The latest Early Pleistocene sabertoothed cat *Homotherium* (Felidae, Mammalia) from Monte Peglia (Umbria, central Italy)

Raffaele SARDELLA & Dawid Adam IURINO

R. Sardella, Dipartimento di Scienze della Terra, Università di Roma “La Sapienza”, P.le A. Moro 5, I-00185 Roma, Italy; IsIPU, Istituto Italiano di Paleontologia Umana, Via U. Aldrovandi 18, I-00197 Roma, Italy; raffaele.sardella@uniroma1.it

D.A. Iurino, Dipartimento di Scienze della Terra, Università di Roma “La Sapienza”, P.le A. Moro 5, I-00185 Roma, Italy; dawid.iurino@uniroma1.it

KEY WORDS - Mammals, biochronology, Early-Middle Pleistocene transition, Italy, taxonomy.

ABSTRACT - The latest Early Pleistocene karst infill deposits outcropping at Monte Peglia (Umbria, central Italy) have been the focus of a variety of field expeditions by researchers from the “Istituto Italiano di Paleontologia Umana” during the period from 1955 to 1968. These studies have led to the discovery of two distinct vertebrate assemblages considered as being similar in age. In 1955 large vertebrate remains were found and, in particular, many isolated teeth were collected that are referable to a single specimen of the saber-toothed cat Homotherium. The taxonomy of Homotherium, mainly based on cranio-dental features, is still controversial and the diverse interpretations are due essentially to the rarity of complete fossil specimens and the high variability of these records. Herein the specimen from Monte Peglia is referred to Homotherium latidens (Owen) and its affinities with the late Villafranchian and Galerian specimens from Eurasia are discussed.

INTRODUCTION

Monte Peglia is located between the towns of Todi and Orvieto in Umbria, central Italy. In the Monte Peglia area, a Meso-Cenozoic carbonatic succession with transitional features between the Scaglia Toscana Formation and the Scaglia Umbria Formation is exposed (Botti et al., 2010). During the Plio-Pleistocene the carbonatic succession of Monte Peglia was affected by karst activity. The Early Pleistocene vertebrate fossiliferous site is a karst filling deposit located near the top of Monte Peglia (837 m), on the left side of the road connecting the town of Orvieto to Marsciano (Blanc, 1955) (Fig. 1).

The site was discovered in 1955 by two collectors (R. Spinola and P. Favella) and in the same year A.C. Blanc promoted a field campaign (July to August 1955) carried out with scientists of the “Istituto Italiano di Paleontologia Umana” (among the others Cardini and von Koenigswald) (Blanc, 1955). In the following years, other field campaigns were carried out on the Istituto in 1957, 1964-66 and 1968 (Piperno et al., 1984) (Fig. 2).

In the deposit “terre rosse” with carbonatic elements, stalagmite levels and bone breccias outcrop. Two assemblages have been discovered: the first, including mostly large vertebrates (generally referred by the authors to a period of subtropical climate conditions) and another one with only microvertebrates (considered as indicating temperate cooler climate) (Piperno et al., 1984). Finally some lithic artefacts (one chopper and four flints) were found not in stratigraphical position near the fossiliferous deposit. The artefacts and the fossil bones were considered as coeval for the occurrence on them of a ferromanganese patina (Piperno, 1972; Piperno et al., 1984).

The faunal assemblages found at M. Peglia are referred to the Colle Curti F.U. (early Biharian-early Galerian, Jaramillo magnethochron) for the presence of *Microtus* (Allocaphioinys) nutiensis and *Microtus* (Allocaphioinys) burgonidiae (Meulen, 1973; Gliozzi et al., 1997; Sala & Masini, 2007).

Bedetti (2003) revised the avifauna and updated the taxa list: *Hieraaetus* nov. sp., *Aquila* sp., Accipitridae indet., *Falco antiquus*, *Coturnix coturnix*, *Perdix* sp., *Columba livia minutula*, *Corvus pliocaenus*. If the taxonomy and the biochronology of the micromammal assemblages is well established and studied, the large mammal assemblage needs a more detailed taxonomical analysis, and the revision of the fossil materials is in progress.

**SYSTEMATIC PALEONTOLOGY**

**Family Felidae Gray, 1821**

**Genus Homotherium Fabrini, 1890**

*Homotherium latidens* Owen, 1846

*Material* - MP 150 right C, MP 151 left C, MP 152 left I3, MP 153 left I2, MP 154 right I1, MP 155 left I1, MP 156 right I2, MP 157 right I3, MP 158 left P4, MP 159 left m1, MP 160 left p4, MP 161 right m1, MP 162 right i2, MP 163 right P4, MP 164 right p4, MP 165 right c, MP 166 right i3, MP 167 right i2, MP 169 left c.

All the fossils are stored at the laboratories of the “Istituto Italiano di Paleontologia Umana” in Anagni (Frosinone, Latium).
Description - Isolated teeth referable to a single large adult specimen (Figs 3-4).

The upper canines are damaged, in particular MP 150 crown is almost complete, serrated, relatively straight and "low", its root is damaged (Fig. 3); MP 151 is fragmentary. MP 158 is a complete left P4, with no trace of preparastyle, a reduced protocone supported by a very little root. In labial view an evident wear surface can be noticed. Such a condition can be observed also on many other teeth (m1 in particular) and suggests that the sabertoothed cat fossil from Monte Peglia should belong to a quite aged adult animal. MP 158 is larger than G21 from Pirro Nord (Sardella, 1994; Petrucci, 2008; Petrucci et al., in press), but they have similar morphologies. No preparastyle occurs in both the specimens, the main differences can be noticed on the parastyle morphology, inclined in Monte Peglia specimen, with a vertical anterior side on Pirro Nord tooth (Figs 4-5).

The lower canine MP 169 has lost its root, the crown is stout, sharp, laterally compressed with finely serrated anterior and posterior ridges. The p4 MP 160 and MP 164 are worn, MP 164 main cusp is slightly broken. Their crowns are directed posteriorly, with a well-separated anterior cusp.

The lower carnassials are elongated and have worn blades on the labial view, with ventrally widened roots.

Discussion - Homotherium spread into Europe around 3 Ma and became one of the most important element in the Plio-Pleistocene Eurasian carnivore guilds. As Sotnikova & Titov (2009) pointed out, the FAD of Homotherium in Europe is recorded in the fauna of Odessa Catacombs (end of MN15). The origin of the genus has been discussed in Werdelin & Sardella (2006), who confuted the presence of Homotherium from the earliest Pliocene South African site of Langenbaanweg.

Fig. 3 - Homotherium latidens (Owen) from Monte Peglia. MP 151 left upper canine: a1) lingual view, a2) labial view; MP 150 right upper canine: b1) labial view, b2) lingual view (Photo Iurino, scale bar 2 cm).

Fig. 4 - Homotherium latidens (Owen) from Monte Peglia. MP 169 left lower canine: a1) labial view, a2) lingual view; MP 160 left p4: b1) labial view, b2) lingual view; MP 164 right p4: c1) lingual view, c2) labial view; MP 158 left P4: d1) labial view, d2) lingual view; MP 159 left m1: e1) labial view, e2) lingual view (Photo Iurino, scale bar 2 cm).

In Eurasia Homotherium becomes rare during the Middle Pleistocene in correspondence to the diffusion of the large pantherine cats and the consequent ecological
competition. The presence of both *Homotherium* and the lion is recorded in many European sites such as Mosbach and Mauer (Germany), Vértesszöllős (Hungary), Westbury (Great Britain), and Atapuerca TD10 (Spain) (Antón et al., 2005).

Evidence for a survival of *Homotherium* in Europe until the Late Pleistocene (late Devensian) comes from a mandible collected from the North Sea (Reumer et al., 2005).

The taxonomy of *Homotherium* is still controversial. Many different species have been referred to the genus *Homotherium* in Eurasia. Among the European species: *Homotherium nestianum* and *Homotherium crenatidens* include most of the Villafranchian specimens, while *Homotherium latidens* and *Homotherium moravicum* characterize the Middle Pleistocene (and possibly Late Pleistocene) assemblages (Sardella, 1994 and references therein; Sotnikova et al., 2002; Galobart et al., 2003; Sotnikova & Titov, 2009 among the others).

Ballesio (1963) and de Bonis (1976) referred the Villafranchian forms to two different species; on the contrary Piccarelli (1979), taking into account the fossil sample from the Upper Valdarno, synonymized *H. nestianum* with *H. crenatidens*, and considered the differences between the two forms as individual variation, possibly due to sexual dimorphism (Tabs 1-2).

The abundant *Homotherium* fossil sample from Incarcar (Spain) (skulls, mandibles and limb bones) shows a great individual variation degree, thus supporting the idea of grouping all the Pliocene and Pleistocene European *Homotherium* within a single species (Pons-Moyá & Moyá-Solá, 1992; Galobart et al., 2003). Therefore Turner & Antón (1997) referred all the Plio-Pleistocene Eurasian homotheres to *Homotherium latidens* because this name has the priority on all the others.

As a matter of fact the differences between Villafranchian and post-Villafranchian Eurasian homotheres can be suitable of different interpretations and the relative paucity and the scantiness of complete material from the Middle Pleistocene sites (mostly fragmentary and isolated teeth) at present do not enable to clarify their taxonomy.

Apart from the “classic” sample from the Upper Valdarno (Fabrini, 1890; Piccarelli, 1979), a very rich sample in Italy is that from Pirro Nord (Apulia) (Sardella, 1994; Petrucci, 2008; Petrucci et al., in press). Pirro Nord
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Domelgiana (I)</td>
<td>Middle Pleist.</td>
<td>V8911</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>45.3</td>
<td>10</td>
<td>9.5</td>
<td>16.5</td>
<td>19.3</td>
</tr>
<tr>
<td>2 Monte Peglia (I)</td>
<td>Middle Pleist.</td>
<td>MP150-158</td>
<td>35.3</td>
<td>14.1</td>
<td></td>
<td></td>
<td>43.8</td>
<td>12.7</td>
<td>9</td>
<td>16</td>
<td>19</td>
</tr>
<tr>
<td>3 Pirro Nord (I)</td>
<td>Early Pleist.</td>
<td>PP 180</td>
<td>30.6</td>
<td>13.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 Pirro Nord (I)</td>
<td>Early Pleist.</td>
<td>PP 184</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>40.6</td>
<td>12.2</td>
<td>7.7</td>
<td>16.6</td>
<td>16.6</td>
</tr>
<tr>
<td>5 Pirro Nord (I)</td>
<td>Early Pleist.</td>
<td>PN 11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 Pirro Nord (I)</td>
<td>Early Pleist.</td>
<td>G 21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>39.3</td>
<td>12.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 Pirro Nord (I)</td>
<td>Early Pleist.</td>
<td>G 93</td>
<td>32</td>
<td>13.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 Stránska Skála (CZ)</td>
<td>Middle Pleist.</td>
<td>S410</td>
<td>30.5</td>
<td>12.7</td>
<td></td>
<td></td>
<td>37.3</td>
<td>10.8</td>
<td>7.1</td>
<td>12</td>
<td>17.5</td>
</tr>
<tr>
<td>9 Koněpy (CZ)</td>
<td>Middle Pleist.</td>
<td>cast</td>
<td>32.8</td>
<td>13.2</td>
<td>6</td>
<td>5.4</td>
<td>38</td>
<td>11.5</td>
<td>9.1</td>
<td>12.6</td>
<td>14.9</td>
</tr>
<tr>
<td>10 Artanac (F)</td>
<td>Middle Pleist.</td>
<td>V.60.1767</td>
<td>27.8</td>
<td>11.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 Gombaszig (SK)</td>
<td>Middle Pleist.</td>
<td>V.69.1220</td>
<td>32</td>
<td>13.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 Verdesszollos (H)</td>
<td>Middle Pleist.</td>
<td>2006 V.10774</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 Betiza (RO)</td>
<td>Early Pleist.</td>
<td>cast</td>
<td>31</td>
<td>15.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 Hundsheim (A)</td>
<td>Middle Pleist.</td>
<td>IGF 825</td>
<td>31</td>
<td>11.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 Hundsheim (A)</td>
<td>Middle Pleist.</td>
<td>IGF 4713</td>
<td>31</td>
<td>15.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16 Hundsheim (A)</td>
<td>Middle Pleist.</td>
<td>cast</td>
<td>31</td>
<td>11.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17 Natiere (F)</td>
<td>Middle Pleist.</td>
<td>V. A. 2057</td>
<td>28</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18 Montmarin (F)</td>
<td>Middle Pleist.</td>
<td>cast</td>
<td>31</td>
<td>15.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19 Valdarno sup. (I)</td>
<td>Early Pleist.</td>
<td>IGF 6090</td>
<td>31.9</td>
<td>13.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20 Valdarno sup. (I)</td>
<td>Early Pleist.</td>
<td>IGF12480</td>
<td>31.9</td>
<td>11.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 Valdarno sup. (I)</td>
<td>Early Pleist.</td>
<td>IGF 817</td>
<td>33.5</td>
<td>13.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22 Valdarno sup. (I)</td>
<td>Early Pleist.</td>
<td>IGF 4713</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>43.1</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23 Valdarno sup. (I)</td>
<td>Early Pleist.</td>
<td>Se 1698</td>
<td>31</td>
<td>13.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24 Ceyssenget (F)</td>
<td>Early Pleist.</td>
<td>V. A. 2057</td>
<td>31.6</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 Ceyssenget (F)</td>
<td>Early Pleist.</td>
<td>cast</td>
<td>34.5</td>
<td>15.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>26 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>n.n.</td>
<td>33.8</td>
<td>14.4</td>
<td></td>
<td></td>
<td>41.5</td>
<td>13.8</td>
<td>8</td>
<td>14</td>
<td>16.5</td>
</tr>
<tr>
<td>27 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>cast</td>
<td>38.2</td>
<td>17.2</td>
<td>10</td>
<td>6.4</td>
<td>41.5</td>
<td>13.8</td>
<td>9</td>
<td>14.5</td>
<td>17.7</td>
</tr>
<tr>
<td>28 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>ind. A/lac. 13</td>
<td>26.8</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>ind. B/lac. 13</td>
<td>32</td>
<td>15</td>
<td></td>
<td></td>
<td>37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>ind. E/lac. 13</td>
<td>25</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>31 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>ind. Z/P 3-867L</td>
<td>30</td>
<td>10.7</td>
<td>8</td>
<td>5.5</td>
<td>38</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>32 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>Teilhard '36</td>
<td>29</td>
<td>11.5</td>
<td>10</td>
<td></td>
<td>38</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>33 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>3120-60</td>
<td>31</td>
<td>15</td>
<td>11</td>
<td>7</td>
<td>37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>34 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>3120-610</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>39</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>Sharapov '86</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>Vekua's 72</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>37 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>Boule 1901</td>
<td>30</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>38 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>Boule 1901</td>
<td>33</td>
<td>15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>39 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>IGF 832</td>
<td>32</td>
<td>14</td>
<td></td>
<td></td>
<td>41.5</td>
<td>11.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>40 Choukoutien (RC)</td>
<td>Middle Pleist.</td>
<td>IGF 53V</td>
<td>30.5</td>
<td>14.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tab. 1 - Upper dention measurements (mm). L= tooth length; W= tooth width. P4/L1= parastyle length; P4/L2= paracone length; P4/L3= metastyle length. I: Italy; CZ: Czech Republic; F: France; SK: Slovakia; H: Hungary; RO: Romania; A: Austria; DZ: Algeria; RC: Democratic Republic of China; TJ: Tajikistan; GE: Georgia; GB: Great Britain.
Tab. 2 - Lower dentition measurements (mm). L= tooth length; W= tooth width. GB: Great Britain; I: Italy; A: Austria; E: Spain; GE: Georgia; F: France; TJ: Tajikistan; SA: South Africa.

(see Sardella, 1994) and are morphologically different if compared to the Monte Peglia and Pirro Nord specimens, but also to the Untermassfeld ones (Thuringia, Germany).

As pointed out in many studies, the Eurasian homotheres show a high degree of variation in the overall size and craniodental morphology and proportions, and such a mosaic of characters cannot be easily put in a clear taxonomic framework.

The analysis of the fossil material suggests, in our opinion, the possibility of a quite gradual evolution, at least in the European homotheres and, despite fossils can be grouped in different "morphotypes", possibly different species (as claimed recently by Sotnikova & Titov, 2009) in this paper we use the term *Homotherium latidens*.

If a splitter approach is adopted, the Eurasian homotheres could be classified as follows:
1) the late Pliocene-earliest Pleistocene specimens, which have relatively longer upper canines and more robust and convex mental area in the mandible, could be referred, respectively, to *H. nestianus* (Western Europe) and to *H. davitasvili* (Kvabebi) in Caucasus (Georgia) (Vekua, 1972; Agustì et al., 2009);
2) the Early Pleistocene forms, characterized by a high variability, could be referred to *Homotherium crenatidens*;
3) finally, the Middle Pleistocene forms, characterized by the presence of a preparastyle in the P4 (a quite primitive feature) and rounded and concave mental area in the mandible, could be classified as *H. latidens* and/or *H. moravicum*.

Nonetheless, taking into account the wide range of variability observed in the fossils, the definition of a
clearly distinct taxonomic categories (at specific level) is still difficult to achieve, and, at present, a conservative approach is preferred. For this reason the Monte Peglia specimen is here referred to *Homotherium latidens*, even if its characters could be related, considering the upper canine and upper carnassials morphology, to an advanced form of *H. crenatidens* morphotype; such “evolutionary stage” in Italy characterized the late Villafranchian (Pirro Nord) and early Galerian (Colle Curti)/Epivillafranchian faunal units (Gliozzi et al., 1997; Torre et al., 2001; Sardella, 2007). The occurrence of a *H. moravicum* morphotype at Domegliara Selvavecchia, a latest Early Pleistocene site, suggests a more complex scenario for the evolution and the diffusion of homotherine sabertoothed cats in Europe.

ACKNOWLEDGEMENTS

We wish to thank Fabio Parenti and Luca Bellucci (“Istituto Italiano di Paleontologia Umana”) and Maria Cristina De Angelis (“Soprintendenza per i Beni Archeologici per l’Umbria”). We are grateful to Lorenzo Rook (University of Firenze) and Lars Werdelin (Naturhistoriska Riksmuseet, Stockholm) for their valuable comments and suggestions. RS acknowledges 2008 - SYNTHESYS project AT 5028 (European Union-funded Integrated Activities grant) “Early and Middle Pleistocene carnivores (Mammalia) of Europe”, Natural History Museum of Vienna, Austria, and 2010 - SYNTHESYS project HU-TAF-707 (European Union-funded Integrated Activities grant) “Early and Middle Pleistocene carnivores (Mammalia) of Europe: taxonomy and palaeobiogeography”, Natural History Museum of Budapest, Hungary; moreover this study was funded by SAPIENZA Ricerche Universitarie 2010 (prot. C26A10YBY3)” “Analisi dei vincoli crono-stratigrafici delle unità biocronologiche a mammiferi, ostracodi e molluschi continentali per mezzo di metodologie stratigrafiche integrate: il caso delle aree costiere quaternarie tosco-umbro-laziali” (resp. RS).

REFERENCES


