, the anguid osteoderms from Verduno show the typical morphological traits of the osteoderms of the anguine genera *Pseudopus* and *Ophisaurus*, and are manifestly distinct from those of *Anguis* whose osteoderms are non-rectangular and bear no keels. Non-*Anguis* anguine lizards are very common in the European and Italian Neogene fossil record (see KLEMBARA et al. in press, for a summary of the taxonomy of extinct European anguines). In modern Europe they are represented solely by *Pseudopus*, which is known only from the Balkans (GASC et al. 1997).

Varanidae GRAY, 1827
Varanus MERREM, 1820
Varanus sp.
 Fig. 6.15

Varanids are represented only by the nearly complete centrum of a caudal vertebra (MGPT-PU 132080; Fig. 6.15). The specimen is relatively large (as preserved, the centrum length is 9.5 mm, but it was originally somewhat longer) and elongated. It shows a set of diagnostic features: two pedestals for the chevron bone; a slight constriction cranially to the condyle (width of the centrum in proximity to the condyle: 4.5 mm); condyle dorsoventrally flattened (although somewhat eroded, the proportions of the condyle are nonetheless well-preserved: width: 5.3 mm; height 3.1 mm) and more extended cranially in its dorsal part than ventrally. A small central area of the cotyle is still preserved; the rest of the cotylar area, together with its rim are completely eroded or broken off. Based on its remnants, the right transverse process was rather dorsoventrally flat.

This set of morphologic features, and the precondylar constriction in particular, indicate that this relatively large vertebra belongs to monitor lizards, which in the Neogene of Europe are represented only by the genus *Varanus* (DELFINO et al. 2013a). The precondylar constriction was more extreme originally (as shown by the slightly different erosion of the condyle and by the evident notch on the best preserved right side of the centrum) to a degree similar to that of modern comparative specimens of *Varanus* spp. It is even stronger than that of the fossil *Varanus* vertebra from Brisighella (BRS 25), where the presence of *Varanus* sp. is testified by isolated teeth together with a fragmentary trunk vertebra (DELFINO 2002; ROOK & DELFINO 2007). At present, Verduno and Brisighella are the only Italian sites that yielded remains of monitor lizards (DELFINO et al. 2013b).

Acrodonta COPE, 1864
 Agamidae SPIX, 1825
 Agamidae gen. et sp. indet.
 Fig. 6.16-6.17

The rostral part of a tiny fragmentary right dentary (MGPT-PU 132081; Fig. 6.16-6.17), still preserves at least the first four positions, and teeth in the first and third position. The first tooth is not complete but seems conical and pleurodont. The third is triangular, labiolingually compressed (with a cutting mesiodistal edge), and clearly acrodont. The sulcus dentalis broadens in correspondence of the second tooth position. The sulcus Meckeli is quite narrow and reaches the symphysis, which is oval and is located where the dental shelf appears thickened. Three foramina open on the lateral surface of the dentary.

Based on the presence of acrodont teeth associated with pleurodont anterior teeth, the specimen can be confidently attributed to the clade Acrodonta and to Agamidae in particular, and not to Chamaeleonidae. Due to its fragmentary state, this single, probably juvenile dentary cannot be classified at genus level. The taxonomy of modern western Palaeartic agamids was recently revised. New genera (i.e., *Stellagama* and *Paralaudakia*: BAIG et al. 2012) have been described, also based on skeletal elements, but there are no elements for referring the fossil material from Verduno to any of these or other genera. Noteworthy is that despite the fact that agamids have been reported from several Italian Neogene and Quaternary localities (DELFINO 2002; ROOK & DELFINO 2007; DELFINO et al. 2008), so far chamaeleontids are absent from Italy (DELFINO 2006).

Amphisbaenia GRAY, 1844
 Amphisbaenia gen. et sp. indet.
 Fig. 6.18

A centrum and left prezygapophysis of the very fragmentary trunk vertebra (MGPT-PU 132082; Fig. 6.18) show features diagnostic of amphisbaenian vertebrae (DELFINO 2002, 2003). These include: prezygapophyseal facet roundish; small prezygapophyseal process, only just visible in dorsal view; diapophysis and parapophysis fused in a single, globular and prominent paradiapophysis; ventral surface of the centrum flat and devoid of any hypapophysis or keel, with slightly concave, well-defined lateral edges; elongated subcentral foramina; condyle and cotyle proportionally large and markedly dorsoventrally depressed.

Amphisbaenian vertebrae do not have characters that permit to classify them at the genus level. However, MGPT-PU 132082 is morphologically compatible with an anterior trunk vertebra of blaniids, which are the only amphisbaenians identified so far in Europe on fairly rare cranial remains (DELFINO et al. 2013c). Amphisbaenians had been already found in the Upper Miocene deposits of Ciabòt Cagna, in Northwestern Italy (CAVALLO et al. 1993).

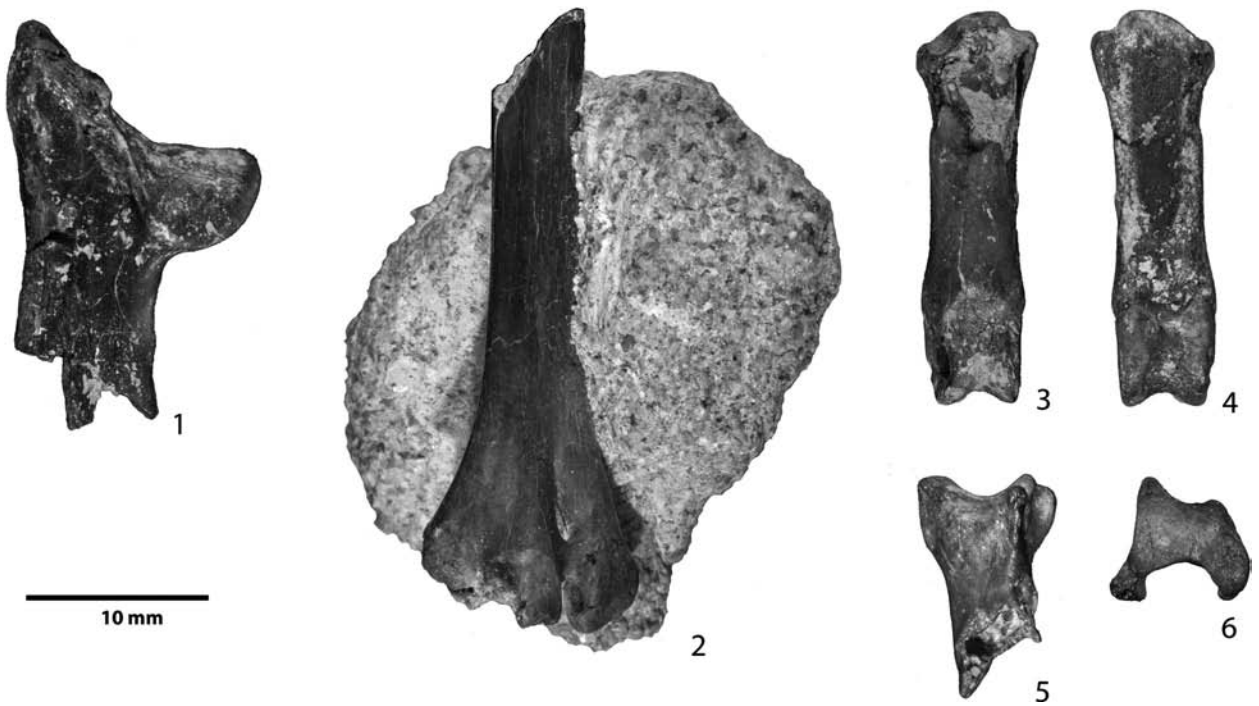


Fig. 7. Bird remains from lithofacies 5 of the Verduno sequence. **1** – Phasianidae gen. et sp. indet., right scapula (MGPT-PU 135006), lateral view. **2** – Galliformes indet., left tarsometatarsus (MGPT-PU 135007), dorsal view. **3-4** – Accipitridae gen et sp. indet., left posterior phalanx 2/II (MGPT-PU 135008), dorsal 3: and plantar 4: views. **5-6** – Strigididae gen. et sp. indet., left posterior phalanx 1/II (MGPT-PU 135009), **5**: dorsal and **6**: proximal views. All the specimens come from lithofacies 5.

Serpentes LINNAEUS, 1758
 Scolecophidia COPE, 1864
 Scolecophidia gen. et sp. indet.
 Fig. 6.19-6.21

The fragmentary trunk vertebra MGPT-PU 132083 (Fig. 6.19-6.21) shows the following characters: small size (length of the centrum: about 1.2 mm); absence of neural spine; elongated depression at the base of the broken cranial edge of the neural arch, which indicates the former presence of zygosphenes; parapophysis well-developed although fragmentary; cotyle and condyle moderately dorsoventrally-depressed and proportionally small; ventral surface of the centrum slightly convex with ill-defined lateral edges; postzygapophyseal facet distinctly elongated; presence of zygantrum indicated by the posterior edge of its facet visible on the left side of the vertebra (reaching the surface of the concretion that fills the neural canal); neural canal very large in posterior view; posterior edge of the neural arch depressed in caudal view.

All these characters, the absence of neural spine in particular, are suggestive of scolecophidians. Isolated vertebrae of scolecophidian, however, are considered not diagnostic at the genus level (SZYNDLAR 1991; MEAD 2013).

Hence, the vertebra from Verduno can be identified simply as Scolecophidia indet. This group of diminutive, fossorial snakes is currently represented in Europe by a single species, *Typhlops vermicularis* MERREM 1820, which inhabits only the Balkan Peninsula (GASC et al. 1997). Although European scolecophidians had a much wider range in the past (MEAD 2013), they were never reported in the Italian fossil record until recently, when another single vertebra was described from the Late Miocene of Moncucco Torinese (DELFINO et al. 2013d; FERRO 2013). Preservational and/or collecting biases (sediments should be wet-screened with mesh less than 1 mm diameter) may account for its absence from other Italian localities.

Caenophidia HOFFSTETTER, 1939
 Colubridae OPPEL, 1811
 “Colubrines” sensu SZYNDLAR, 1991
 “Colubrines” gen. et sp. indet.
 Fig. 6.22-6.25

Six fragmentary trunk vertebrae (MGPT-PU 132084-9; Fig. 6.22-6.25) are referred to the informal taxon “colubrines” for the absence of the hypapophysis (SZYNDLAR 1991). The

fragmentary state of these specimens renders their identification difficult, but morphological differences in the haemal keel indicate the presence of at least two taxa. MGPT-PU 132084 (Fig. 6.22) shows a low, broad and blunt haemal keel, quite different from the thin and prominent keel of MGPT-PU 132087 (Fig. 6.25); the fragmentary centrum of the latter is also associated to an isolated prezygapophysis characterized by a long, thin, and pointed process.

Squamata gen. et sp. indet.

A number of fragmentary or otherwise well-preserved, but not informative elements were referred to Squamata gen. et sp. indet. In particular, a few fragmentary trunk vertebrae or well-preserved caudal vertebrae can be only referred to Serpentes gen. et sp. indet. These remains likely belong to some of the taxa listed above.

4.4. Birds

Galliformes TEMMINCK, 1820

Phasianidae HORSFIELD, 1821

Phasianidae gen. et sp. indet.

Fig. 7.1

This family is represented by a right scapula (MGPT-PU 135006; Fig. 7.1) with a well-preserved cranial end and crushed cranial part of the diaphysis. The specimen shows the typical galliform triangular-shaped facies articularis humeralis, with the mediolateral diameter that exceeds the dorsoventral diameter. The acromion is not bent laterally, like in Phasianidae and unlike Tetraonidae. Dimensionally, the scapula falls in the variability of the scapulae of the largest Phasianidae of the European Miocene, *Miogallus altus*. Morphologically, however, the ventral angle of the facies articularis humeralis of MGPT-PU 135006 is not bent cranially (GÖHLICH & GROSS in press). MGPT-PU 135006 also differs from modern *Phasianus* and *Gallus* in having a wider, rounded and not medially bent acromion. It is also smaller than *Pavo bravardi*, described from the Pliocene of France and found in various Pliocene localities in Europe (MOURER-CHAUVIRÉ 1989, 2004). Avian scapulae are rarely found fossil and seldom preserve morphological characters that are taxonomically diagnostic.

Galliformes indet.

Fig. 7.2

This second galliform is attested to by the distal half of a left tarsometatarsus (MGPT-PU 135007; Fig. 7.2), with heavily damaged distal end. Only the trochela metatarsi IV is still preserved. The specimen can be referred to Galliformes for the well-developed crista medianoplantaris, as well as the shape of the foramen vasculare distale. The bad state of preservation prevents any accurate specific identification.

Accipitriformes SHARPE, 1874

Accipitridae VIEILLOT, 1816

Accipitridae gen. et sp. indet.

Fig. 7.3-7.4

These diurnal birds of prey are represented by the damaged proximal end of a large left posterior phalanx 2/II (MGPT-PU 135008; Fig. 7.3-7.4). The plantoproximal process of the bone is blunt and does not protrude proximally, the depressions on the side of the distal end are very deep and well-defined, and in dorsal view the depression located proximally to the distal end is not as deep as in Strigiformes. Based on all these features the specimen is accommodated in Accipitridae. Dimensionally, the phalanx has a size comparable to that of the extant *Aquila pomarina*. Nonetheless, because the systematic affinities of the Neogene Accipitridae are awaiting revision (MLÍKOVSKÝ 2002), MGPT-PU 135008 is not assigned to named species.

Strigiformes WAGLER, 1830

Strigidae RIDGWAY, 1914

Strigidae gen. et sp. indet.

Fig. 7.5-7.6

The proximal end of a left posterior phalanx 1/II (MGPT-PU 135009; Fig. 7.5-7.6) with damaged distal end, has the typical morphological traits of Strigiformes. The bone is stout and the dorsal side of its proximal end is concave in proximal view and not convex as in Tytonidae (PAVIA & MOURER-CHAUVIRÉ 2011). For this reason it can be referred to Strigidae. MGPT-PU 135009 belongs to a large-sized Strigidae, intermediate in size between modern *Strix aluco* and *Bubo bubo*. Because of the bad state of preservation, which obliterated useful diagnostic features, but also of the absence of suitable reference fossil material to compare with, MGPT-PU 135009 can not be reliably attributed to any given species.

4.5. Mammals

Proboscidea ILLIGER, 1811

Gomphotheriidae gen. et sp. indet.

Figs. 8.1-8.2, 9

A gomphothere proboscidean is represented by few fragments of tusks, two very worn second upper molars, one right (MCEA P01086) and one left (MCEA P01087; Fig. 8.1-8.2), 14 thoracic vertebrae, 17 ribs, a left scapula (MCEA P01088), coxal bone fragments, two fragments of femur, four phalanges, plus other six undetermined fragments. All the bones belong to a single individual. Part of them were found in anatomical connection (Fig. 9). Most of these fossil bones are under restoration and still unlabelled.

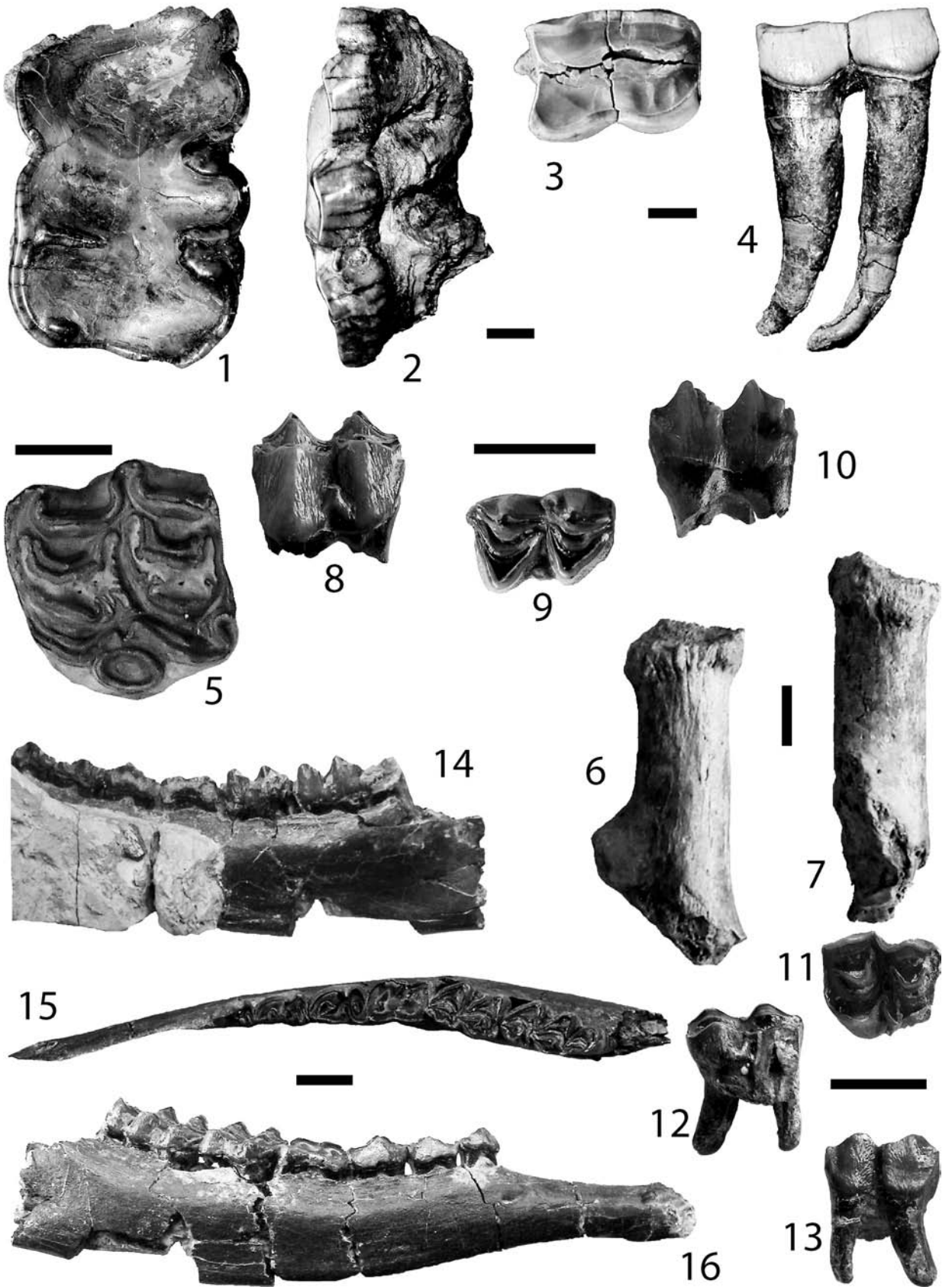


Fig. 8.

Perissodactyla OWEN 1848
 Rhinocerotidae gen. et sp. indet.
 Fig. 8.3-8.4

Three rhinoceros cheek teeth, a small fragment of an upper one (MCEA P00944), a right lower premolar (MCEA P00968; Fig. 8.3-8.4) and the distal half of a right lower molar (MCEA P00912), are included in the bone assemblage. The upper tooth is only a small part of the ectoloph, and the two lower teeth are excessively worn to permit any sure taxonomical attribution.

Equidae GRAY 1821

Cremohipparion cf. *C. macedonicum* (KOUFOS, 1984)
 Fig. 8.5

A quite worn left upper first molar (MCEA P00977; Fig. 8.5) is morphologically and dimensionally suggestive of *Cremohipparion macedonicum* (KOUFOS, 1987), to which the isolated specimen is therefore ascribed to this species. The fossettes are free and closed with a fairly high enamel plication, especially in the prefossette and the mesial border of the postfossette. The hypocone is elliptical. The hypocoanal groove is short, simple and fairly shallow, probably due to wear. The pli-caballin is simple. The protocone is isolated, small and moderately elliptical. Although it falls in the size-ranges of the first upper molars of *Hippotherium malpassii* from Monticino Quarry (BERNOR et al. 2011; ROOK & BERNOR 2013), it differs morphologically from the latter in having much simpler pre- and postfossette borders and single, and not complexly ornamented, pli caballin.

Artiodactyla OWEN, 1848
 Cervidae GOLDFUSS, 1820

Euprox sp.
 Fig. 8.6-8.10

Three specimens belong to *Euprox* sp., an isolated left pedicle (MCEA P00959; Fig. 8.6-8.7) and three right lower second molars (MCEA P00935, MCEA P00938; Fig. 8.8-8.10). The pedicle includes a fragment of the frontal bone at its base and the burr (or coronet) at the distal end. The cross-section is roughly circular.

In the lower molars the metaconid and entoconid ribs are very prominent. Mesostylid and metastylid are well-developed, entostylid very weak. The external postprotocristid (= "*Palaeomeryx* fold") is absent. A fairly-developed cingulid occurs on the mesial and distal sides of the teeth. The teeth bear also a marked ectostylid. The enamel is rugose.

The pedicle (MCEA P00959) has the characters of AZANZA et al. (2013) large morphotype 1. It is moderately long ($1.5 < \text{length/transverse diameter} = 1.97 < 3.0$), strongly inclined backwards and set partially on the cranial cavity.

Pliocervus sp.
 Fig. 8.11-8.16

A number of specimens show characters typical of a primitive cervid. They include: a right upper second premolar (MCEA P00957), a right upper first molar (MCEA P00936; Fig. 8.11-8.13), a left upper third molar (MCEA P00952), a left hemimandible (MCEA P01085), still preserving most of its cheek toothrow (p3-m3), two fragmental hemimandibles, one left (MCEA P00960a), also preserving most of its cheek toothrow (p3-m3), and one right (MCEA P00960b; Fig. 8.14-8.16), with p2-m3, the two almost complete hemimandibles of a senile mandible (MCEA P00907), a right lower third premolar (MCEA P00937), a cervical vertebra (MCEA P00965), a thoracic vertebra (MCEA P00998), a fragmental left radius (MCEA P00919), a left calcaneum (MCEA P00972), a right naviculocuboid (MCEA P00993), two fragmental left metatarsal bones (MCEA P00962, MCEA P00994), a fragmental metapodial (MCEA P00925), two complete phalanges (MCEA P00995 and MCEA P00996).

The second upper premolar has a rounded lingual outline. The anterior style is strong and the labial rib of the anterolabial cone well-developed. The posterolabial cone and the posterior style are not preserved in the available specimen. A single cone appears lingually. A very strong and long enamel fold issues anterolingually from the lingual cone. The anterolingual and posterolingual cristae are fused to the anterior and posterior styles, respectively.

The upper molars have robust paracone rib, and well-developed parastyle and mesostyle. The labial column of the metacone and the metastyle are weaker. A tiny external postprotocristid (= "*Palaeomeryx* fold") occurs: in advanced stages it fuses to the premetaconulecrista forming a fossetta at the center of the tooth. A weak cingulum is

Fig. 8. Large mammal remains from Verduno. **1-2** – Gomphotheiidae gen. et sp. indet., left M2 (MCEA P01087), 1: occlusal view, 2: lingual view. **3-4** – Rhinocerotidae gen. et sp. indet., right lower premolar (MCEA P00968), **3**: occlusal view, 4: lateral view. **5** – *Cremohipparion* cf. *C. macedonicum*, left upper first molar (MCEA P00977), occlusal view. **6-7** – *Euprox* sp., left pedicle (MCEA P00959), 6: dorsal view, 7: medial view. **8-10** – *Euprox* sp., right lower second molar (MCEA P00938), 8: buccal view, 9: occlusal view, 10: lingual view. **11-13** – *Pliocervus* sp., right upper first molar (MCEA P00936), 11: occlusal view, 12: lingual view, 13: buccal view. **14-16** – *Pliocervus* sp., right hemimandible (MCEA P00960b), 14: medial view, 15: dorsal view, 16: lateral view (detail). Scale bars equal 1 cm. Specimens **1-2**, **5-7**, **14-16** come from lithofacies 1, **3-4**, **8-13** from lithofacies 5.



Fig. 9. Partial skeleton of Gomphotheriidae from Verduno during the excavation.

present at the mesial base of the protocone and along the distal border of the tooth. An entostyle issues from the distal base of the protocone.

The lower second premolar has an anterior conid, whereas the anterior stylid is missing. The mesolabial and mesolingual conids are fused and the posterolingual cristid is well-developed. The posterior and back valleys are squeezed between the posterolingual cristid and the strongly backward oriented posterior cristid, and between the latter and the posterior stylid, respectively. The posterior stylid is oriented transversely to the tooth axis. The posterolabial conid is weak. The lower third premolar bears a well-developed anterior conid and anterior stylid. The anterolabial cristid bends markedly lingually. The transverse cristid is strongly inclined backwards. A strong posterolingual cristid emerges from the mesolingual conid. The anterolingual

cristid is weak and seems emerging from the base of the mesolingual conid. The posterior cristid is as long as the posterior stylid and both are slightly inclined backwards. The posterior stylid is oriented transversely. The posterolabial conid protrudes labially and is separated from the mesiolabial conid by a strong depression. In p4 anterior stylid and anterior conid are fused to the anterolingual cristid. The anterior valley is isolated and forms a large fossette. The transverse cristid is inclined backward. A strong posterolingual cristid emerges from a well-developed mesolingual conid. The posterior cristid is markedly oriented backward and fused to the robust posterior stylid. The back valley forms an isolated fossette. The posterolabial conid is strong, very prominent labially, and is separated from the mesiolabial conid by a very marked depression. The lower molars have a prominent labial metaconid rib, and a weaker entoconid

rib. The mesostylid and entostylid are weak, whereas the metastylid is well-developed. The metaconid-complex and entoconid-complex are slightly inclined to the tooth axis. All the molars bear a strong ectostylid and mesial cingulid. There is no distal cingulid. In m3 there is a tiny posterior ectostylid at the base of the hyponulid. The external post-protocristid (= "*Palaeomeryx* fold") is absent. The enamel is rugose in all cheek teeth.

The mandible is long and slender. The anterior edge of the ascending ramus reclines at an angle of about 127° to the alveolar margin of the cheek tooththrow. The ventral profile of the horizontal ramus is gently concave under the cheek tooththrow and turns slightly concave under the long and slender rostral portion. The c-p2 diastema is elongated. The processus angularis does not appear to protrude.

The cervical vertebra has a vaguely pentagonal cranial articular surface, which appears slightly inclined to the axis of the vertebral corpus in lateral view. Ventrally the corpus is distinctly keeled and markedly concave. The transverse foramina are fairly small. In cranial view they open by the sides of the upper half of the articular surface.

The spinous process of the thoracic vertebra is slender and inclined caudally. The transverse processes are robust, laterally fairly short and relatively elongated cranio-caudally. The cranial articular surface is oval. The vertebral corpus is short and slightly concave ventrally in lateral view.

The head of the radius (caput radii) is transversely enlarged and narrow in antero-posterior diameter. The proximal articular surface of the radius has two concavities of quite different size. The medial concavity is wide and sub-circular, the lateral is much smaller and roughly kidney shaped. The two concavities are separated from each other by a wide and deep groove for the crest of the distal humeral trochlea.

The calcaneum is slender. The distal part of the bone, from the articular surfaces for the astragalus, is about 1/3 the greatest length of the bone. The tuber calcanei is compressed latero-medially, with an acute dorsal margin. In medial view the plantar border of the sustentaculum does not protrude beyond the plantar margin of the bone. The distal articulation for the naviculocuboid is narrow and concave.

The naviculocuboid is narrow and low. On the proximal articular surface for the astragalus the two plantar processes have a rounded outline. The medial one surpasses the lateral one in height. The astragalal ligamentous fossa is narrow, deep and located in the naviculocuboid suture, at the base of the lateral plantar process.

The metatarsal bone is distinctly grooved both dorsally and plantarly. The distal articular surfaces for the first phalanges have well-developed keels extended completely around the articular surface. The keels of the two pulleys are parallel to one another. The first phalanx is long and slender. The second is one third shorter than the first phalanx.

The teeth from Verduno closely resemble those of *Cervavitus*, *Procapreolus*, and *Pliocervus*. Dentally, *Pliocervus* is relatively more advanced than *Cervavitus* and *Procapreolus* in the lack of the "*Palaeomeryx* fold" and in the tendency to lose the cingulids in the lower molars (CZYZEWSKA 1968). For this reason, the remains of primitive cervid from Verduno are referred to *Pliocervus* sp.

Palaeomerycidae FRICK, 1937

aff. *Palaeomeryx*

Fig. 10.1-10.5

A relatively small giraffid is represented by only a few specimens: a fragmental right mandible, with no teeth preserved (MCEA P01006; Fig. 10.1-10.3), an upper tooth fragment (MCEA P00908; Fig. 10.4-10.5), a complete axis (epistropheus) (MCEA P00980), a fragmental left radius (MCEA P01008), a fragmental juvenile right ulna (MCEA P00997), two fragmental left metacarpal bones (MCEA P00927, MCEA P01007), and a complete sesamoidal (MCEA P00999).

The tooth is brachyodont and shows a very strong labial column and a well-developed style. The enamel is rugose.

The mandible fragment includes the rostral part of the horizontal ramus from under the molars to the mental foramen and part of the mandibular symphysis. The specimen is very slender, with an extended diastema and a distinctly straight ventral profile.

The axis is elongated. The vertebral corpus has a median ventral crest, which terminates in a slender, elongated tubercle behind. The dens has a convex articular surface ventrally and is deeply concave dorsally. The dorsal face of the dens shows two irregular depressions for the attachment of the odontoid ligament. The cranial articular surface is saddle-shaped: it surrounds the dens and is confluent below with its ventral surface. The transverse processes are relatively small and project backward and downward. The transversarium foramina are wide. The spinous process is high and markedly inclined cranially. The caudal articular processes are rhomboidal. The caudal articular surface is deep and circular.

The head of the radius (caput radii) is transversely enlarged and very narrow in antero-posterior diameter. The proximal articular surface of the radius has two concavities quite different in size. The medial concavity is wide and sub-circular, the lateral is much smaller and roughly rectangular. The two concavities are separated from each other by a wide, but not very deep groove for the crest of the distal humeral trochlea.

The tuber (tuber olecrani) of the ulna is long and wide in medio-lateral view, and slender cranially with a smooth crest-like anterior margin. The medial and lateral coronoid processes (processi coronoideus medialis et lateralis) are fairly broad. The trochlear notch (incisura trochlearis) is relatively wide latero-medially. The radial notch (incisura radialis) is wide and deep.

This species is also present at Moncucco Torinese (ANGELONE et al. 2011). The characters of the fragmental upper cheek tooth and of the mandible resemble those of giraffids or cervids. The tooth, however, is much larger than the teeth of any cervid of the time. Morphologically and dimensionally, it recalls the cheek teeth of *Palaeotragus*, and in particular of *P. rouenii*. The mandibular diastema, however, is far too short for *Palaeotragus* (p2 alveolus – symphysis distance: ~ 70 mm). A suitable alternative is *Palaeomeryx*, which combines giraffid-like teeth with relatively short mandibular diastemas. In Europe, however, *Palaeomeryx* becomes extinct around 9 Ma (MN 10).

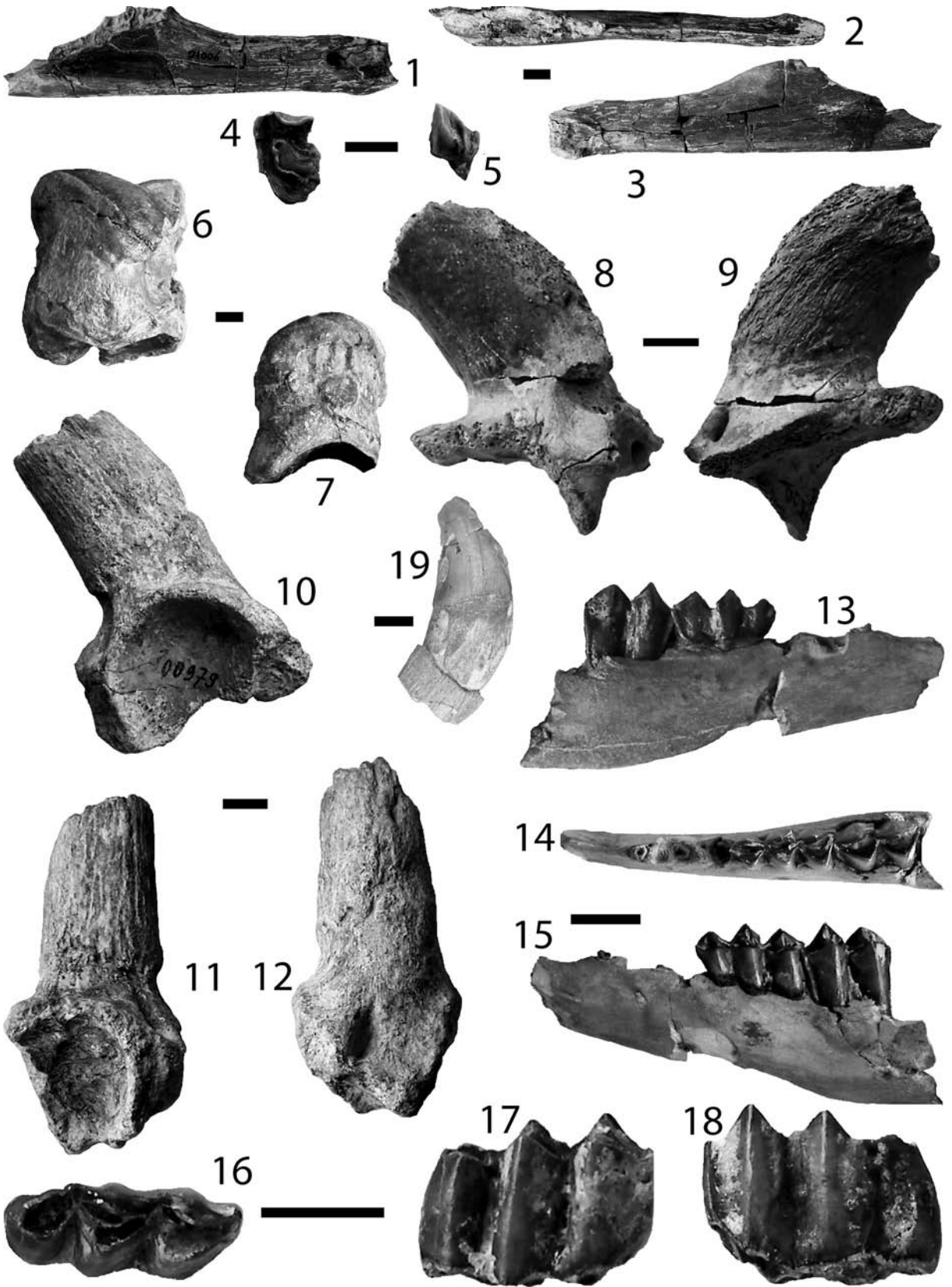


Fig. 10.

The specimens have been also compared with the remains of the enigmatic giraffid *Umbrotherium azzarolii* from several Italian Late Miocene localities (Fiume Santo, Sardinia; Baccinello V2 and Casteani, southern Tuscany). The tooth Verduno, however, is far more brachyodont than the latter species.

Giraffidae GRAY, 1821

Helladotherium sp. (?*Bramatherium*)

Fig. 10.6-10.7

A complete and fairly well preserved second phalanx (MCEA P00992; Fig. 10.6-10.7) belong to a huge Sivatheriinae giraffid. The proximal articular surface consists of two concave facets for the first phalanx, which are separated by a smooth ridge. The two facets are somewhat inclined and are of different transversal size. Distally, the articular surface is markedly oblique. It consists of two very convex and inclined facets, one extended dorsally over the other.

The specimen is slightly larger and more massive than the second phalanges of the Asian *Samotherium sinense*. Huge Macedonian Late Miocene sivatheriine giraffids, among which *Helladotherium duvernoyi*, have been recently described by GERAADS (2009). The Balkan *Helladotherium* is closely related, or even congeneric, with *Bramatherium*, another huge giraffid from Iran. Unfortunately, the phalanges of Macedonian representatives are not preserved. Nonetheless, considering that Sivatheriinae grew progressively larger over time, the dimensions of the second phalanx from Verduno would be compatible with those of a late, very large-sized *Helladotherium* (pers. comm. D. GERAADS, 2013).

Bovidae GRAY, 1821

?*Paraoioceros* (*Hispanodorcas*?) *occidentalis*

(MASINI & THOMAS, 1989)

Fig. 10.8-10.9

A spiral-horned antelope is present at Verduno with a right frontal bone with part of the orbital cavity and basal stump of the horncore (MCEA P00975; Fig. 10.8-10.9), a fragmental left horncore (MCEA P00974), a right upper third molar (MCEA P00953), a right lower fourth deciduous premolar

(MCEA P00923), and a cervical vertebra (MCEA P00966).

The horncore is massive at the base, slightly divergent laterally, twisted helicoidally counter-clockwise, and moderately grooved. The basal cross section is elliptical. The pedicle is short, inserted above the orbit, weakly inclined posteriorly with a gently curved posterior edge. The postcornual fossa is wide, but not very deep. The supraorbital foramen is moderately-sized and located in a deep pit close to the pedicle. A shallow lateral longitudinal groove on the horncore is aligned to the postcornual fossa, but does not extend on to the pedicle. The frontal bone is thick. Distally, the horncore is slender, gently twisted, and still elliptical in cross section.

The upper third molar is hypsodont. It has a strong paracone rib, a much weaker metacone rib, fairly strong styles, and prominent, but not very robust mesostyle. The metaconule crescent is U-shaped, whereas the protocone crescent is slightly more angulate. A very weak cingulum occurs at the base of the metaconule. The entostyle is absent.

In the lower fourth deciduous premolar the anterolingual conid has a lingual rib more prominent than those of the metacond and entoconid. The anterior styloid is hardly developed, the antostyloid is relatively stronger, the metastyloid is very weak, and the mesostyloid is absent. The labial crescents are moderately angulate. The tooth bears a small anterior ectostyloid, a much larger ectostyloid, and a very weak "goat" fold. No other cingulids occur.

The enamel is weakly wrinkled in these teeth.

In lateral view, the cervical vertebra has a cranial articular surface markedly inclined to the axis of the vertebral corpus. The transverse foramina are large. In cranial view they open by the sides of the articular surface.

The set of horncore, cranial and dental characters, and in particular the short pedicle, wide postcornual fossa, elliptical and moderately grooved horncore, strong cheek teeth styles, and absence of entostyle resemble *Paraoioceros occidentalis* (originally *Samotragus occidentalis* MASINI & THOMAS, 1989, emended by KOSTOPOULOS in press). Nonetheless, the weakly inclined horncore inserted above the orbit and the shallow lateral longitudinal groove are also remotely reminiscent of *Hispanodorcas*. This genus is reported from Spain and Greece from Vallesian to Ruscinian times (MN10-MN14; KOSTOPOULOS, in press).

The species from Verduno is the second spiral-horned antelope known from Italy. In fact, it adds to the holotype of *Paraoioceros occidentalis*, from Monticino Quarry (Brisighella, north-eastern Italy). Yet another fragmental

Fig. 10. Large mammal remains from Verduno. **1-3** – aff. *Palaeomeryx*, right mandible (MCEA P01006), 1: lateral view, 2: dorsal view, 3: medial view. **4-5** – aff. *Palaeomeryx*, upper tooth fragment (MCEA P00908), 4: occlusal view, 5: buccal view. **6-7** – *Helladotherium* sp., second phalanx (MCEA P00992), 6: dorsal view, 7: side view. **8-9** – *Paraoioceros occidentalis*, right frontal bone (MCEA P00975), 8: lateral view, 9: medial view. **10-12** – *Gazella* aff. *G. pilgrimi*, skull fragment (MCEA P00979), 10: lateral view, 11: medial view, 12: dorsal view. **13-15** – *Gazella* sp., juvenile left horizontal ramus (MCEA P00956), 13: medial view, 14: dorsal view, 15: lateral view. **16-18** – *Gazella* sp., right lower third molar (MCEA P00958), 16: occlusal view, 17: buccal view, 18: lingual view. **19** – cf. Camelidae from Verduno, right lower canine (MCEA P01084), labial view. Scale bars equal 1 cm. Specimens **1-4**, **8-12**, **16-19** come from lithofacies 5, **6-7** and **13-15** from lithofacies 1.

skull roof with both horncores, yet unpublished, was found at Borro Strolla, a Late Miocene fossiliferous locality near Siena (central Italy) (ABBAZZI et al. 2008b). The specimen is kept in the Paleontological Section of the Museum of Natural History of Florence and is classified as *Samotragus occidentalis*. Italian spiral-horned antelopes seem to have been more frequent than hitherto believed.

If the spiral-horned antelope from Verduno actually belongs in *Hispanodorcus*, it adds to the representatives from Monticino Quarry and Borro Strolla bridging the gap between the Iberian and Balkan distribution of this genus. If not, the two antelopes might have been somehow related to one another.

Gazella aff. *G. pilgrimi* (BOHLIN, 1935)

Fig. 10.10-10.12

A second antilopine bovid is attested to by a skull fragment (MCEA P00979; Fig. 10.10-10.12), the apical part of a left horncore (MCEA P00940), and the distal part of a left metatarsal cannon (MCEA P00971). Another specimen tentatively ascribed to the same taxon is a right pubis (MCEA P00930).

The skull fragment includes part of the right frontal bone with part of the braincase, the basal stump of right horncore and the dorsal part of the right orbital cavity. The horncore is compressed latero-medially, flatter laterally and more convex medially, has a short pedicle, and is very closely situated to the orbital cavity. Its surface is densely streaked by thin, shallow, straight longitudinal grooves. The basal part curves gently backwards. The postcornual groove is fairly deep. The DT (24.6) × 100/DAP (31.7) index at the base of the horncore is 77.6. The supraorbital foramen is a relatively long and deep pit.

In the metatarsal cannon the dorsal gully is open at its distal end. The distal articular surfaces for the first phalanges bear strongly developed keels, which extend completely around the articular surfaces. The keels of the two pulleys are parallel to one another.

The horncore of the skull fragment MCEA P00979 has basal sizes that fall in the dimensional ranges of *G. deperdita* (HEINTZ 1971), but is more compressed latero-medially than in the latter species. *Gazella pilgrimi* has horncores strongly inclined backwards and compressed mediolaterally, with a well grooved surface, and with short pedicles (BOHLIN 1935). The horncore (MCEA P00979) shows most of these features. It is quite close to, and as large as, *Gazella* aff. *G. pilgrimi* from Kohfidisch (VISLOBOKOVA 2007), and somewhat larger-sized than the same taxon from Akkaşdağı (KOSTOPOULOS 2005). For this, this antelope from Verduno is referred to *Gazella* aff. *G. pilgrimi*.

Gazella sp.

Fig. 10.13-10.18

A third antilopine ruminant is relatively well represented in the Verduno sample. The remains include a right deciduous upper second premolar (MCEA P00983), a fragmental left deciduous upper third premolar (MCEA P00984), a

right upper second molar (MCEA P00943), a fragmental left horizontal ramus with d4 and m1 (MCEA P00956; Fig. 10.13-10.15), the proximal part of ascending ramus (MCEA P00922) with condyle and coronoid process, a left lower first molar (MCEA P00934), a right lower third molar (MCEA P00958; Fig. 10.16-10.18), a fragmental right scapula (MCEA P00928), a fragmental left radius (MCEA P00931), a fragmental distal epiphysis of right femur (MCEA P00961), an unfused distal epiphysis of right tibia (MCEA P00946), five astragali, a right one (MCEA P00939) and four left ones (MCEA P00954, MCEA P00945, MCEA P01004, MCEA P00964), and two naviculocuboids, a right one (MCEA P01000) and a left one (MCEA P01003). A fragmental cervical vertebra (MCEA P00955) is also tentatively attributed to this taxon. The specimens are morphologically and dimensionally suggestive of *Gazella*. The cheek teeth are hypsodont. The deciduous upper second premolar has no anterior cone. The tooth has a strong paracone rib and a weaker metacone rib. The parastyle and mesostyle are robust, the metastyle, in contrast, is weaker. A preprotocrista fuses to the parastyle and the postmetaconulecrista to the metastyle. The external premetaconulecrista fuses with the protocone, whereas the internal premetaconulecrista is directed labially and closes partially the posterior fossa, without reaching the lingual walls of the labial cones. A tiny style emerges between the labial end of the internal premetaconulecrista and the metacone. A strong fold issues from the metaconule and stretches toward the base of the metacone. The deciduous upper third premolar has acute lingual crescents. The postprotocrista fuses to the premetaconulecrista, and a strong metaconule fold issues from the postmetaconulecrista. The tooth shows a mesial, distal, and lingual cingulum, and the latter bears a tine entostyle. There are no cingula in the deciduous teeth and the enamel surface is smooth. In the upper second molar the labial column of the paracone is prominent while that of the metacone is weaker. The parastyle is stronger than the metastyle, but not as robust and labially protruding as the mesostyle. The lingual crescents are fairly acute. The tooth bears a small metaconule fold and a tine entostyle. The external postprotocristid (= "*Palaeomeryx* fold") is absent. There are no cingula. The enamel is faintly rugose. In the deciduous lower fourth premolar the anterolingual and metaconid have fairly prominent lingual columns, whereas the lingual entoconid rib is relatively less robust. The anterior stylid is very weak, the entostylid is somewhat more developed, the mesostylid is absent, while the metastylid is very protruding. The posterior cristid of the anterolabial conid is fused to the posterior cristid of the anterolingual conid. The tooth bears a tiny anterior ectostylid and a small ectostylid. There are no cingulids. The lower molars have a well-developed labial metaconid rib, whereas the entoconid rib is weaker. The mesostylid, entostylid, and metastylid are weak. The lingual crescents are acute. The tooth shows a marked anterocingulid (= "goat fold"). The ectostylid may be either absent or thin and elongated. In m3 the rear lobe (entoconulid-hypoconulid complex) is elliptical and the posterior ectostylid is absent. The labial and distal cingulids are absent in all molars. The enamel is faintly rugose in the lower cheek teeth.

The head of the radius (caput radii) is weakly transversely enlarged. The proximal articular surface of the radius has two concavities of very different size. The medial concavity

is very broad with a fairly large antero-posterior diameter; the lateral is much smaller and elliptical. The groove for the crest of the distal humeral trochlea is narrow and deep.

The astragalus is narrow and elongated proximo-distally. The proximal trochlea for the tibia has a high, wide, but relatively short lateral lip and a low, narrow and long medial lip. The trough between the two trochleae is deep and asymmetrical, much steeper against the medial lip and more gently sloping against the lateral lip. Dorsally, the proximal and distal trochleae are attached to one another and the depression at the center of the bone is very deep and narrow. The lateral lip of the proximal trochlea ends distally with a short, very weak, oblique crest. The distal end of the medial lip is raised dorsally and protrudes medially. The distal trochlea is less than half the greatest length of the bone and approximately as wide as the proximal trochlea. The two distal parallel trochleae are separated by a wide and shallow trough. The axis of the trough is aligned with that of the trough of the proximal trochleae. The ridge marking the boundary between the navicular and the cuboid is blunt and smooth. Plantarily, the depression under the lateral lip of the proximal trochlea is deep, convex proximally and flat distally. The plantar trochleae (calcaneal facet) is fused to the distal trochleae medially, bounding only medially a moderately deep ligamentous fossa.

This gazelle is smaller than *Gazella* aff. *G. pilgrimi*. Its size is compatible with that of *?Nisidorcas* sp. from Kohfidisch (VISLOBOKOVA 2007). Nonetheless, lacking horns and any other skeletal or dental element possibly to compare with the latter taxon, the small-sized gazelle antelope from Verduno is referred here to *Gazella* sp.

Artiodactyla indet. cf. Camelidae

Fig. 10.19

Three remains of a large-sized ungulate, the fragment of a left scapula (MCEA: P01082), a robust right pyramidal bone (MCEA P01083), and a large right lower canine (MCEA P01084; Fig. 10.19), are referred to cf. Camelidae. The scapula lacks the proximal part of the blade. Part of the medial margin of the glenoid fossa is not preserved. The articular surface appears fairly shallow. The neck is robust. The spine is stout and robust, and bears a prominent acromion process that extends close to the distal margin of the glenoid cavity. These characteristics are suggestive of Camelidae and are associated with the adaptation to a pacing gait (JANIS et al. 2002). In the pyramidal bone, the articular facets for the lunar and as well as the postero-medial extension of the facet for the pisiform are morphologically similar to those of extant species of Camelidae. Also the lower canine is morphologically strongly reminiscent of Camelinae, in particular in the marked anteromedial and posterior enamel ridges.

Carnivora BOWDICH, 1821
Mustelidae gen. et sp. indet.

Fig. 11.1-11.2

An isolated tooth (MCEA P00914; Fig. 11.1-11.2) has the shape and size of a mustelid right lower second premolar. The specimen shows two roots, a very high, acute protocone and a distal cingulum that forms a small platform. The tooth is very asymmetric with a mesial margin that falls abruptly because of the lack of a mesial cingulum.

Canidae FISCHER, 1817

Eucyon monticinensis (ROOK, 1992)

Fig. 11.3-11.9

A left upper first molar (MCEA P01080), a complete fourth and incomplete fifth right metacarpal bone, and a first and second phalanx (all registered as MCEA P00991; Fig. 11.3-11.9) are referred to *Eucyon monticinensis*. The upper molar was referred to this species by SARDELLA (2008). The metacarpal bones have been found in anatomical connection. They are very similar morphologically and dimensionally to the equivalent metacarpals of the Monticino Quarry species. The diaphysis of the IV metacarpal is straight, while that of the V metacarpal is arched dorsally, as normally occurs in these lateral metapodials. Both have quite flat dorsal surfaces.

Felidae GRAY, 1821

Pristifelis attica (WAGNER, 1857)

Fig. 11.10-11.12

A fragmental left ulna (MCEA P00926; Fig. 11.10-11.12) is referred to *Pristifelis attica*. The tuber olecrani and the distal half of the diaphysis are not preserved. Two shallow grooves extend longitudinally close to the caudal border of the diaphysis, one on each side of it. The coronoid processes (processi coronoideus medialis et lateralis) are abraded. The medial one is prominent, the lateral one very reduced. The trochlear notch (incisura trochlearis) is partially preserved and relatively wide latero-medially. The radial notch (incisura radialis) is hardly marked and very shallow. The specimen is dimensionally and morphologically very similar to the ulnae of *Felis silvestris*. The fairly widespread, though scarcely documented, Late Miocene small-sized Felinae are traditionally classified as *Felis attica*. It was generally agreed that *F. attica* is quite similar to *F. silvestris*. SALESA et al. (2012), however, revealed important differences between the two cats and proposed the new generic name *Pristifelis* for *Felis attica*.

Amphimachairodus sp.

Fig. 11.13-11.17

A saber-tooth cat is documented by two complete and very well preserved specimens, a left scaphosemilar (MCEA P00989; Fig. 11.13-11.14) and a right calcaneum (MCEA P00973; Fig. 11.15-11.17). The wide proximal articular surface of the scaphosemilar is largely occupied by a broad, convex, latero-medially elongated facet for articulation with



Fig. 11. Large mammal remains from Verduno. **1-2** – Mustelidae, right lower second premolar (MCEA P00914), 1: lingual view, 2: buccal view. **3-4** – *Eucyon monticinensis*, fourth right metacarpal bone (MCEA P00991), 3: dorsal view, 4: lateral view. **5** – *Eucyon monticinensis*, fifth metacarpal bone (MCEA P00991), dorsal view. **6-9** – *Eucyon monticinensis*, 6-8: first phalanx (MCEA P00991), 6: dorsal view, 7: palmar view, 8: lateral view. 9: second phalanx (MCEA P00991), dorsal view. **10-12** – *Pristifelis attica*, left ulna (MCEA P00926), 10: lateral view, 11: dorsal view, 12: medial view. **13-14** – *Amphimachairodus* sp., left scaphosemilar (MCEA P00989), 13: proximal view, 14: distal view. **15-17** – *Amphimachairodus* sp., right calcaneum (MCEA P00973), 15: dorsal view, 16: medial view, 17: distal view. Scale bars equal 1 cm. All specimens come from lithofacies 5.

the radius. At the postero-medial end it continues in an up-lifted palmar protrusion. The distal articulation is characterized by three depressed articular surfaces for the trapezium, trapezoid, and capitatum. The three articular surfaces are separated by two ridges, a blunt, oblique, medial one, between the trapezium and trapezoid articulations, and a dorso-palmarly oriented and crest-like lateral one, between the trapezoid, and capitatum articulations. At the latero-distal border of the bone there is a tiny elongated and flat articular surface for the uncinat.

The calcaneum is massive. The distal part of the bone, from the articular surfaces for the astragalus, is massive. It is about 1/3 the length of the bone. The tuber calcanei is long and thick and compressed latero-medially. The lateral articular surface for the astragalus is strongly convex in dorsal view and its distal part is almost at a right angle to the long axis of the bone. The medial articular surface for the astragalus is fairly wide and oval-shaped and borne by a short and massive sustentaculum tali. It is connected with the the cuboid surface by a narrow, uninterrupted articular surface. In plantar view a fairly deep longitudinal groove extends at the base of the sustentaculum. The cuboid surface is irregularly oval-shaped. It makes an angle of slightly less than 90° with the long axis of the bone.

The scaphosemilar (MCEA P00989) is morphologically similar to that of *Paramachairodus* cf. *P. orientalis* from Crevillente 15 (MONTROYA & ALBERDI 1995), but its size is compatible with that of *Amphimachairodus giganteus*. For this reason the saber-tooth remains from Verduno are referred to *Amphimachairodus* sp.

Hyaenidae GRAY, 1821

Hyaenictitherium sp.

A left upper third premolar (MCEA P01081) has a large, conical main cusp, a relatively strong accessory cuspid placed behind and next to it, and a marked mesial and distal cingulum. Based on its size and morphological features suggestive of a large dog-like hyaena SARDELLA (2008) referred the tooth to *Hyaenictitherium* sp.

Lagomorpha BRANDT, 1855

Ochotonidae THOMAS, 1897

Prolagus POMEL, 1853

Prolagus sorbinii MASINI, 1989

Fig. 12.1

All the lagomorph remains from Verduno (isolated teeth: six p3s, two m1s, five P3s, four P4s, one M1 and one M2, Fig. 12.1) pertain to the ochotonid *Prolagus sorbinii*, a Late Miocene-Pliocene species distributed in central-western Italy and NE Greece (ANGELONE 2007; ABBAZZI et al. 2008b). The sizes of the teeth of *P. sorbinii* from Verduno fall in the range of the species (ANGELONE 2007), but differ from those of the holotype (MASINI 1989) and also of the specimens from Brisighella 25 (northern Italy, post-evaporitic Messinian; ANGELONE 2007) in having a slender p3 with triangular metaconid and entoconid shorter than the metaconid, simi-

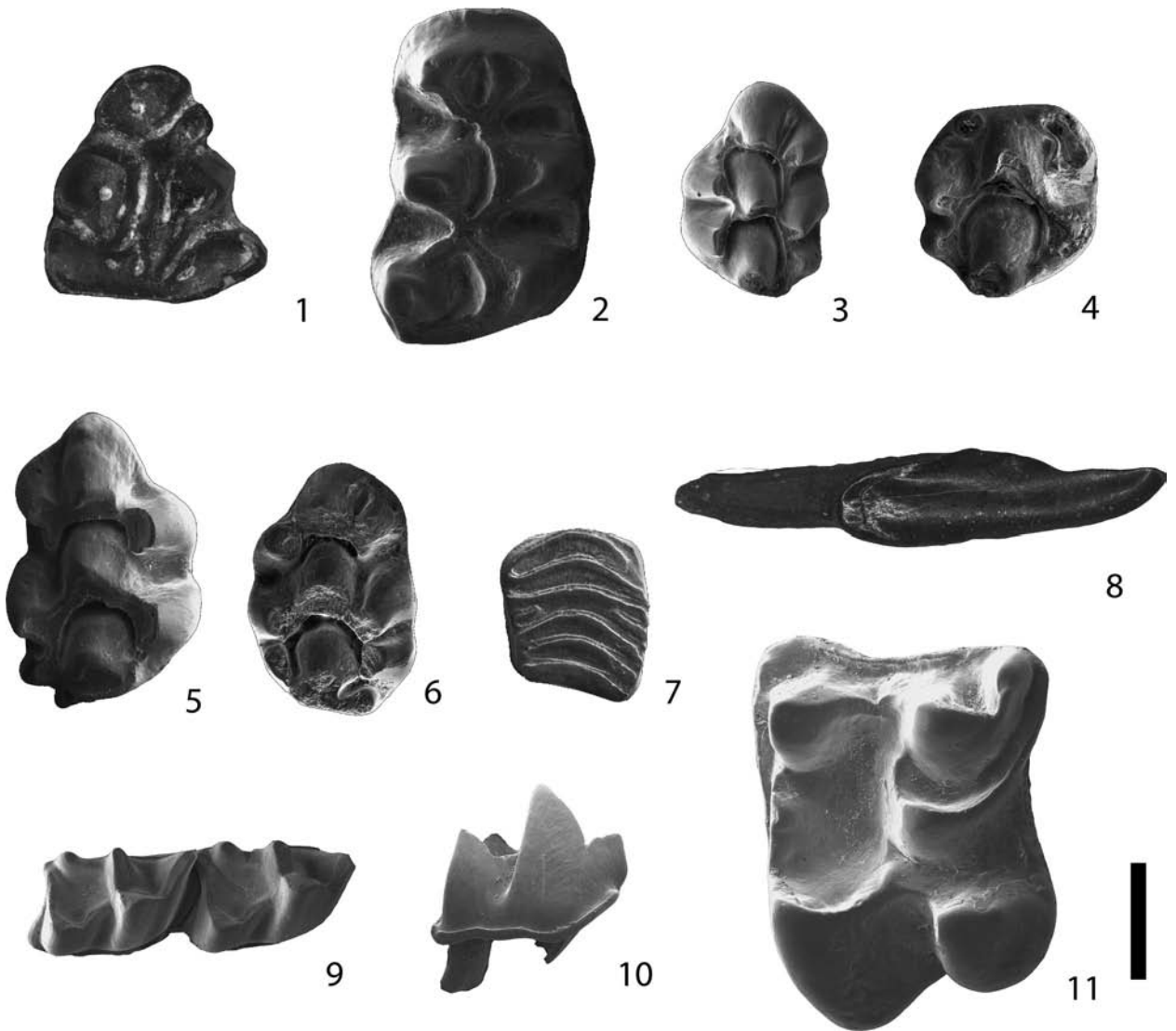


Fig. 12. Small mammal remains from Verduno. **1** – *Prolagus sorbinii*, right p3, (MGPT-PU 131500), occlusal view, **2** – *Apocricetus barrierei*, right M1 (MGPT-PU131767), occlusal view. **3** – *Centralomys benericettii*, left M1 (MGPT-PU131772), occlusal view. **4** – *Occitanomys* sp. left M2 (MGPT-PU131799), occlusal view. **5** – *Paraethomys meini*, right M1 (MGPT-PU131717), occlusal view. **6** – *Apodemus gudrunae*, left M1 (MGPT-PU131009), occlusal view. **7** – *Muscardinus vireti*, left m2 (MGPT-PU131978), occlusal view. **8-10** – cf. *Asoriculus gibberodon*, **8**: right lower incisor (MGPT-PU 131638), labial view, **9**: right m1 and m2 (MGPT-PU 131607), occlusal view, **10**: right m1 (MGPT-PU 131606) labial view, **11** – *Parasorex* sp. left M2 (MGPT-PU131602), occlusal view. Scale bars equal 1 mm. Specimens **1**, **6**, **9** and **10** come from lithofacies 2; **2**, **3**, **7** and **11** from lithofacies 5; **4**, **5**, **8** from lithofacies 1.

larly to the populations from Brisighella 3 and 6, Tuscany (Velona, Early Messinian; Borro Strolla, earliest Pliocene; ANGELONE & ROOK 2012) and eastern Europe (Maramena, Mio/Pliocene boundary; BRUIJN 1995). It is worth noting that some of the morphological features distinctive of *P. sorbinii* are particularly accentuated in the populations from Verduno. In p3 the entoconid is very thick, and in P3, in the lingual side the enamel bridge connecting lagicone and lagiloph, is often deformed by a deep notch. A peculiar

feature possessed by 50% of the specimens from Verduno is an undulated anterior border of the metaconid in p3.

The material of *P. sorbinii* from Verduno is the third retrieved from the uppermost Messinian deposits of NW Italy, after those recovered from Ciabòt Cagna and Moncucco Torinese (ANGELONE & CAVALLO 2010; ANGELONE et al. 2011). No leporids have been found in Verduno and Ciabòt Cagna, whereas an undetermined leporid is reported from Moncucco Torinese.

Rodentia BOWDICH, 1821

Rodents from the locality of Verduno have been extensively discussed and described in recent works (COLOMBERO et al. 2013; COLOMBERO & PAVIA 2013). The systematic list of the species recorded from the samples is given below, together with a description of their main morphological features.

Cricetidae FISCHER, 1817

Apocricetus FREUDENTHAL et al., 1998

Apocricetus barrierei (MEIN & MICHAUX, 1970)

Fig. 12.2

Few remains (two M1s, three M2s, one M3, three m1s, one m2, one m3, Fig. 12.2) of a large species of cricetine were recovered at Verduno. The total lack of mesoloph(id)s in the molars, the presence of stout and crest-like anteroconids in m1s and the occurrence of elongate m3s rule out the genus *Neocricetodon* and *Kowalskia*. On the contrary, these features are suggestive of the genus *Apocricetus*. The teeth are large and stout, and fall in the average size-ranges of *Apocricetus barrierei* (MEIN & MICHAUX 1970). The classification of the fossil cricetine from Verduno to this species is also corroborated by the absence of an anterior protoloph in M1s. *A. barrierei* occurs in the uppermost Miocene to Pliocene deposits of Spain, France and Italy (MEIN & MICHAUX 1970; DE GIULI 1989; FREUDENTHAL et al. 1998; GARCÍA-ALIX et al. 2008; COLOMBERO et al. 2013).

Muridae ILLIGER, 1811

Centralomys DE GIULI, 1989

Centralomys benericettii (DE GIULI, 1989)

Fig. 12.3

A dominant murid (40 M1s, 30 M2s, six M3s, 35 m1s, 36 m2s, 14 m3s, Fig. 12.3) is a small-sized species with moderately stephanodont teeth. Morphologically, the upper molars of this taxon display an intermediate degree of stephanodony between those of *Castillomys* (more hypsodont and stephanodont molars) and *Occitanomys* (less stephanodont molars) (see DE GIULI 1989 and COLOMBERO & PAVIA 2013). The longitudinal connections between t3 and t5 in M1s are present in only 2/3 of M1s. They are very thin and never in the form of high crests. In m1s the longitudinal connections between the metaconid-protoconid and hypoconid-entocoid complexes are present in about 50% of the specimens and are quite low and weak. Moreover M1s and M2s constantly show a t1bis, and a tiny tma is present in 30% of m1s. Based on personal observations of one of the authors (SC) on the fossil material from the type locality of Brisighella 1 (latest Miocene, Italy; see DE GIULI 1989), as well as on the plentiful remains from Brisighella 25, the small murid from Verduno can be confidently assigned to *Centralomys benericettii* with which it shares all the above-cited morphological features and nearly identical dimensions.

Occitanomys (MICHAUX, 1969)

Occitanomys sp.

Fig. 12.4

Three brachyodont teeth, one partially preserved M1 (MGPT-PU131771) and two M2s (MGPT-PU131738, MGPT-PU 131799, Fig. 12.4), of a large-sized murid show moderate stephanodont arrangement of the tubercles (t4-t5-t6-t9-t8 forming a fairly rather well-developed stephanodont crest, t1 connected to t5, t3 far from the t5-t6 connection). The specimens can therefore be assigned to genus *Occitanomys*. The low number of remains prevents identification at the species level. However, the large dimensions and the general morphology are suggestive of either *Occitanomys brailloni* or *Occitanomys montheleni*.

Paraethomys PETTER, 1968

Paraethomys meini (MICHAUX, 1969)

Fig. 12.5

A large-sized murid with stout tubercles, moderately stephanodont teeth and strong reduction or even absence of t9 in M1s and M2s is assigned to the species *Paraethomys meini*. This species is very abundant in the rodent assemblages from Verduno (29 M1s, 12 M2s, five M3s, 14 m1s, 18 m2s, eight m3s, Fig. 12.5). Together with *Centralomys benericettii*, they constitute more than 90% of the recovered rodent remains (COLOMBERO et al. 2013). *P. meini* entered (western?) Europe from Africa slightly before the onset of the Messinian Salinity Crisis (AGUSTÍ et al. 2006a; GIBERT et al. 2013) and then spread out to the entire Mediterranean basin, reaching also the Aegean region at Maritsa (DE BRUIJN et al. 1970). Its remains are commonly found in the uppermost Miocene to Lower Pliocene deposits of Spain, France and Italy (ADROVER et al. 1988, 1993; AGUILAR et al. 1991; DE GIULI 1989; GARCÍA-ALIX et al. 2008; MINWER-BARAKAT et al. 2009a, 2009b).

Apodemus KAUP, 1826

Apodemus gudrunae VAN DE WEERD, 1976

Fig. 12.6

Teeth of *Apodemus* are rare in the rodent assemblages from Verduno (three M1s, seven M2s, two m1s, four m2s, Fig. 12.6). The upper molars assigned to this taxon (M1s and M2s) are all characterized by a t7, a well developed tma in the m1s, well-developed labial cingula and two to four additional cusplets in m1s and m2s. Morphologically, these medium-size teeth are indicative of *Apodemus gudrunae*, a species commonly found in the upper Turolian deposits of France and Spain (see VAN DE WEERD 1976; AGUILAR et al. 1991; ADROVER et al. 1993; MARTÍN-SUÁREZ & MEIN 1998; MARTÍN-SUÁREZ et al. 2001; MINWER-BARAKAT et al. 2009b, among others) and also Greece (KOUFOS 2006) and Turkey (SARICA-FILOREAU 2002). Size considerations rule out an attribution to the larger-sized *Apodemus gorafensis*. Moreo-

ver, according to SARICA FILOREAU (2002), *A. gudrunae* differs from *A. gorafensis* in the less developed t1 of M1. As a matter of fact, the larger-sized t1 produces a deep incision between t1 and t2 on the lingual side of the M1 of *A. gorafensis*.

Gliridae THOMAS, 1897

Muscardinus KAUP, 1829

Muscardinus vireti HUGUENEY & MEIN, 1965

Fig. 12.7

Only one m2 (MGPT-PU 131978, Fig. 12.7) and one m3 (MGPT-PU131979) are included in the rodent assemblages from Verduno. The two molars are extremely bacyodont and have six roughly parallel crests. The occurrence of a lingual (in m2 and m3) and labial (only in m2) portion of an incomplete extra-ridge are characteristic of *Muscardinus vireti*. This species was identified at Lissieu (MN13 of France, HUGUENEY & MEIN 1965) and also at Baccinello V3 (MN13, central Italy, ENGESSER 1983) and Can Vilella (MN13, Pyrenees, Spain, AGUSTÍ et al. 2006b).

Eulipotyphla WADDELL et al., 1999

The insectivores from Verduno are currently under study. However, preliminary analyses have revealed the presence of a small soricid and of a larger galericine.

Soricidae FISCHER, 1814

Soricidae indet. cf. *Asoriculus gibberodon* (PETÉNYI, 1864)

Fig. 12.8-12.10

A medium-sized soricid (one M2, one lower incisor, nine mandibular fragments, eight isolated lower molars, Fig 12.8-12.10) characterized by stout teeth, well-developed entoconid crests, and lower incisors without cuspules is tentatively referred to cfr. *Asoriculus gibberodon*. This taxon occurred in Europe for a long time-span ranging from the latest Miocene (FURIÓ 2007) to the Early Pleistocene (FURIÓ & ANGELONE 2010). Until now, the oldest occurrence in Italy of *A. gibberodon* is that of Capo Mannu (Sardinia, ? MN13/MN14-MN15, FURIÓ & ANGELONE 2010). Should the record from Verduno be confirmed by further studies, it would represent one of the earliest occurrences of this taxon in Europe and in Italy.

Erinaceidae FISCHER, 1817

Galericinae POMEL, 1848

Parasorex VON MEYER, 1865

Parasorex sp.

Fig. 12.11

A rare erinaceomorph is referred to *Parasorex* sp. (one M2, one M3, one p4 and one partially preserved m1 or m2, Fig. 12.11). The mesostyles are quite reduced and undivided, and are markedly different from those of *Schizogalerix*. This morphology is instead suggestive of *Parasorex* (see VAN DEN HOEK OSTENDE 2001). The p4 is high-crowned, with well-developed metaconid and paralophid, and moderately-developed labial cingulum. Only the talonid of an m1 or an m2 is preserved. The posterior cingulum is strongly reduced and the tooth is wide bucco-lingually. The genus *Parasorex* includes two Late Miocene to Early Pliocene species: the smaller-sized *Parasorex ibericus* (MEIN & MARTÍN SUÁREZ 1994) and *Parasorex depereti*, which is comparable in size to the Verduno representative. Nonetheless, the latest Miocene-earliest Pliocene *P. ibericus* (see MINWER-BARAKAT et al. 2009b) from Negratín 1 and Purcal 4 (Spain) is dimensionally similar to the specimens from Verduno. The main morphological differences separating *P. ibericus* from *P. depereti* are the degree of molarization of the upper premolars, as well as the development of the labial cingula in the lower molars. However, these traits cannot be assessed in the scanty Verduno specimens. This prevents a confident classification at the species level.

5. Discussion

5.1. Biochronology

Pending a more thorough analysis of the Moncucco Torinese fossil assemblages, at the moment Verduno links biochronologically to the latter, dating to the time span of the Messinian Salinity Crisis (5.55-5.33 Ma), based only on the occurrence of a set of small mammals, i.e., *Asoriculus gibberodon*, *Apocricetus barrierei*, *Centralomys benericettii*, *Prolagus sorbinii*, and the genera *Parasorex*, *Apodemus* and *Muscardinus*. Nonetheless, preliminary cross-comparisons between the fossil assemblages of the two sites show the existence of several other unequivocal taxonomic correlates, for instance among rhinos, cervids, and bovids. The differences that occur in the vertebrate assemblages of Moncucco Torinese and Verduno can be explained by possible palaeoenvironmental differences (COLOMBERO & PAVIA 2013).

It is worth noting that the small murid *C. benericettii* characterizes all the post-evaporitic Messinian rodent-faunas of Piedmont, Romagna and Tuscany, but it is absent from slightly older localities, such as Velona and Baccinello V3. *Apocricetus barrierei* is absent from the rodent assemblages of Moncucco Torinese, but it is present in those of Borro Strolla (ABBAZZI et al. 2008b) and Monticino Quarry (DE GIULI 1989), which date very close to the Mio/Pliocene boundary.

5.2. Palaeoenvironment

The Verduno taxa have restricted use as palaeoenvironmental proxies. They collectively indicate an open, semi-arid, woodland savanna landscape not far from the coastline. The bones accumulated in a variety of subaqueous palaeobiotopes. The remains of aquatic taxa (charophytes, molluscs, ostracods, fishes) collected from lithofacies 1, 2 and 4 are relevant palaeoenvironmental proxies. The charophyte gyrogonites assigned to *Lychnothamnus* cf. *barbatus* from lithofacies 1 and 2 indicate that sedimentation occurred in permanent waterbodies. This taxon grows at depths of 2 to 8 meters in small oligotrophic lakes and permanent ponds (e.g., KRAUSE 1997; BATHIA et al. 1998). The presence of water bodies is also testified by bufonids and ranids whose larvae develop mandatorily in fresh water. In contrast, at least some geoemydid turtles (as *Mauremys*) can survive in brackish water. All the ostracod valves collected from lithofacies 1 and 2 belong to the genus *Cyprideis*. This genus includes prevalently euryhaline species which are tolerant of a wide range of salinities, from freshwater to hyperhaline conditions, with an optimum in oligo- and meso-haline waters of coastal ponds, lagoons, estuaries, deltas and salt marshes (see MORKHOVEN 1963; MEISCH 2000; GROSS et al. 2008).

The Late Miocene cyprinodontid *Aphanius crassicaudus*, including the so-called pachyostotic phenotype recorded in Verduno's lithofacies 1 and 4, inhabited a broad variety of aquatic palaeobiotopes characterized by thalassogenic waters, from oligo-mesohaline to normal marine to hyperhaline (GAUDANT 1979; GAUDANT et al. 1988; CAPUTO et al. 2009). Like for other extant and extinct congeners, the weak competitive ability of this Late Miocene euryhaline species may account for its distribution (see REICHENBACHER & KOWALKE 2009) and its abundance in the lithofacies 4 sediments may indicate strong environmental instability, possibly because of periodic oscillations in the physico-chemical parameters of the waterbody. Overall, the aquatic biota of lithofacies 1 and 2 suggests that deposition took place in a coastal, oligo-mesohaline lake characterized by permanent oligotrophic waters and at several meters of depth. On the other hand, the exclusive presence of *Aphanius crassicaudus* in lithofacies 4 suggests very unsuitable environmental conditions. Hence, sedimentation possibly occurred in a coastal lagoon subjected to broad salinity excursions.

Large mammals are varied, but their remains are scant. *Gazella* sp. is present with four specimens, *Euprox* sp., aff. *Palaeomeryx*, and *?Paraoioceros occidentalis* with three, all other taxa with one each. The

list of large mammals shows a fairly proportionate occurrence of woodland and open space dwellers. Browsers with typical brachyodont dentition (e.g., *Euprox*, *Pliocervus*, aff. *Palaeomeryx*) are indicative of the presence of juicy and tender dicotyledon leaves, in contrast to grazers (e.g., *Cremohipparion*, *?Paraoioceros*) which are concentrate selectors and eat grass and roughage. Nonetheless, due to the exiguity of the sample, any palaeoenvironmental inference based on the large mammalian community of Verduno would be fraught with speculation.

The Verduno small mammal assemblage is dominated by the small *Centralomys benericettii* as well as the large *Paraethomys meini* murids. The latter, in particular, is an indicator of warm and dry conditions (GARCÍA ALIX et al. 2008). Glirids are extremely rare, with just two teeth of *Muscardinus vireti* making up less than 1% of the rodent assemblage (COLOMBERO et al. 2013). They nonetheless indicate the presence of a forested area in the surroundings. The association of *P. meini* with *Apodemus gudrunae* indicates warm conditions (MARTÍN-SUÁREZ et al. 2001). Among insectivores, the presence of a neomyin (cf. *Asoriculus gibberodon*) is consistent with the presence of fresh waterbodies.

The herpetofauna is varied, but can rarely be identified below order level. Its usefulness as palaeoenvironmental indicator is therefore limited. The ecological requirements of the taxa that have been identified indicate semi-arid, woodland savanna conditions with sparse freshwater bodies. The fossil bird taxa corroborate the presence of local woodlands.

5.3. Palaeobiogeography

The varied Verduno community includes taxa of both Asian and European origin. These findings confirm Piedmont's key biogeographic role in the faunal exchanges between the different quarters of the Mediterranean at the very end of the Miocene (ANGELONE et al. 2011). More specifically, Piedmont was part of a dispersal route connecting western, central and eastern Europe, but also, through the latter, Asia. The presence of agamids, non-*Anguis* anguines, varanids and scolecophidians, which in the northern Mediterranean area currently inhabit the Balkan or the Anatolian Peninsula only (GASC et al. 1997), does not imply any direct dispersal from that area, because these taxa were quite widespread in southern Europe during the Late Miocene (RAGE 2013). More informative under a biogeographic perspective are some of the Verduno

mammals. The enigmatic giant giraffid, classified to *Helladotherium*, suggests possible connections with eastern Europe and, through the latter, with Anatolia (GERAADS 2009). *Apocricetus barrierei* and *Muscardinus vireti* spread westwards to France and Spain, whereas *Prolagus sorbinii* is reported from northeastern Greece (DE BRUIJN 1995).

Verduno shows that Piedmont was also the doorway to western and eastern Italian districts. In fact, it shares taxa with several localities, such as Monticino Quarry (*Varanus*, Agamidae, Amphisbaenia, Hipparionini, *Eucyon*, *P. sorbinii*, *C. benericettii*, *Apodemus* cf. *A. gudrunae*, *A. cf. A. barrierei*), which is situated on the northeastern margin of the northern Apennine Chain, but also with Casino (Hipparionini, *Euprox*), Baccinello V3 (*Amphimachairodus*, *Muscardinus*), Velona (*Prolagus*) and Podere La Crocina (Hipparionini), which are located in what was the Tusco-Sardinian palaeobioprovince. We cannot exclude the possibility, pending revisions, that some differences from the faunal compositions of these Italian Miocene communities may simply reflect discrepancies in the systematic attributions of the same taxa. *Stephanorhinus megarhinus*, for example, which is reported both at Baccinello V3 and Monticino Quarry, may likely be the equivalent of the indetermined rhinoceros from Verduno; *Paracervulus*, which is included in the faunal lists from Baccinello V3, Borro Strolla, and Monticino Quarry (ABBAZZI 2001; ABBAZZI et al. 2008b) may perhaps be *Pliocervus*.

These faunal connections can be used to detect the pathways and trace the movement of faunas into the different corners of Europe. As information increases, generalizations are broken down and gaps in the distributions that originally appeared discontinuous are progressively filled in.

6. Conclusions

Piedmont was an important palaeobiogeographical domain at the crossroads of vertebrate dispersions between western and eastern Europe, and between the latter regions and other Italian districts during the latest Miocene. This is certainly not an original breakthrough because previous studies on other relevant fossiliferous sites of Piedmont had already supposed such a Late Miocene role of the region (i.e., Ciabòt Cagna and Moncucco Torinese: CAVALLO et al. 1993; ANGELONE et al. 2011). Verduno, however, provided a significant amount of additional information, disclosing a variety of taxa that lead to a more comprehensive view of the patterns

of these inter-regional faunal exchanges. The area of Verduno was involved in the broad biotic interactions that led, in the latest Miocene, to the homogenization of the faunas dispersed in the different parts of the peri-Mediterranean. The fall of several significant geographic barriers during the Late Miocene “Messinian Salinity Crisis” permitted a freer circulation of fauna from eastern and southeastern ranges. Most of the taxa that figure in the Verduno faunal list (e.g., *Euprox*, *Pliocervus*, *Helladotherium*, *Gazella*, *Eucyon*, *Amphimachairodus*) were widespread in Eurasia. Others (e.g., *Paraethomys*) are reported also from Africa (AGUSTÍ et al. 2006a), and still others only from eastern or western Europe. Piedmont, for instance, represents the western limit of distribution of *Prolagus sorbinii* and together with Borro Strolla and Brisighella, the eastern limit of distribution of the genus *Apocricetus*.

Therefore, Piedmont was a crucial check-point during the latest Miocene that controlled the interchange of animals across the different parts of the circum-Mediterranean region. The varied movements of fauna during the Miocene were an important factor in the broad distribution of many of the taxa that figure in Verduno’s faunal list. The eastward and westward migrations to France and Spain, to central and eastern European reaches and down to Greece, together with the transfers from and to south-western and south-eastern areas of the then-forming peninsular Italy should supply palaeontologists, palaeobiogeographers, and taxonomists with new prospects for further inquiries and studies.

Acknowledgements

ILARIA MAZZINI (Roma) helped with identification of ostracods and INGEBORG SOULIÉ-MÄRSCHÉ (Montpellier) discussed the identification of charophyte gyrogonites. HUGUES ALEXANDRE BLAIN (Tarragona), ARNAU BOLET (Barcelona), IGOR DANILOV (Saint Petersburg) and ANGEL HERNÁNDEZ LUJÁN (Barcelona) discussed the identification of the reptile material. SIMONA CAVAGNA (Torino) helped us with SEM images. We are grateful to the late CRISTINA PREACCO (Torino) for obtaining the needed excavation permits (reg. 587, 20/01/2011 from the Italian “Ministero per i Beni e le Attività Culturali”, by means of the “Soprintendenza per i Beni Archeologici del Piemonte”). We also would like to thank all those who collaborated with us during the field works. The draft greatly benefited from the critical reading of NIKOLAI SPASSOV, JEAN-PIERRE SUC and two anonymous reviewers. The study was funded by MIUR (Ministry of Education, University and Research grants: PRIN 2009MSSS9L_002 - resp. G. PAVIA). CHIARA ANGELONE and MASSIMO DELFINO received support by the Spanish Ministerio de Economía y Competitividad (CGL2011-28681).

References

- ABBAZZI, L. (2001): Cervidae and Moschidae (Mammalia, Artiodactyla) from the Baccinello V3 assemblage (late Miocene, late Turolian, Grosseto, Italy). – *Rivista Italiana di Paleontologia e Stratigrafia*, **107**: 107-123.
- ABBAZZI, L., BENVENUTI, M., CECI, E., ESU, D., FARANDA, C., ROOK, L. & TANGOCCI, F. (2008b): The end of the Lago-Mare time in the SE Valdelsa Basin (Central Italy): interference between local tectonism and regional sea-level rise. – *Geodiversitas*, **30**: 611-639.
- ABBAZZI, L., DELFINO, M., GALLAI, G., TREBINI, L. & ROOK, L. (2008a): New data on the vertebrate assemblage of Fiume Santo (North-western Sardinia, Italy), and overview on the Late Miocene Tusco-Sardinia paleobioprovince. – *Palaeontology*, **51**: 425-451.
- ADROVER, R., MEIN, P. & MOISSENET, E. (1988): Contribución al conocimiento de la fauna de roedores del Plioceno de la región de Teruel. – *Teruel*, **79**: 91-151.
- ADROVER, R., MEIN, P. & MOISSENET, E. (1993): Roedores de la transición Mio-Plioceno de la región de Teruel. – *Paleontologia i Evolució*, **26-27**: 47-84.
- AGUILAR, J.P., MICHAUX, J., BACHELET, B., CALVET, M. & FAILLAT, J.P. (1991): Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocène en Roussillon. Implications biostratigraphiques et biogéographiques. – *Palaeovertebrata*, **20**: 147-174.
- AGUSTÍ, J., GARCÉS, M. & KRIJGSMAN, W. (2006a): Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238**: 5-14.
- AGUSTÍ, J., OMS, O., FURIÓ, M., PÉREZ-VILA, M.-J. & ROCA, E. (2006b): The Messinian terrestrial record in the Pyrenees: the case of Can Vilella (Cerdanya Basin). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238**: 179-189.
- ALBA, D.M., DELSON, E., CARNEVALE, G., COLOMERO, S., DELFINO, M., GIUNTELLI, P., PAVIA, M. & PAVIA, G. (2014): First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. – *Journal of Human Evolution*, **67**: 1-18.
- ALCALÁ, L. & MONTOYA, P. (1998): *Hystrix primigenia* (WAGNER, 1848) (Rodentia, Mammalia) del Turoliense superior (MN 13) de Las Casiones (Teruel, España). – *Revista Española de Paleontología*, **13**: 139-147.
- ANGELONE, C. (2007): Messinian *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) of Italy. – *Geobios*, **40**: 407-421.
- ANGELONE, C. & CAVALLO, O. (2010): A new look to *Prolagus* (Ochotonidae, Lagomorpha) from the late Messinian of Ciabòt Cagna (Piedmont, NW Italy). – *Rivista Italiana di Paleontologia e Stratigrafia*, **116**: 267-270.
- ANGELONE, C., COLOMERO, S., ESU, D., GIUNTELLI, P., MARCOLINI, F., PAVIA, M., TRENKWALDER, S., VAN DEN HOEK OSTENDE, L., ZUNINO, M. & PAVIA, G. (2011): Moncucco Torinese, a new post-evaporitic Messinian fossiliferous site from Piedmont (NW Italy). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **259**: 89-104.
- ANGELONE, C. & ROOK, L. (2011): *Alilepus meini* nov. sp. (Leporidae, Lagomorpha) from the Early Messinian of Tuscany (central-western Italy). – *Geobios*, **44**: 151-156.
- ANGELONE, C. & ROOK, L. (2012): Late Neogene and Quaternary lagomorphs from Tuscany: a revision based on specimens in Basel Naturhistorisches Museum and Florence University collections. – *Swiss Journal of Palaeontology*, **131**: 127-145.
- ANGELONE, C. & SESÉ, C. (2009): New characters for species discrimination within the genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia). – *Journal of Palaeontology*, **83**: 80-88.
- ARNOLD, E.N., ARRIBAS, O. & CARRANZA, S. (2007): Systematics of the Palaeoartctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. – *Zootaxa*, **1430**: 1-86.
- AUGÉ, M. & RAGE, J.-C. (2000): Les Squamates (Reptilia) du Miocène moyen de Sansan. – In: GINSBURG, L. (Ed.): La faune miocène de Sansan et son environnement. – *Mémoires du Muséum nationale d'Histoire naturelle*, **183**: 263-313.
- AZANA, B., RÖSSNER, G.E. & ORTIZ-JAUREGUIZAR, E. (2013): The early Turolian (late Miocene) Cervidae (Artiodactyla, Mammalia) from the fossil site of Dorn-Dürkheim 1 (Germany) and implications on the origin of crown cervids. – *Palaeobiodiversity and Palaeoenvironments*, **93**: 217-258.
- BACHMAYER, F. & MEYNARSKI, M. (1981): *Testudo kalksburgensis* TOULA, 1896, eine valide Schildkrötenart aus den miozänen Strandbildungen von Kalksburg bei Wien. – *Österreichische Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse*, **190**: 11-119.
- BAIG, K.J.P., WAGNER, N.B., ANANJEVA & BÖHME, W. (2012): A morphology-based taxonomic revision of *Laudakia* GRAY, 1845 (Squamata: Agamidae). – *Vertebrate Zoology*, **62** (2): 213-260.
- BARAHONA, F. & BARBADILLO, L.J. (1997). Identification of some Iberian lacertids using skull characters. – *Revista Española de Herpetología*, **11**: 47-62.
- BATHIA, S.B., SOULIÉ-MÄRSCHKE, I. & GEMAYEL, P. (1998): Late Pliocene and Early Pleistocene charophyte floras of the Hirpur Formation, Karewa Group, Kashmir, India. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **210**: 185-209.
- BERNARDI, E., DELA PIERRE, F., IRACE, A., LOZAR, F., NATALICCHIO, M., CLARI, P., MARTIRE, L. & VIOLANTI, D. (2010): The Messinian sediments of the Tertiary Piedmont Basin: new data from outcrop sections. – *GEOSED 2010. Post congress field trip (24-25 September 2010)*, 35 pp.
- BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (1996a): The Evolution of Western Eurasian Neogene Mammal Faunas. – 488 pp.; New York (Columbia University Press).
- BERNOR, R.L., FORTELIUS, M. & ROOK, L. (2001): Evolutionary biogeography and paleoecology of the *Oreopithecus bambolii* "Faunal Zone" (Late Miocene, Tusco-Sardinian Province). – *Bollettino della Società Paleontologica Italiana*, **40** (2): 139-148.
- BERNOR, R.L., KAISER, T., NELSON, S. & ROOK, L. (2011): Systematics and paleobiology of *Hippotherium malpascii* n. sp. (Equidae, Mammalia) from the latest Miocene of Baccinello V3 (Tuscany, Italy). – *Bollettino della Società Paleontologica Italiana*, **50**: 175-208.

- BERNOR, R.L., KOUFOS, G.D., WOODBURN, M.O. & FORTELIUS, M. (1996b): The evolutionary history and biochronology of European and southwest Asian late Miocene and Pliocene hipparionine horses. – In: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (Eds.): *The Evolution of Western Eurasian Neogene Mammal Faunas*, 307-338; New York (Columbia University Press).
- BERTINI, A. & MARTINETTO, E. (2011): Reconstruction of vegetation transects for the Messinian-Piacenzian of Italy by means of comparative analysis of pollen, leaf and carpological records. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **304**: 230-246.
- BOHLIN, B. (1935): *Cavicornier der Hipparion-Fauna Nord-Chinas*. – *Palaeontologia Sinica*, (C), **9** (4): 1-166.
- BONIS, L. DE (2005): Carnivora (Mammalia) from the late Miocene of Akkasdagi, Turkey. – *Geodiversitas*, **27**: 567-589.
- BOSSIO, A., MAZZEI R., SALVATORINI, G. & SANDRELLI, F. (2001): Geologia dell'area compresa tra Siena e Poggibonsi ("Bacino del Casino"). – *Atti della Società Toscana di Scienze Naturali Memorie*, (A), **107**: 69-85.
- CAPUTO, D., CARNEVALE, G. & LANDINI, W. (2009): Fish otoliths from the Messinian of Strada degli Archi (Tuscany, Italy) – Taxonomy and paleoecology. – *Annalen des Naturhistorischen Museums, Wien*, **111A**: 257-280.
- CARNEVALE, G., CAPUTO, D. & LANDINI, W. (2006a): Late Miocene fish otoliths from the Colombacci Formation (Northern Apennines, Italy): Implications for the Messinian 'Lago-mare' event. – *Geological Journal*, **41**: 537-555.
- CARNEVALE, G., LANDINI, W. & SARTI, G. (2006b): Mare versus Lago-mare: marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. – *Journal of the Geological Society, London*, **163**: 75-80.
- CARNEVALE, G., LONGINELLI, A., CAPUTO, D., BARBIERI, M. & LANDINI, W. (2008): Did the Mediterranean marine re-flooding precede the Mio-Pliocene boundary? Paleontological and geochemical evidence from upper Messinian sequences of Tuscany, Italy. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **257**: 81-105.
- CAVALLO, O. & REPETTO, G. (1988): Un nuovo giacimento della Facies a Congerie nell'Albese (Piemonte, Italia NW). – *Rivista Piemontese di Storia Naturale*, **9**: 43-62.
- CAVALLO, O., ŞEN, Ş., RAGE, J.-C. & GAUDANT, J. (1993): Vertébrés messiniens du Faciès à Congéries de Ciabòt Cagna, Corneliano d'Alba (Piémont, Italie). – *Rivista Piemontese di Storia Naturale*, **14**: 3-22.
- CERDEÑO, E. (1989): Revisión de la Sistemática de los rinocerontes del Neógeno de España. – *Colección Tesis Doctorales Universidad Complutense de Madrid*, **306/89**: 1-429.
- CERDEÑO, E. (1992): Spanish Neogene rhinoceroses. – *Palaeontology*, **35** (2): 297-308.
- CHESI, F. (2009): Il registro fossile italiano dei cheloni. – PhD Thesis, Dipartimento di Scienze della Terra, Università degli studi di Firenze, unpublished.
- CHESI, F., DELFINO, M., ABBAZZI, L., CARBONI, S., LECCA, L. & ROOK, L. (2007): New fossil vertebrate remains from San Giovanni di Sinis (Late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the Central Mediterranean. – *Rivista Italiana di Paleontologia e Stratigrafia*, **113** (2): 287-297.
- CHESI, F., DELFINO, M. & ROOK, L. (2009): Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): evidence of terrapin persistence after a mammal turnover. – *Journal of Paleontology*, **83** (3): 379-388.
- COLOMBERO, S., BONELLI, E., KOTSAKIS, T., PAVIA, G., PAVIA, M. & CARNEVALE, G. (2013): Late Messinian rodents from Verduno (Piedmont, NW Italy): biochronological, palaeoecological and palaeobiogeographic implications. – *Geobios*, **46**: 111-125.
- COLOMBERO, S. & PAVIA, G. (2013): *Centralomys benericetti* (DE GIULI, 1989) (Mammalia, Rodentia): a latest Messinian murid from Northern and Central Italy. New data from Piedmont. – *Bollettino della Società Paleontologica Italiana*, **52**: 27-34.
- COLOMBERO, S., PAVIA, G. & CARNEVALE, G. (in press): Messinian rodents from Moncucco Torinese, NW Italy: palaeobiodiversity and biochronology. – *Geodiversitas*.
- CZYZEWSKA, T. (1968): Deer from Weze and their relationship with the Pliocene and Recent Eurasiatic Cervidae. – *Acta Palaeontologica Polonica*, **13**: 537-593.
- DAMIANI, M. (2009): I vertebrati fossili del Messiniano superiore di Verduno (Alba, Cuneo). – University of Turin, unpublished bachelor thesis.
- DE BRUIJN, H. (1995): The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 11-Lagomorpha (Mammalia). – *Münchener Geowissenschaftliche Abhandlungen*, (A), **28**: 133-136.
- DE BRUIJN, H., DAWSON, M.R. & MEIN, P. (1970): Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). I-III. – *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, (B), **73**: 535-584.
- DE GIULI, C. (1989): The rodents of the Brisighella latest Miocene fauna. – *Bollettino della Società Paleontologica Italiana*, **28**: 197-212.
- DE GIULI, C., MASINI, F., TORRE, D., BENERICETTI, A., COSTA, G.P., FOSELLA, M. & SAMI, M. (1988): The mammal fauna of the Monticino quarry. – In: DE GIULI, C. & VAI, G.B. (Eds.): *Guide Book of the Workshop "Continental Faunas at the Mio-Pliocene Boundary"*, 65-69; Faenza.
- DELA PIERRE, F., BERNARDI, E., CAVAGNA, S., CLARI, P., GENNARI, R., IRACE, A., LOZAR, F., LUGLI, S., MANZI, V., NATALICCHIO, M., ROVERI, M. & VIOLANTI, D. (2011): The record of the Messinian salinity crisis in the Tertiary Piedmont Basin (NW Italy): the Alba section revisited. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **310**: 238-255.
- DELA PIERRE, F., FESTA, A. & IRACE, A. (2007): Interaction of tectonic, sedimentary and diapiric processes in the origin of chaotic sediments: an example from the Messinian of the Torino Hills (Tertiary Piedmont Basin, northwestern Italy). – *Bulletins of the Geological Society of America*, **119**: 1107-1119.
- DELFINO, M. (2002): Neogene and Quaternary Herpetofaunas of Italy. – Ph.D. thesis, Università di Modena e Reggio Emilia, 382 pp.
- DELFINO, M. (2003): A Pleistocene amphibaenian from Sicily. – *Amphibia-Reptilia*, **24** (4): 407-414.

- DELFINO, M. (2006): Fossil records of modern reptile and amphibian species in Italy. – In: SINDACO, R., DORIA, G., RAZZETTI, E. & BERNINI, F. (Eds.): Atlas of Italian Amphibians and Reptiles, 96-119; Firenze (Societas Herpetologica Italica).
- DELFINO, M., ABELLA, J., ALBA, D.M. & ROOK, L. (2013b): The Italian fossil record of monitor lizards (Squamata, Varanidae). – In: BALDANZA, A. & MONACO, P. (Eds.): Abstract book “XIII Giornate di Paleontologia” della Società Paleontologica Italiana, 31; Perugia. 23-25 May 2013.
- DELFINO, M., BOLET, A., FORTUNY, J. & ALBA, D.M. (2013c): A new extinct *Blanus* species based on the first European amphisbaenian skull (Middle Miocene, NW Iberia). – Journal of Vertebrate Paleontology, **33** (Suppl. 1): 113-114.
- DELFINO, M., BÖHME, M. & ROOK, L. (2007): First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). – Zoological Journal of the Linnean Society, **149**: 293-307.
- DELFINO, M., FERRO, L., GIUNTELLI, P. & PAVIA, M. (2013d): First Italian record of scolecophidian snakes (late Miocene, Moncucco Torinese). – In: SCILLITANI, G., LIUZZI, C., LORUSSO, L., MASTROPASQUA, F. & VENTRELLA, P. (Eds.): Atti IX Congresso Nazionale della Societas Herpetologica Italica, 106-107; Bari - Conversano, 26-30 September 2012.
- DELFINO, M., KOTSAKIS, T., ARCA, M., TUVERI, C., PITRUZZELLA, G. & ROOK, L. (2008): Agamid lizards from the Pliocene of Sardinia (Italy) and an overview of the European fossil record of the family. – Geodiversitas, **30**: 641-656.
- DELFINO, M., RAGE, J.-C., BOLET, A. & ALBA, D.M. (2013a): Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. – Acta Palaeontologica Polonica, **58**: 731-735.
- DELFINO, M. & ROOK, L. (2008): African crocodylians in the Late Neogene of Europe. A revision of *Crocodylus bambolii* RISTORI, 1890. – Journal of Paleontology, **82**: 336-343.
- DELFINO, M. & ROSSI, M.A. (2013): Fossil crocodylid remains from Scontrone (Tortonian, Southern Italy) and the Late Neogene Mediterranean biogeography of crocodylians. – Geobios, **46**: 25-31.
- EINSELE, G. (1992): Sedimentary Basins: Evolution, Facies and Sediment Budget. – 628 pp.; Berlin (Springer).
- ENGESSER, B. (1983): Die jungtertiären Kleinsäuger des Gebietes der Maremma (Toskana, Italien). 1. Teil: Gliridae (Rodentia, Mammalia). – Eclogae Geologicae Helveticae, **76**: 763-780.
- FERRO, L. (2013): The snakes of the late Miocene of Moncucco Torinese (Italy). – Bachelor Thesis, University of Torino, unpublished.
- FREUDENTHAL, M. (1971): Neogene vertebrates from the Gargano Peninsula. – Scripta Geologica, **3**: 1-10.
- FREUDENTHAL, M., MEIN, P. & MARTÍN-SUÁREZ, E. (1998): Revision of Late Miocene and Pliocene Cricetinae (Rodentia, Mammalia) from Spain and France. – Treballs del Museu de Geologia de Barcelona, **7**: 11-93.
- FROST, D.R., GRANT, T., FAIVOVICH, J., BAIN, R.H., HAAS, A., HADDAD, C.F.B., DE SÁ, R.O., CHANNING, A., WILKINSON, M., DONNELLAN, S.C., RAXWORTHY, C.J., CAMPBELL, J.A., BLOTTO, B.L., MOLER, P., DREWES, R.C., NUSSBAUM, R.A., LYNCH, J.D., GREEN, D.N. & WHEELER, W.C. (2006): The Amphibian tree of life. – *Bulletins of the American Museum of Natural History*, **297**: 1-370.
- FURIÓ, M. (2007): Los Insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno Superior del Levante Ibérico. – PhD Thesis, Departament de Geologia, Universitat Autònoma de Barcelona, unpublished.
- FURIÓ, M. & ANGELONE, C. (2010): Insectívoros (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu DI (Mandriola, central-western Sardinia, Italy). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **258**: 229-242.
- GALLAI, G. & ROOK, L. (2011): *Propotamochoerus provincialis* (Gervais, 1859) (Suidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino quarry (Brisighella, Emilia-Romagna, Italy). – Bollettino della Società Paleontologica Italiana, **50**: 29-34.
- GARCÍA-ALIX, A., MINWER-BARAKAT, R., MARTÍN-SUÁREZ, E. & FREUDENTHAL, M. (2008): Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada Basin (southern Spain). Biostratigraphic and phylogenetic implications. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **248**: 183-215.
- GASC, J.P., CABELA, A., CRNOBRNJA-ISAILOVIC, J., DOLMEN, D., GROSSENBACHER, K., HAFFNER, P., LESCURE, J., MARTENS, H., MARTÍNEZ RICA, J.P., MAURIN, H., OLIVEIRA, M.E., SOFIANIDOU, T.S., VEITH, M. & ZUIDERWIJK, A. (1997): Atlas of amphibians and reptiles in Europe. – 496 pp.; Paris (Collection Patrimoines Naturels, 29, Societas Europaea Herpetologica, Muséum National d'Histoire Naturelle & Service du Patrimoine Naturel).
- GAUDANT, J. (1979): “*Pachylebias*” *crassicaudus* (AGASSIZ) (Poisson Téléostéen, Cyprinodontiformes), un constituant majeur dell'ichtyofaune du Messinien continental du Bassin Méditerranéen. – Geobios, **12**: 47-73.
- GAUDANT, J., GUERRERA, F. & SAVELLI, D. (1988): Nouvelles données sur le Messinien de Méditerranée occidentale : les gisements à *Aphanius crassicaudus* (AGASSIZ) (poissons téléostéens, Cyprinodontiformes) des Marches (Italie). – Geodinamica Acta, **2**: 185-196.
- GENTRY, A.W. (1966): Fossil Antilopini of East Africa. – *Bulletins of the British Museum of Natural History (Geology)*, **12**: 45-106.
- GERAADS, D. (2009): Giraffidae (Mammalia) de la fin du Néogène de la République de Macédoine (ARYM). – Geodiversitas, **31** (4): 893-908.
- GERAADS, D. & SPASSOV, N. (2009): Rhinocerotidae (Mammalia) from the late Miocene of Bulgaria. – *Palaeontographica*, (A), **287**: 99-122.
- GHETTI, P., ANADÓN, P., BERTINI, A., ESU, D., GLIOZZI, E., ROOK, L. & SOULIÉ-MARSCHÉ, I. (2002): The Early Messinian Velona Basin (Siena, central Italy): Palaeoenvironmental and paleobiogeographical reconstructions. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **187**: 1-33.
- GHIBAUDO, G., CLARI, P. & PERELLO, M. 1985: Litostratigrafia, sedimentologia ed evoluzione tettonico-sedimentaria dei depositi miocenici del margine sud-orientale del Bacino Terziario Ligure-Piemontese (Valli Borbera,

- Scrivia e Lemme). – *Bollettino della Società Geologica Italiana*, **104**: 349-397.
- GIAOURTSAKIS, I.X. (2003): Late Neogene Rhinocerotidae of Greece: distribution, diversity and stratigraphical range. – *Deinsea*, **10**: 235-253.
- GIAOURTSAKIS, I., THEODOROU, G., ROUSIAKIS, S., ATHANASSIOU, A. & ILIOPOULOS, G. (2006): Late Miocene horned rhinoceroses (Rhinocerotinae, Mammalia) from Kerassia (Euboea, Greece). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **239**: 367-398.
- GIBERT, L., SCOTT, G.R., MONTOYA, P., RUIZ-SÁNCHEZ, F.J., MORALES, J., LUQUE, L., ABELLA, J. & LERÍA, M. (2013): Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. – *Geology*, **41** (6): 691-694.
- GÖHLICH, U.B. & GROSS, M. (in press): The Sarmatian avian fauna from Gratkorn (late Middle Miocene), Austria. – *Palaeobiodiversity and Palaeoenvironments*.
- GROSS, M., MINATI, K., DANIELOPOL, D. & PILLER, W. (2008): Environmental changes and diversification of *Cyprideis* in the Late Miocene of the Styrian Basin (Lake Pannon, Austria). – *Senckenbergiana Lethaea*, **88**: 161-181.
- HEINTZ, E. (1971): *Gazella deperdita* (GERVAIS) 1847 (Bovidae, Artiodactyla, Mammalia) du Pontien du Mont Lubéron, Vaucluse, France. – *Annales de Paléontologie*, **57** (2): 209-229.
- HOWELL, F.C. & GARCÍA, N. (2007): Carnivora (Mammalia) from Lemudong'o (late Miocene: Narok District, Kenya). – *Kirtlandia*, **46**: 121-139.
- HUGUENEY, M. & MEIN, P. (1965): Lagomorphes et rongeurs du Néogène de Lissieu (Rhône). – *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon, Nouvelle Serie*, **12**: 109-123.
- JANIS, C.M., THEODOR, J.M. & BOISVERT, B. (2002): Locomotor evolution in camels revisited: a quantitative analysis of pedal anatomy and the acquisition of the pacing gait. – *Journal of Vertebrate Paleontology*, **22** (1): 110-121.
- KLEMBARA, J., MIROSLAV, J. & DOBIAŠOVÁ, K. (in press): Comparative anatomy of the lower jaw and dentition of *Pseudopus apodus* and the interrelationships of species of subfamily Anguinae (Anguimorpha, Anguidae). – *New advances in morphology and evolution of living and extinct Squamates*. – *Anatomical Records*, special volume.
- KOSTOPOULOS, D.S. (2005): The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkasdagi, Turkey. – *Geodiversitas*, **27**: 747-791.
- KOSTOPOULOS, D.S. (in press): Taxonomic re-assessment and phylogenetic relationships of Miocene homonymously spiral-horned antelopes. – *Acta Palaeontologica Polonica*.
- KOUFOS, G.D. (1987): Study of the Turolian hipparions of the lower Axios valley (Macedonia, Greece). 1. Locality "Ravin des Zouaves-5" (RZO). – *Geobios*, **20**: 293-312.
- KOUFOS, G.D. (2006): The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. – *Hellenic Journal of Geosciences*, **41**: 183-214.
- KOUFOS, G.D., KOSTOPOULOS, D.S., VLACHOU, T.D. & KONIDARIS, G.E. (2011): A synopsis of the late Miocene mammal fauna of Samos Island, Aegean Sea, Greece. – *Geobios*, **44**: 237-251.
- KRAUSE, W. (1997): Charales (Charophyceae). – *Süßwasserflora von Mitteleuropa*, **18**: 202 pp.; Jena (G. Fischer).
- LAPPARENT DE BROIN, F., BOUR, R. & PERÄLÄ, J. (2006a): Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): first part. – *Annales de Paléontologie*, **92**: 255-304.
- LAPPARENT DE BROIN, F., BOUR, R. & PERÄLÄ, J. (2006b): Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): second part. – *Annales de Paléontologie*, **92**: 325-357.
- LUGLI, S., MANZI, V., ROVERI, M. & SCHREIBER, B.C. (2010): The Primary Lower Gypsum in the Mediterranean: a new facies interpretation for the first stage of the Messinian salinity crisis. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **297**: 83-99.
- MANZI, V., GENNARI, R., HILGEN, F., KRIIGSMAN, W., LUGLI, S., ROVERI, M. & SIERRA, F.J. (2013): Age refinement of the Messinian salinity crisis onset in the Mediterranean. – *Terra Nova*, **25** (4): 315-322.
- MARABINI, S. & VAL, G.B. (1988): Geology of the Monticino Quarry (Brisighella, Italy). Stratigraphic implications of its late Messinian mammal fauna. – In: GIULI, C. DE & VAL, G.B. (Eds.): *Fossil vertebrates in the Lamone valley, Romagna Apennines*. – *Field trip guidebook*, 39-52.
- MARRA, A.C. (2009): Pleistocene mammal faunas of Calabria. – *Bollettino della Società Paleontologica Italiana*, **48**: 113-122.
- MARRA, A.C., SOLOUNIAS, N., CARONE, G. & ROOK, L. (2011): Palaeogeographic significance of the giraffid remains (Mammalia, Artiodactyla) from Cessaniti (Late Miocene, Southern Italy). – *Geobios*, **44**: 189-197.
- MARTÍN-SUÁREZ, E., FREUDENTHAL, M. & CIVIS, J. (2001): Rodent palaeoecology of the Continental Upper Miocene of Crevillente (Alicante, SE Spain). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **165**: 349-356.
- MARTÍN SUÁREZ, E. & MEIN, P. (1998): Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). – *Geobios*, **31**: 87-97.
- MASINI, F. (1989): *Prolagus sorbinii* n. sp., a new Ochotonid (Mammalia, Lagomorpha) from the Messinian of Italy. – *Bollettino della Società Paleontologica Italiana*, **28**: 295-306.
- MASINI, F., RINALDI, P.M., PETRUSO, D. & SURDI, G. (2010): The Gargano Terre Rosse insular faunas: an overview. – *Rivista Italiana di Paleontologia e Stratigrafia*, **116**: 421-435.
- MASINI, F., RINALDI, P.M., SAVORELLI, A. & PAVIA, M. (2013): A new small mammal assemblage from the M013 Terre Rosse fissure filling (Gargano, South-Eastern Italy). – *Geobios*, **46**: 49-61.
- MASINI, F. & THOMAS, H. (1989): *Samotragus occidentalis* n. sp., a new bovid from the late Messinian of Italy. – *Bollettino della Società Paleontologica Italiana*, **28**: 307-316.
- MAZZA, P.P.A. (2013): The systematic position of *Hoplitomerycidae* revisited. – *Geobios*, **46**: 33-42.
- MEAD, J. (2013): *Scolecophidia* (Serpentes) of the Late Oligocene and Early Miocene, North America, and a fossil history overview. – *Geobios*, **46**: 225-231.
- MEIN, P. & MARTÍN-SUÁREZ, E. (1994): *Galerix iberica* sp.

- nov. (Erinaceidae, Insectivora, Mammalia) from the Late Miocene and Early Pliocene of the Iberian Peninsula. – *Geobios*, **26**: 723-730.
- MEIN, P. & MICHAUX, J. (1970): Un nouveau stade dans l'évolution des rongeurs pliocènes de l'Europe sud-occidentale. – *Comptes rendus de l'Académie des Sciences (D)*, **270**: 2780-2783.
- MEISCH, C. (2000): Freshwater Ostracoda of Western and Central Europe. – In: SCHWOERBEL, J. & ZWICK, P. (Eds.): Süßwasserfauna von Mitteleuropa, **8**: 522 pp.; Heidelberg & Berlin (Spektrum).
- MINWER-BARAKAT, R., GARCÍA-ALIX, A., MARTÍN-SUAREZ, E. & FREUDENTHAL, M. (2009a): Late Turolian micromammals from Rambla de Chimeneas-3: considerations on the oldest continental faunas from the Guadix Basin (Southern Spain). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **83**: 854-879.
- MINWER-BARAKAT, R., GARCÍA-ALIX, A., AGUSTÍ, J., MARTÍN-SUAREZ, E. & FREUDENTHAL, M. (2009b): The micromammal fauna from Negratín-1 (Guadix Basin, Southern Spain): New evidence of African-Iberian mammal exchanges during the late Miocene. – *Journal of Paleontology*, **251**: 95-108.
- MLÍKOVSKÝ, J. (2002): Cenozoic birds of the World. Part 1: Europe. – 406 pp.: Praha (Ninox Press).
- MEYNARSKI, M. (1976): Testudines. *Handbuch der Paläoherpetologie*, part 7. – VI + 129 pp.; Stuttgart & New York (G. Fischer).
- MONTOYA, P. (1994): Los macromamíferos del Mioceno superior del área de Crevillente (Alicante). – PhD Thesis, Universitat de Valencia, unpublished.
- MONTOYA, P. & ALBERDI, M.T. (1995): Crevillente 15 y Crevillente 16, dos nuevos yacimientos con macromamíferos en el Mioceno superior de Alicante (España). – *Estudios Geológicos*, **51**: 159-182.
- MONTOYA, P., GINSBURG, L., ALBERDI, M.T., VAN DER MADE, J., MORALES, J. & SORIA, M.D. (2006): Fossil large mammals from the Early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. – *Geodiversitas*, **28**: 137-173.
- MOURER-CHAUVIRÉ, C. (1989): A Peafowl from the Pliocène of Perpignan, France. – *Palaeontology*, **32**: 439-446.
- MOURER-CHAUVIRÉ, C. (2004): Les oiseaux du Pliocène supérieur de Saint-Vallier (Drome, France). – *Geobios*, **37**: S97-S114.
- NOLF, D. (1985): Otolithi Piscium. – In: SCHULTZE, H.-P. (Ed.): *Handbook of Paleichthyology*, **10**: 1-145.
- NOLF, D. (2013): The Diversity of Fish Otoliths Past and Present. – 350 pp.; Bruxelles (Royal Belgian Institute of Natural Sciences).
- PARENTI, L.R. (1981): A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). – *Bulletins of the American Museum of Natural History*, **168**: 339-557.
- PATACCA, E., SCANDONE, P. & CARNEVALE, G. (2013): The Miocene vertebrate-bearing deposits of Scontrone (Abruzzo, Central Italy): stratigraphic and paleoenvironmental analysis. – *Geobios* **46**: 5-23.
- PAVIA, M. & MOURER-CHAUVIRÉ, C. (2011): Redescription of *Tyto sanctialbani* LYDEKKER, 1893 (Aves, Strigiformes), from its type locality of La Grive-Saint-Alban (middle Miocene, France). – *Journal of Vertebrate Paleontology*, **31**: 1093-1101.
- PESQUERO, M.D. (2003): *Hipparion* del Turoliense superior de Las Casiones (Fosa de Teruel). – *Coloquios de Paleontología, Vol. Extr.*, **1**: 511-548.
- PESQUERO, M.D., SALESA, M.J., ESPÍLEZ, E., MAMPEL, L., SILICEO, G. & ALCALÁ, L. (2011): An exceptionally rich hyaena coprolites concentration in the Late Miocene mammal fossil site of La Roma 2 (Teruel, Spain): taphonomical and palaeoenvironmental inferences. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**: 30-37.
- PORTIS, A. (1880): Di alcuni fossili terziarii del Piemonte e della Liguria appartenenti all'ordine dei Chelonii. – *Memorie della Regia Accademia delle Scienze di Torino, serie 2*, **32**: 113-134.
- RAGE, J.-C. (2013): Mesozoic and Cenozoic squamates of Europe. – *Palaeobiodiversity and Palaeoenvironment*, **93**: 517-534.
- REICHENBACHER, B. & KOWALKE, T. (2009): Neogene and present-day zoogeography of killifishes (*Aphanius* and *Aphanolebias*) in the Mediterranean and Paratethys areas. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**: 43-56.
- ROČEK, Z. (1984): Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Boemia, Czechoslovakia). – *Rozpravi Československé Akademie Ved Řada matematických a Přírodních Ved*, **94**: 3-69.
- ROOK, L. (2009): The wide ranging genus *Eucyon* TEDFORD & QIU, 1996 (Mammalia, Carnivora, Canidae, Canini) in the Mio-Pliocene of the Old World. – *Geodiversitas*, **31**: 723-741.
- ROOK, L. & BERNOR R.L. (2013): *Hippotherium malpasi* (Equidae, Mammalia) from the latest Miocene (late Messinian; MN13) of Monticino gypsum quarry (Brisighella, Emilia-Romagna, Italy). – *Bollettino della Società Paleontologica Italiana*, **52**: 95-102.
- ROOK, L., GALLAI, G. & TORRE, D. (2006): Lands and endemic mammals in the Late Miocene of Italy: constraints for paleogeographic outlines of Tyrrhenian area. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238**: 263-269.
- ROOK, L. & DELFINO M. (2007): La fauna preistorica di Brisighella e i popolamenti continentali del Mediterraneo nel Miocene superiore. – In: SAMI, A. (Ed.): *Il parco museo geologico Cava Monticino, Brisighella. Una guida e una storia*, 97-121; Faenza (Tipografia Carta Bianca).
- ROOK, L., OMS, O., BENVENUTI, M. & PAPINI, M. (2011): Magnetostratigraphy of the Late Miocene Baccinello-Cinigliano basin (Tuscany, Italy) and the age of *Oreopithecus bambolii* faunal assemblages. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **305**: 286-294.
- ROVERI, M., LUGLI, S., MANZI, V. & SCHREIBER, B.C. (2008): The Messinian Sicilian stratigraphy revisited: new insights for the Messinian salinity crisis. – *Terra Nova*, **20**: 483-488.
- ROVERI, M. & MANZI, V. (2006): The Messinian salinity crisis: looking for a new paradigm? – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238**: 386-398.
- ROVERI, M. & MANZI, V. (2007): Gessoso-Solfifera. – In:

- CITA, M.B., ABBATE, E., BALINI, M., CONTI, M.A., FALORNI, P., GERMANI, D., GROPELLI, G., MANETTI, P. & PETTI, F.M. (Eds.): Carta Geologica d'Italia 1:50000, Catalogo delle Formazioni, Unità tradizionali (2). Quaderni Servizio Geologico d'Italia, serie III, 7: 303-310.
- RYAN, W.B.F., PITMAN, W.C. III, MAJOR, C.O., SHIMKUS, K., MOSKALENKO, V., JONES, J.A., DIMITROV, P., GÖRÜR, N., SAKINÇ, M. & YÜCE, H. (1997a): An abrupt drowning of Black Sea shelf at 7.5 kyr BP. – *Geo-Eco-Marina*, 2, Proc. International Workshop on Fluvial-Marine Interactions, Mainas, Romania, 1-7 October, 1997: 115-125.
- RYAN, W.B.F., PITMAN, W.C. III, MAJOR, C.O., SHIMKUS, K., MOSKALENKO, V., JONES, J.A., DIMITROV, P., GÖRÜR, N., SAKINÇ, M. & YÜCE, H. (1997b): An abrupt drowning of Black Sea shelf. – *Marine Geology*, 138: 119-126.
- SALESA, M.J., PESQUERO, M.D., SILICEO, G., ANTÓN, M., ALCALÁ, L. & MORALES, J. (2012): A rich community of Felidae (Mammalia, Carnivora) from the Late Miocene (Turolian, MN 13) site of Las Casiones (Villalba Baja, Teruel, Spain). – *Journal of Vertebrate Paleontology*, 32: 658-676.
- SANCHÍZ, B. (1998): Salientia. – *Handbuch der Paläoherpetologie*, 4: 275 pp.; München (Pfeil).
- SARDELLA, R. (2008): Remarks on the Messinian carnivores (Mammalia) of Italy. – *Bollettino della Società Paleontologica Italiana*, 47: 195-202.
- SARDELLA, R. & WERDELIN, L. (2007): *Amphimachairodus* (Felidae, Mammalia) from Sahabi (latest Miocene-earliest Pliocene, Libya), with a review of African Miocene Machairodontinae. – *Rivista Italiana di Paleontologia e Stratigrafia*, 113: 67-77.
- SARICA-FILOREAU, N. (2002): Faunes de rongeurs néogènes et quaternaires des grabens d'Anatolie occidentale. Systématique, biochronologie et implications tectoniques. – PhD thesis, Muséum National d'Histoire Naturelle, Paris, unpublished.
- SEGUENZA, L. (1902): I vertebrati fossili della provincia di Messina: Parte II. Mammiferi e geologia del piano Pontico. – *Bollettino della Società Geologica Italiana*, 21: 115-172.
- SEGUENZA, L. (1907): Nuovi resti di mammiferi fossili di Gravittelli presso Messina. – *Bollettino della Società Geologica Italiana*, 26: 7-119.
- SELLI, R. (1973): An outline of the Italian Messinian. – In: DROOGER, C.W. (Ed.): *Messinian Events in the Mediterranean*, 150-171; Amsterdam (North-Holland Publishing Company).
- SPASSOV, N., TZANKOV, T. & GERAADS, D. (2006): Late Neogene stratigraphy, biochronology, faunal diversity and environments of south-western Bulgaria (Struma River valley). – *Geodiversitas*, 28: 477-498.
- SPEYBROECK, J., BEUKEMA, W. & CROCHET, P.A. (2010): A tentative species list of the European herpetofauna (Amphibia and Reptilia) – an update. – *Zootaxa*, 2492: 1-27.
- STURANI, C. (1973): A fossil eel (*Anguilla* sp.) from the Messinian of Alba (Tertiary piedmontese basin). Palaeoenvironmental and palaeogeographic implications. – *Messinian events in the Mediterranean*. – Koninklijke Nederlandse Academie van Wetenschappen: 243-255.
- STURANI, C. (1976): Messinian facies in the Piedmont Basin. – *Memorie della Società Geologica Italiana*, 16: 11-25.
- SZYNDLAR, Z. (1991): A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. – *Estudios geológicos*, 47: 103-126.
- SZYNDLAR, Z. (1984): Fossil snakes from Poland. – *Acta Zoologica Cracoviensia*, 28: 1-156.
- VAN DEN HOEK OSTENDE, L.W. (2001): A revised generic classification of the Galericiini (Insectivora, Mammalia) with some remarks on their palaeobiogeography and phylogeny. – *Geobios*, 34: 681-695.
- VAN MORKHOVEN, F.P.C.M. (1963): Post-Paleozoic Ostracoda. Vol II, Generic Description. – 478 pp.; Amsterdam (Elsevier).
- VILLIER, B. & CARNEVALE, G. (2013): A new skeleton of the giant hedgehog *Deinogalerix* from the Miocene of Gargano, southern Italy. – *Journal of Vertebrate Paleontology*, 33: 902-923.
- VISLOBOKOVA, I. (2005): The importance of Late Miocene faunal exchange between Eastern Mediterranean areas and central Europe. – *Annales de Paléontologie*, 91: 241-255.
- VISLOBOKOVA, I.A. (2007): New data on late Miocene mammals of Kohfidisch, Austria. – *Paleontological Journal*, 41 (4): 451-460.
- VON DEN DRIESCH, A. (1976): A guide to the measurement of animal bones from archaeological sites. – *Peabody Museum Bulletin*, 1: 1-136.
- WEERD, A. VAN DE (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. – *Utrecht Micropaleontological Bulletin*, 2: 1-217.

Manuscript received: January 15th, 2014.

Revised version accepted by the Stuttgart editor: March 28th, 2014.

Addresses of the authors:

SIMONE COLOMBERO, GIORGIO CARNEVALE, MASSIMO DELFINO, PIERO GIUNTELLI, GIULIO PAVIA, MARCO PAVIA, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, 35, 10125 Torino, Italy;

CHIARA ANGELONE, MASSIMO DELFINO, Grup de recerca de Faunes del Neogen i Quaternari, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICP, Campus de la UAB s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain;

EDOMONDO BONELLI, ORESTE CAVALLO, GIOVANNI REPETTO, Museo Civico "Federico Eusebio", Via Vittorio Emanuele, 19, 12051 Alba (Cuneo), Italy;

PAUL PETER ANTHONY MAZZA (corresp. author), Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via La Pira 4, 50121 Firenze, Italy.
e-mail: paul.mazza@libero.it

Appendix

Table 1. Measurements (in mm) of the bird remains from Verduno. **GL**, greatest length; **Pw**, proximal width; **Pd**, proximal depth; **Dw**, distal width; **Dd**, distal depth; **Sw**, smallest width of shaft. Coracoid: **Lm**, medial length; **Wdf**, width of distal facies. Scapula: **W**, proximal width from caudal margin of facies articularis humeralis to acromion; **Lfah**, length of facies articularis humeralis; **Wfah**, width of facies articularis humeralis; **Wc**, width of the column.

Phasianidae gen et sp. indet.					
scapula	GL	W	Lfah	Wfah	Wc
MGPT-PU 135006	–	15.8	8.3	6.2	7.4
Galliformes indet.					
Tarsometatarsus	GL	Pw	Pd	Dw	Sw
MGPT-PU 135007	–	–	–	11.5	4.8
Accipitridae gen. et sp. indet.					
Post. phalanx 2/II	GL	Pw	Pd	Dw	Sw
MGPT-PU 135008	21.6	6.7	–	5.4	4.9
Strigidae gen. et sp. indet.					
Post. phalanx 1/II	GL	Pw	Pd	Dw	Sw
MGPT-PU 135009	12.2	7.4	6.6	–	4.8

Next double page

Table 2. Osteometrics of Verduno's large mammals. Legend, in alphabetic order: B: greatest breadth; Bcaud art surf: breadth of the caudal articular surface; Bcran: cranial breadth; BD: breadth of the distal epiphysis; BDa: breadth of the distal articular surface; Bdens: breadth of the dens; Bdiart art: breadth across the diarthrodial articulations; Bpost art surf: breadth across the posterior articular surfaces; BP: breadth of the proximal epiphysis; BPa: breadth of the proximal articular surface; BS: breadth of the shaft (diaphysis); Btub olecran: greatest breadth of the olecranon; DAP: antero-posterior diameter; DAPbeak: antero-posterior diameter at the olecranic beak; DAPneck: antero-posterior diameter of the neck; DAPolecran: antero-posterior diameter of the olecranon; DD: depth of the distal epiphysis; DL: lateral depth; DM: medial depth; DP: depth of the proximal epiphysis; DS: depth of the shaft (diaphysis); DT: transverse diameter; DTglen: transverse diameter across the glenoid articular surface; DTolecran: transverse diameter of the olecranon; H: height; Hcaud art surf: dorso-ventral diameter of the caudal articular surface; Hglen: dorso-ventral diameter of the glenoid articular surface; L: greatest length; Ldist half: length between the margin of the articular surfaces for the astragalus and the distal tip of the bone; LL: lateral length; ML: medial length.

