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REINTERPRETATION OF THE LATE PLEISTOCENE INGARANO CAVE DEPOSIT BASED ON THE FOSSIL BIRD ASSOCIATIONS (APULIA, SOUTH-EASTERN ITALY)

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Abstract. We present a study of Late Pleistocene fossil bird remains from Ingarano (Apulia, SE Italy), based on the revision of previously published material and the study of unpublished fossils bones. New field observations make it possible to simplify the stratigraphy of the deposit compared to previous work. The systematic study of the fossil bird bones revealed the presence of 17 taxa, including two hypothetical ones: *Circus aeruginosus*, *Buteo rufinus*, *Aquila chrysaëtos*, *Falco columbarius*, *Falco cherrug*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Otus scops*, *Nyctea scandiaca*, *Nyctea scandiaca* vel *Bubo bubo*, *Athene noctua noctua*, *Pyrrhocorax graculus*, *Pyrrhocorax pyrrhocorax*, *Corvus corone*, *Corvus corone* vel *Corvus frugilegus*, *Corvus corax*. Our detailed study also helps improve the taphonomical interpretation of the deposit: the remains from the lower layers were accumulated after mammalian predator activity and were transported over short distances, while the ones from the upper layers show sings of intense transport, such as fractures and surface abrasion. Two different bird assemblages were recognized, respectively from the lowermost and the upper layers of the clastic succession exposed in the Ingarano deposit; this difference is also confirmed by the fossil mammal remains. The systematic study makes it possible to make palaeoenvironmental and palaeoclimatic reconstructions: both assemblages indicate open environments, and the taxa of the lower layers indicate the presence of woods and wetlands with colder characteristics, while birds of the upper layers indicate drier and warmer conditions. This analysis, and the dating established through geochemical analyses and study of lithic artefacts, lead us to date the formation of the Ingarano deposit to the Late Pleistocene, in particular to the MIS 3. The presence of a layer dated to the MIS 2 at the base of the succession indicated in previous works cannot be confirmed.

Riassunto. In questo lavoro vengono analizzati i resti di uccelli provenienti dal giacimento del Pleistocene superiore di Ingarano (Puglia, Italia meridionale) con la revisione dei materiali editi e lo studio di resti inediti. È stata effettuata una nuova interpretazione stratigrafica del deposito, semplificata rispetto a quella proposta dagli autori precedenti. Lo studio sistematico delle ossa di uccelli ha permesso di determinare diciassette taxa, due dei quali in modo dubitativo: *Circus aeruginosus*, *Buteo rufinus*, *Aquila chrysaëtos*, *Falco columbarius*, *Falco cherrug*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Otus scops*, *Nyctea scandiaca*, *Nyctea scandiaca* vel *Bubo bubo*, *Athene noctua noctua*, *Pyrrhocorax graculus*, *Pyrrhocorax pyrrhocorax*, *Corvus corone*, *Corvus corone* vel *Corvus frugilegus*, *Corvus corax*. Lo studio del materiale fossile ha inoltre fornito nuovi elementi per l'interpretazione tafonomica del giacimento, rivelando che i resti presenti nei livelli inferiori hanno subito un trasporto molto ridotto e sono stati in parte originati dall'attività di un mammifero predatore, mentre quelli conservati nei livelli superiori presentano segni di un maggiore trasporto, quali fratture e abrasioni. È stato così possibile riconoscere due associazioni faunistiche nettamente distinte, una che caratterizza livelli inferiori, l'altra peculiare dei livelli superiori; questa divisione, non evidenziata negli studi precedenti, trova conferme anche da nuovi dati provenienti dall'associazione a mammiferi. Vengono inoltre ipotizzate ricostruzioni paleoambientali e paleoclimatiche sulla base delle due diverse associazioni; entrambe sono tipiche di ambienti aperti, ma mentre le associazioni dei livelli inferiori indicano un clima più freddo e umido con vegetazione sparsa, le associazioni provenienti dai livelli superiori danno invece indicazioni di un clima più caldo e secco. Da un punto di vista cronologico i dati inediti, uniti alle datazioni effettuate in precedenza, permettono di collocare la formazione del deposito di Ingarano nel Pleistocene superiore, più precisamente all'interno dello Stadio Isotopico 3, ma in due momenti climatici distinti. Nei precedenti studi un livello riccamente fossilifero posto alla base della successione era stato attribuito allo Stadio Isotopico 2 sulla base del suo contenuto paleontologico. Il presente studio rivela come questo livello rappresenti il prodotto dell'erosione del livello immediatamente soprastante.

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Fig. 1 - Map of Italy with the position of the Ingarano fossil locality.

Introduction

The Ingarano Late Pleistocene succession consists of a cave deposit made up of different layers outcropping in an abandoned quarry, at about 270 m a.s.l., along the Gargano railway, near Apricena (Foggia, south-eastern Italy) (Fig. 1).

The locality was discovered in the first half of the 1980's, but only since 1992 has it been possible to analyse the complete stratigraphy, which appears chaotic and partially disturbed by quarry activities. The palaeontological site of Ingarano has documented a very rich vertebrate fauna together with some lithic artefacts indicative of a Mousterian age (Capasso Barbato et al. 1992; Petronio et al. 1996; Petronio & Sardella 1998; Sardella 2000; Curcio et al. 2005). The vertebrate list up to that point included 41 taxa with Amphibians: *Rana* sp.; Reptiles: *Lacerta* sp., Ophidae indet.; Birds: *Circus* nov. sp., *Aquila chrysaëtos*, *Falco tinnunculus*, *Falco peregrinus*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Nyctea scandiaca*, *Pyrrhocorax graculus*, *Pyrrhocorax* sp., *Corvus monedula*, *Corvus corax*; Mammals: *Erinaceus europaeus*, *Myotis blythi*, *Oryctolagus cuniculus*, *Lepus europaeus*, Arvicolidae indet., *Microtus* sp., *Microtus* gr. *arvalis/agrestis*, *Terricola savii*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Canis lupus*, *Canis* ex gr. *arnensis-mosbachensis*, *Vulpes vulpes*, *Ursus arctos*, *Mustela nivalis*, *Martes* sp., *Gulo gulo*, *Crocuta crocuta*, *Felis silvestris*, *Lynx lynx*, *Panthera pardus*, *Equus hydruntinus*, *Cervus elaphus*, *Dama dama dama*, *Capreolus capreolus*, *Rupicapra* sp., *Bos primigenius*.

Remains of *Panthera spelaea*, *Hippopotamus amphibius*, *Coelodonta antiquitatis*, *Stephanorhinus hemitoechus* and *Elephas antiquus* have been collected in a sandy-clay level in unclear stratigraphic relationships with the karst succession (Petronio & Sardella 1998). This level was destroyed by quarry activities and no additional information could be obtained, so that it is not considered in the present paper.

The analysis of the fossil material enabled previous authors to define the palaeoclimatic and biochronological significances of the Ingarano vertebrate remains. Three different faunal assemblages were identified: the first, exemplified by the large mammals found outside the cave succession, represents the MIS 4, while two different faunal assemblages in the cave succession represent the MIS 3 and MIS 2 (Petronio & Sardella 1998).

In this paper we consider the fossil bird remains of the Ingarano deposit, collected in various layers of the karst succession. The analysis of the fossil birds leads us to propose a new interpretation of the different layers of the cave succession and a new palaeoclimatic and palaeoenvironmental reconstruction of the deposit based on the palaeoecologic characteristics of the bird taxa we recorded.

Bird remains, together with other vertebrate remains, were previously collected by a University of Roma "La Sapienza" research team, coordinated by prof. Carmelo Petronio; two preliminary analyses were made by Cassoli (in Capasso Barbato et al. 1992) and by Parry (in Petronio et al. 1996; see also Petronio & Sardella 1998). New data on the fossil bird remains were elaborated in a master thesis by one of the authors (Bedetti 1999) and later reported by Pavia (2000). In this paper we present a systematic analysis of nearly two thousand bones, including a revision of the material already studied by Bedetti (1999) and a study of the new material collected thereafter.

Stratigraphic framework

New information obtained during recent surveys enable us to partially modify the stratigraphy sketched out by Petronio & Sardella (1998). The Pleistocene Ingarano deposit is a karst filling succession within the Jurassic-Cretaceous limestone of the "Calcare di Sannicandro" Formation. It probably represents the infilling of a sinkhole, the structure of which is no longer visible now that quarry activities have exposed the entire succession. The Ingarano succession includes at least five depositional events of terrigenous sedimentation during Late Pleistocene, each indicated by a different layer in the cave succession with its own fossil vertebrate assemblage.

The succession is made up of five layers of various thickness (Figs. 2-3). The first one is an alabastrine level (Layer A) from a few centimetres up to over one meter thick, and includes some stalagmite and stalactite fragments; it directly overlies the Mesozoic limestone. The alabastrine level is locally encrusted by phosphatic material interpreted as the product of the guano decomposition of a bird colony (Petronio & Sardella 1998). A geochemical analysis of the phosphatic material by ^{239}Th/^{234}U method gave an age of 40.000 ± 2000 years BP. The phosphatic encrustations (Layer B), several centimetres thick, are locally rich in middle- and small-sized vertebrate remains, including birds. The layers A and B are overlain by a massive conglomerate bed whose texture is homogeneous with flattened calcareous pebbles of small size, while the silty reddish matrix is locally poorly cemented. This conglomerate (Layer C) shows a variable thickness from one to three metres and is rich in vertebrate remains, including both macro- and micromammals and an abundance of birds. A discontinuity surface indicates the passage to another conglomerate two to four metres thick (Layer D) with angular clasts, some larger than 10 cm, and a prevalently calcareous matrix. This level is rich in vertebrate remains, especially macromammals, with local concentrations of micromammal and some bird bones. The Ingarano Pleistocene succession is closed by a two to three m-thick conglomerate with large angular clasts (Layer E) cemented by calcareous matrix; the frequent vertebrate remains are mostly represented by macromammals. The passage between layers D and E corresponds to a change in the present topography of the deposit; on the terrace, at the passage between D and E, several

Fig. 2 - View of the Ingarano locality with the outline of the different layers described in the text.

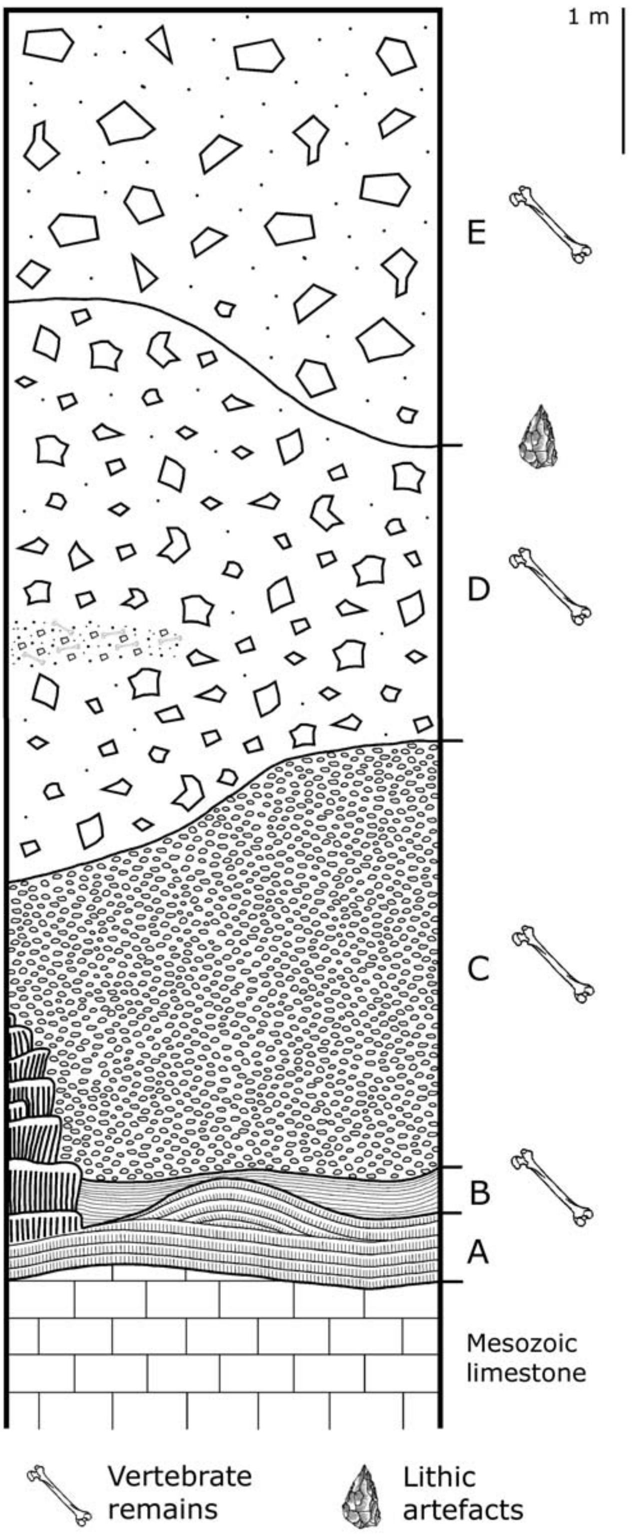

Fig. 3 - Schematic interpreted composite log of the Late Pleistocene Ingarano succession, mainly aimed to represent the stratigraphic relationships of the different layers. Thicknesses are only indicative. For the description of the different layers, see text.

lithic artefacts have been collected and attributed to the Mousterian period (Mussi in Petronio et al. 1996).

At the base of the layer C some open fissures are present, partially filled with loosely cemented bones and calcareous pebbles. They were previously interpreted as a younger level of the succession (Layer G) dated to the MIS 2 by Petronio & Sardella (1998), on the basis of the faunal content and its relationship with the other levels of the Ingarano succession. After the new observations we consider these infillings to be the product of the erosion of layer C, including both sediments and vertebrate remains.

Systematic Palaeontology

The fossil material, collected by researchers of the University of Roma "La Sapienza" and by the authors, is currently stored in the Dipartimento di Scienze della Terra of the University of Roma "La Sapienza" and provisionally catalogued with the acronym "Ing. A.". Some fossil remains are also stored at the Museo di Geologia e Paleontologia of the University of Torino and catalogued with the acronym "PU". A few *Aquila chrysaëtos* remains are also in the collections of the Dipartimento di Scienze della Terra of the University of Firenze; they are still uncatalogued (F. Masini pers. com.).

Systematic analyses of the fossil remains were conducted through comparisons with modern bird skeletons of the "Marco Pavia Osteological Collection" (MPOC), held at the Dipartimento di Scienze della Terra of the Torino University, the collection of the Université Claude Bernard Lyon 1 at Villeurbanne, Lyon (UCBL), the collection of the Museo Civico di Storia Naturale of Carmagnola, Torino (MCC) and the Insitut für Paläoanatomie of München. Some recent *Falco* skeletons were loaned by the Natural History Museum of London (NHM). Taxonomy follows Del Hoyo et al. (1994, 1999) and Cramp & Perrins (1994). Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimetres, in accordance with the indications proposed by Mourer-Chauviré (1975b).

This analysis identified the following bird taxa from the Ingarano outcrop: *Circus aeruginosus*, *Buteo rufinus*, *Aquila chrysaëtos*, *Falco columbarius*, *Falco cherrug*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Otus scops*, *Nyctea scandiaca*, *Nyctea scandiaca* vel *Bubo bubo*, *Athene noctua noctua*, *Pyrrhocorax graculus*, *Pyrrhocorax pyrrhocorax*, *Corvus corone*, *Corvus corone* vel *Corvus frugilegus*, *Corvus corax*. They are described hereafter.

Class **Aves** Linnaeus, 1758
Order **Falconiformes** Sharpe, 1874
Family Accipitridae Vieilliott, 1816
Genus *Circus* Lacépède, 1799

Circus aeruginosus (Linnaeus, 1758)

Pl. 2, fig. J

1996 *Circus* n. sp. - Petronio et al., p. 334.
1998 *Circus* n. sp. - Petronio & Sardella, p. 289.

Material. 8 bones coming from layer C. In detail: one coracoid, one humerus, two ulnae, one carpometacarpus, two tibiotarsi, one tarsometatarsus.

Description and comparisons. Middle-sized Accipitridae, similar in size to *Buteo buteo* and *Accipiter gentilis*, from which it can be distinguished by morphological characteristics of the long bones. The coracoid is slender and not as stout as in *Buteo buteo*, although it less slender than in *Accipiter gentilis*; the sulcus musculi supracoracoideus forms a deep pneumatic foramen, absent in *Buteo buteo*. *Circus aeruginosus* lacks the incisura musculi supracoracoidei, but shows a small vascular foramen between the sulcus nervi supracoracoidei and the facies articularis scapularis. The facies articularis clavicularis is more developed in *Circus aeruginosus* than in *Buteo buteo* and in *Accipiter gentilis* and the processus procoracoideus is more connected to the diaphysis. In the distal part of the humerus of *Circus aeruginosus* the processus supracondylaris is larger than in *Accipiter gentilis*; in *Buteo buteo* the fossa muscoli brachialis is larger and the condylus ventralis more developed distally than in *Circus aeruginosus*, as is the tuberculum supracondylare ventrale, which is larger and more separated from the epicondylus ventralis in *Buteo buteo* than in *Circus aeruginosus*. In *Circus aeruginosus* the sulcus intercondylaris of the distal ulna is more pronounced than in *Buteo buteo*, the tuberculum carpale is pointed and more developed than in *Accipiter gentilis*, and the condylus ventralis ulnaris is less developed than in *Accipiter gentilis*. The tibiotarsus is thin and slender in *Circus aeruginosus* with the distal part as large as the diaphysis; in the distal part the two condyli are more protruding than in *Buteo buteo*, while the canalis extensorius is smaller and the pons supratendineum is wider than in *Accipiter gentilis*, and the incisura intercotylaris is less protruding. The tarsometatarsus of *Circus aeruginosus* is a slender bone with the epiphyses not as wide as in *Buteo buteo* and *Accipiter gentilis*; both the foramen of the distal part of the tarsometatarsus and the fossa metatarsi I are reduced.

The other European species of the genus *Circus* can be easily excluded because they are clearly smaller than *C. aeruginosus* (Otto 1981; Schmidt-Burger 1982).

Biochronological and ecological remarks. *Circus aeruginosus* is an extant species rarely recorded in the fossil record of the Palearctic Pleistocene (Tyrberg 1998, 2006). It is known since the Middle/Late Pleistocene of Binagady in Azerbaijan; in Italy it is recorded from four localities of the Late Pleistocene (Tyrberg 1998, 2006).

This species lives in open marshy environments, and feeds mainly on middle-sized aquatic birds, in particularly during the breeding season when it builds its nest in extensive reedbeds or other open wetlands (Cramp & Simmons 1980). The record of *Circus aeruginosus* in the layer C of Ingarano indicates the presence of open wetlands at the base of the Gargano plateau.

Genus *Buteo* Lacépède, 1799

Buteo rufinus (Cretzschmar, 1827)

Pl. 2, fig. H

Material. 3 bones coming from layers C and E. In detail: one carpometacarpus (Layer E), one tarsometatarsus (Layer C), one posterior phalanx (Layer C).

Description and comparisons. The carpometacarpus shows the typical features of the genus *Buteo*, differing from *Accipiter gentilis* in having a plain wider fovea carpalis cranialis and a larger os metacarpale minus; the Ingarano specimen also shows a relatively short processus extensorius, which is longer and more pointed in *Circus aeruginosus*. The morphology of the proximal part of the tarsometatarsus is typical of the genus *Buteo* and is more enlarged than the one of *Circus aeruginosus*; furthermore *Accipiter gentilis* differs in having a deeper fossa infracotylaris dorsalis and a more protruding eminentia intercotylaris

Within the genus *Buteo*, *B. rufinus* is the largest species and the Ingarano remains fall outside the range of variation of *Buteo buteo* and *B. lagopus* (Otto 1981; Schmidt-Burger 1982). The morphology of the posterior phalanx is stout as in *Buteo*, while in *Accipiter* and *Circus* it is slender, and the size lies within the range of variation of *Buteo rufinus* (Mourer-Chauviré 1975a).

In the Middle Pleistocene of Saint-Estève-Janson, in Southern France, Mourer-Chauviré (1975a) described the extinct subspecies *Buteo rufinus jansoni* on the basis of a nearly complete skeleton and some other bones; the extinct subspecies differs from the extant one in having a shorter tarsometatarsus and minor morphological differences in the humerus and carpometacarpus. The Ingarano remains are too fragmented to be identified to subspecies and so they are left as *Buteo rufinus* s.l.

Biochronological and ecological remarks. *Buteo rufinus* is an extant species known since the Middle Pleistocene and it is rarely reported in fossil assemblages, most such records being from France. It had never previously been found in Italy as a fossil, thus the Ingarano remains constitute the first Italian record of this species (Tyrberg 1998, 2006).

This species ranges widely from Eastern Europe to Africa, but it occurs mainly in open environments, characterized by low vegetation, exposed rocks and cliffs (Cramp & Simmons 1980), probably similar to that of Ingarano area during the Late Pleistocene.

Genus *Aquila* Linnaeus, 1758

Aquila chrysaëtos (Linnaeus, 1758)

Pl. 1, figs A, B, C, H

1992 *Aquila chrysaëtos* - Capasso Barbato et al., p. 325.
1996 *Aquila chrysaëtos* - Petronio et al., p. 334.
1998 *Aquila chrysaëtos* - Petronio & Sardella, p. 288-289.

Material. 74 bones coming from layer C. In detail: two skulls, three quadrati, one mandible, two sterni, three coracoids, three furculae, four scapulae, seven humeri, two ulnae, two radii, four ossi carpi ulnare, four carpometacarpi, three synsacri, four femora, nine tibiotarsi, three tarsometatarsi, eighteen posterior phalanges.

Description and comparisons. The bones examined here show the morphological characteristics of the Accipitridae, particularly the larger ones, such as eagles and vultures. They cannot refer to the latter, such as *Gypaëtus barbatus*, *Gyps fulvus* and *Aegypius monachus*, because these are even larger and show more pneumatization in all the long bones, unlike the Ingarano material; they must refer to an eagle of the genus *Aquila,* according to the characteristics indicated by Louchart et al. (2005). The identification of the different *Aquila* species based on osteological characteristics is not easy and not always possible, as suggested by Olson (1994) and Louchart et al. (2005). Among the different *Aquila* species, *Aquila chrysaëtos* shows larger size in all the long bones (Louchart et al. 2005); in terms of size the Ingarano material is comparable to this species, and some elements, such as humerus and tarsometatarsus, are slightly larger.

In conclusion, the morphological characteristics of the genus *Aquila* and the large size allow us to determine the Ingarano remains as *Aquila chrysaëtos*.

The extinct subspecies *Aquila chrysaëtos bonifacti* described from the Middle Pleistocene of France (Mourer-Chauviré 1975b) is significantly smaller than the extant subspecies, and so it was not considered in the determination of the Ingarano material. We do not consider the slightly larger size of the Ingarano remains compared to the present-day animals used for comparison to be significant, as we consider it to be a local variation probably due to ecological pressures, as observed in the Ingarano population of *Lynx lynx* as well (D'Aguanno 1997).

Biochronological and ecological remarks. *Aquila chrysaëtos* is known in the Palearctic since the Early Pleistocene and is very abundant in Late Pleistocene localities throughout Europe (Tyrberg 1998, 2006).

This species is currently distributed in rocky, usually mountainous areas throughout Europe, from Northern Europe to the Mediterranean region. It builds its nest on cliffs close to open areas used for hunting its main prey items, middle-sized mammals and birds (Cramp & Simmons 1980). In the Ingarano deposit several individuals have been found, and show that this predator was one of the most important species at the top of the food chain during the Late Pleistocene.

Family Falconidae Vigors, 1824

Genus *Falco* Linnaeus, 1758

Falco columbarius Linnaeus, 1758

Pl. 2, fig. I

1992 *Falco tinnunculus* - Capasso Barbato et al., p. 325.
1996 *Falco tinnunculus* - Petronio et al., p. 334.
1998 *Falco tinnunculus* - Petronio & Sardella, p. 289.

Material. One humerus coming from layer C.

Description and comparisons. The measurements are comparable with those of the smallest European falcons (*Falco naumanni*, *F. tinnunculus*, *F. columbarius*, *F. vespertinus*) according to Solti (1996). The morphology of the diaphysis shows a well marked curvature in the middle part, that allows to exclude any other European falcon and identify the Ingarano remain as *Falco columbarius*; the determination is also confirmed by the shape of the processus supracondylaris dorsalis more similar to that of *Falco columbarius* than to the other species.

Biochronological and ecological remarks. This species is known since the Middle Pleistocene and commonly reported in Middle and Late Pleistocene localities in Europe and Italy (Tyrberg 1998, 2006).

Falco columbarius, as also other bird species found at Ingarano, testifies the presence of open environments in which it was feeding on middle- and small-sized birds (Cramp & Simmons 1980).

Falco cherrug Gray, 1834

Pl. 1, figs D, F, I, J, K, L

1992 *Falco peregrinus* - Capasso Barbato et al., p. 325.
1996 *Falco peregrinus* - Petronio et al., p. 334.
1998 *Falco peregrinus* - Petronio & Sardella, p. 289.

Material. 84 bones coming from layer C. In detail: two skulls, one bill, two mandibles, one quadratum, one sternum, three furculae, two scapulae, five coracoids, twelve humeri, nine ulnae, one radius, one os carpi ulnare, twelve carpometacarpi, one first anterior phalanx, three synsacri, eight femurs, eleven tibiotarsi, nine tarsometatarsi.

Description and comparisons. In the Ingarano material many bones referable to a large species of *Falco* have been found. The bones can be grouped in two size classes, in accordance with the sexual dimorphism commonly reported in the genus *Falco* (Cramp & Simmons 1980); however, we found no morphological differences between these two groups.

These fossil bones are larger than recent *Falco biarmicus* and *F. peregrinus* bones and are comparable to those of *F. cherrug* and *F. rusticolus* (Solti 1980, 1981a, 1981b). The latter two species are comparable in size, although *Falco rusticolus* is larger, and can be identified thanks to certain morphological characteristics, (see also Solti 1980, 1981b). In particular, the distal humerus shows the processus supracondylaris dorsalis more pronounced and closer to the condylus dorsalis in *Falco cherrug* than in *F. rusticolus*. In the distal part of the ulna of the latter species the condylus dorsalis ulnae shows a step between the condylus and the distal epiphysis, while it is jointed in *F. cherrug*. In the proximal carpometacarpus of *Falco rusticolus* a small tuberculum is present, which is absent in *F. cherrug*. In the proximal femur the crista trochanteris is more protruding in *F. cherrug*, with a pointed outline, while it is rounded in *F. rusticolus*; in the distal part of the bone proximally to the crista supracondylaris medialis a tuberculum is present in the latter species, which is absent in *F. cherrug*, where the trochlea fibularis shows a 90° shape, while it is deeper and shows a U shape in *F. rusticolus*. The tarsometatarsus tends to be proportionately shorter and stouter in *F. rusticolus*, with the three trochleae being rounded, whereas they are pointed in *F. cherrug*; the sulcus hypotarsi in the proximal part is also deeper and more rounded in *F. rusticolus* than in *F. cherrug*. After the comparison of the Ingarano material with recent skeletal material and with the characteristics listed in the literature we can identify them as *Falco cherrug*. The Ingarano remains are similar in size and proportions to recent remains (Tabs. 1-2; Figs. 4-7), although they are slightly stouter, especially in the distal elements, such as the carpometacarpus and the tarsometatarsus (Figs. 5-7). Solti (1981b) indicates some ratios between common measurements, including epiphyses, some of them with no overlap between *Falco cherrug* and *F. peregrinus*. Applying some of these indications to the Ingarano remains reveals that they fit well with the recent *Falco cherrug* (Tab. 3).

Mourer-Chauviré (1975b) described the extinct *Falco antiquus* from the Middle Pleistocene of France as the probable ancestor of both *F. cherrug* and *F. rusticolus,* as it combines characteristics of the two species; *Falco antiquus* is characterised by the tarsometatarsus,

	Total length	Proximal width	Proximal depth	Distal width	Distal depth	Width in the middle
Humerus						
Falco cherrug - Ing. A 72	84.6	-	-	16.2	9.7	7.6
Falco cherrug - Ing. A 76	99.7	-	7.9	18.9	11.1	9.2
Falco cherrug - Ing. A. 1129	82.8	-	-	15.7	10.1	7.5
Falco cherrug - Ing. A. 1133	-	-	-	18.5	10.9	-
Falco cherrug - Ing. A. 1134	83.1	20.3	-	17.2	10.4	7.0
Falco cherrug - Ing. A. 1135	84.9	20.7	10.0	16.6	9.3	7.2
Falco cherrug - Ing. A. 1182	-	-	-	16.0	-	-
Falco cherrug - Ing. A. 1221	87.3	19.5	11.0	17.1	10.2	8.3
Falco cherrug – recent	87.1 - 99.3 (n = 9)	19.3 - 22.5 (n = 7)	10.0 - 11.1 (n = 3)	16.5 - 18.9 (n = 9)	9.4 - 10.4 (n = 3)	7.4 - 8.3 (n = 9)
Falco rusticolus – recent	96.5 - 110.0 (n = 7)	19.4 - 24.8 (n = 9)	10.1 - 12.6 (n = 8)	18.2 - 21.0 (n = 8)	10.8 - 12.1 (n = 6)	8.3 - 9.6 (n = 8)
Falco biarmicus – recent	74.8 - 84.1 (n = 6)	17.5 - 18.7 (n = 6)	9.1 - 9.2 (n = 2)	13.3 - 15.7 (n = 6)	8.7 - 9.4 (n = 2)	6.2 - 7.3 (n = 6)
Falco peregrinus – recent	66.8 - 91.4 (n = 21)	16.5 - 21.3 (n = 20)	7.2 - 11.6 (n = 20)	13.7 - 18.0 (n = 20)	8.0 - 10.5 (n = 17)	6.7 - 9.0 (n = 21)
Ulna						
Falco cherrug - Ing. A. 1	117.0	13.5	-	10.7	9.7	6.8
Falco cherrug - Ing. A. 2	-	11.3	10.4	-	-	-
Falco cherrug - Ing. A. 3	-	-	10.9	-	-	-
Falco cherrug - Ing. A. 9	-	-	-	10.9	8.7	-
Falco cherrug - Ing. A. 11	-	-	-	10.3\	8.8	-
Falco cherrug - Ing. A. 12	-	-	-	10.0	8.0	-
Falco cherrug - Ing. A. 14	-	-	-	9.1	7.9	-
Falco cherrug - Ing. A. 1186	-	-	-	9.7	8.0	-
Falco cherrug – recent	100.2 - 117.7 (n = 8)	11.2 - 13.3 (n = 8)	10.3 - 12.2 (n = 8)	9.6 - 12.6 (n = 8)	8.6 - 9.1 (n = 3)	5.7 - 7.5 (n = 8)
Falco rusticolus – recent	107.7 - 124.7 (n = 8)	12.6 - 14.3 (n = 8)	11.6 - 13.0 (n = 8)	10.4 - 13.7 (n = 8)	9.1 - 10.6 (n = 6)	6.4 - 7.6 (n = 6)
Falco biarmicus – recent	87.3 - 98.1 (n = 6)	9.7 - 10.9 (n = 6)	9.0 - 10.9 (n = 6)	9.5 - 10.8 (n = 5)	7.8 - 8.2 (n = 2)	5.2 - 6.0 (n = 6)
Falco peregrinus – recent	77.0 - 105.8 (n = 20)	9.3 - 12.3 (n = 18)	9.4 - 12.4 (n = 15)	8.0 - 11.2 (n = 15)	7.1 – 9.3 (n = 15)	4.8 - 6.7 (n = 21)
Carpometacarpus						
Falco cherrug - Ing. A. 87	60.5	15.3	6.8	-	5.7	4.6
Falco cherrug - Ing. A. 89	-	-	7.5	-	-	-
Falco cherrug - Ing. A. 90	69.5	-	7.6	11.9	7.3	5.0
Falco cherrug - Ing. A. 91	58.5	15.4	6.6	9.7	-	5.8
Falco cherrug - Ing. A. 94	56.9	14.8	6.6	9.6	7.2	4.1
Falco cherrug - Ing. A. 1121	-	15.0	6.7	-	-	-
Falco cherrug - Ing. A. 1122	68.8	17.2	7.4	11.1	7.1	4.7
Falco cherrug - Ing. A. 1123	-	17.2	7.5	-	-	-
Falco cherrug - Ing. A. 1137	-	-	6.3	-	-	-
Falco cherrug – recent	59.4 - 69.3 (n = 9)	14.8 - 17.7 (n = 8)	5.6 - 5.8 (n = 2)	9.0 - 11.0 (n = 8)	6.5 - 7.5 (n = 2)	3.7 - 4.4 (n = 9)
Falco rusticolus – recent	66.2 - 72.5 (n = 7)	17.4 - 19.6 (n = 7)	6.3 - 7.7 (n = 6)	10.8 - 12.0 (n = 8)	6.8 - 8.0 (n = 6)	4.2 - 5.1 (n = 8)
Falco biarmicus – recent	52.5 - 58.7 (n = 6)	13.5 - 15.5 (n = 6)	5.7 - 5.8 (n = 2)	9.0 - 9.9 (n = 6)	5.8 - 6.0 (n = 2)	3.3 - 4.2 (n = 6)
Falco peregrinus – recent	48.0 - 65.2 (n = 25)	13.4 - 17.3 (n = 19)	5.0 - 7.3 (n = 18)	8.6 - 11.5 (n = 19)	5.1 - 6.5 (n = 19)	3.5 - 4.7 (n = 25)

Tab. 1 - Measurements of the forelimb bones of Late Pleistocene *Falco cherrug* from Ingarano, compared with those of recent *Falco cherrug*, *F. rusticolus*, *F. biarmicus* and *F. peregrinus* (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

	Total length	Proximal width	Proximal depth	Distal width	Distal depth	Width in the middle
Femur						
Falco cherrug - Ing. A. 68	-	13.4	8.1	13.8	-	6.5
Falco cherrug - Ing. A. 69	76.5	-	-	15.6	11.9	7.4
Falco cherrug - Ing. A. 1124	-	13.2	8.6	-	-	-
Falco cherrug - Ing. A. 1131	-	13.8	8.4	13.7	11.9	6.2
Falco cherrug - Ing. A. 1132	77.5	-	-	15.9	13.4	7.2
Falco cherrug – recent	69.3 - 77.1 (n = 7)	13.3 - 14.5 (n = 7)	8.3 - 10.6 (n = 6)	13.7 - 15.5 (n = 7)	10.3 - 11.9 (n = 6)	6.2 - 7.4 (n = 7)
Falco rusticolus – recent	82.0 - 92.3 (n = 9)	15.3 - 18.3 (n = 9)	9.4 - 11.3 (n = 9)	15.8 - 19.0 (n = 9)	12.4 - 14.0 (n = 9)	7.2 - 9.1 (n = 9)
Falco biarmicus – recent	60.5 - 66.6 (n = 6)	11.2 - 12.6 (n = 6)	7.7 - 8.4 (n = 5)	11.3 - 13.3 (n = 6)	8.6 - 11.2 (n = 6)	5.4 - 6.5 (n = 6)
Falco peregrinus – recent	55.3 - 73.2 (n = 27)	11.2 - 15.0 (n = 25)	6.5 - 9.3 (n = 25)	11.2 - 14.7 (n = 25)	9.2 - 12.6 (n = 25)	5.3 - 7.4 (n = 27)
Tibiotarsus						
Falco cherrug - Ing. A. 24	-	-	-	12.8	8.8	-
Falco cherrug - Ing. A. 43	92.6	-	-	14.3	10.5	6.9
Falco cherrug - Ing. A. 46	-	-	-	14.9	9.7	-
Falco cherrug - Ing. A. 55	-	12.2	12.8	-	-	-
Falco cherrug - Ing. A. 1125	-	-	-	-	9.1	-
Falco cherrug - Ing. A. 1225	96.9	14.9	12.1	15.1	9.7	6.7
Falco cherrug – recent	88.0 - 97.9 (n = 8)	12.0 - 12.2 (n = 2)	12.8 - 13.8 (n = 2)	12.1 - 15.3 (n = 8)	9.1 - 9.7 (n = 3)	4.3 - 6.3 (n = 8)
Falco rusticolus – recent	99.5 - 110.5 (n = 8)	13.2 - 15.0 (n = 6)	13.9 - 16.1 (n = 6)	13.8 - 17.2 (n = 8)	9.8 - 12.1 (n = 6)	5.3 - 7.2 (n = 6)
Falco biarmicus – recent	79.2 - 87.0 (n = 6)	10.3 - 12.1 (n = 5)	11.6 - 12.6 (n = 2)	11.0 - 12.1 (n = 4)	6.4 - 8.5 (n = 2)	4.0 - 5.4 (n = 6)
Falco peregrinus – recent	71.5 - 92.7 (n = 21)	9.5 - 15.0 (n = 19)	9.2 - 14.2 (n = 19)	10.2 - 14.5 (n = 19)	7.1 - 9.9 (n = 19)	4.1 - 6.7 (n = 21)
Tarsometatarsus						
Falco cherrug - Ing. A. 21	-	-	-	15.2	10.1	-
Falco cherrug - Ing. A. 22	-	-	-	13.8	9.3	-
Falco cherrug - Ing. A. 29	-	14.7	-	-	-	-
Falco cherrug - Ing. A. 31	-	13.2	10.3	-	-	-
Falco cherrug - Ing. A. 1223	54.4	13.2	-	14.0	9.2	6.8
Falco cherrug - Ing. A. 1124	58.3	14.6	-	15.8	10.2	6.2
Falco cherrug - Ing. A. 1226	55.4	13.7	-	13.6	9.2	5.8
Falco cherrug - Ing. A. 1227	52.9	13.2	10.1	14.1	9.3	6.3
Falco cherrug - Ing. A. 1228	-	-	-	13.8	9.3	-
Falco cherrug – recent	53.8 - 60.5 (n = 9)	13.3 - 15.9 (n = 9)	10.0 - 11.2 (n = 3)	13.0 - 15.8 (n = 8)	9.3 - 9.5 (n = 2)	5.0 - 6.3 (n = 9)
Falco rusticolus – recent	60.4 - 62.3 (n = 8)	14.6 - 18.8 (n = 8)	11.3 - 13.6 (n = 6)	15.1 - 17.3 (n = 8)	9.7 - 12.0 (n = 6)	5.3 - 7.6 (n = 8)
Falco biarmicus – recent	51.1 - 53.0 (n = 5)	11.5 - 13.2 (n = 6)	9.9 - 10.0 (n = 2)	10.7 - 12.9 (n = 4)	8.8	4.6 - 5.8 (n = 6)
Falco peregrinus – recent	44.4 - 56.0 (n = 23)	11.0 - 14.4 (n = 21)	8.3 - 11.0 (n = 21)	10.8 - 15.0 (n = 21)	7.4 - 10.2 (n = 15)	4.3 - 6.2 (n = 21)

Tab. 2 - Measurements of the hindlimb bones of Late Pleistocene *Falco cherrug* from Ingarano, compared with those of recent *Falco cherrug*, *F. rusticolus*, *F. biarmicus* and *F. peregrinus* (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

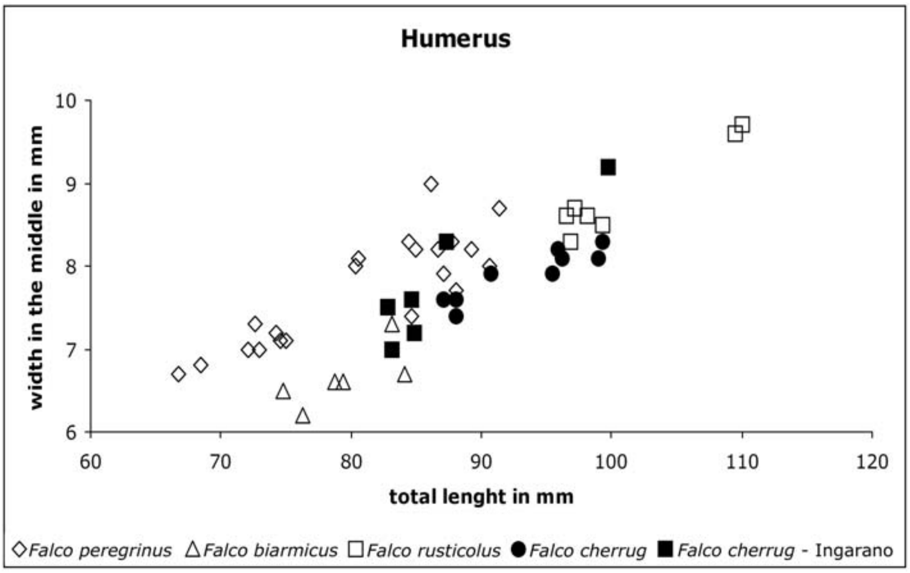

Fig. 4 - Scatter diagrams of the measurements of humerus of recent *Falco peregrinus*, *F. biarmicus*, *F. rusticolus*, *F. cherrug* and the fossil *F. cherrug* from the Late Pleistocene of Ingarano (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

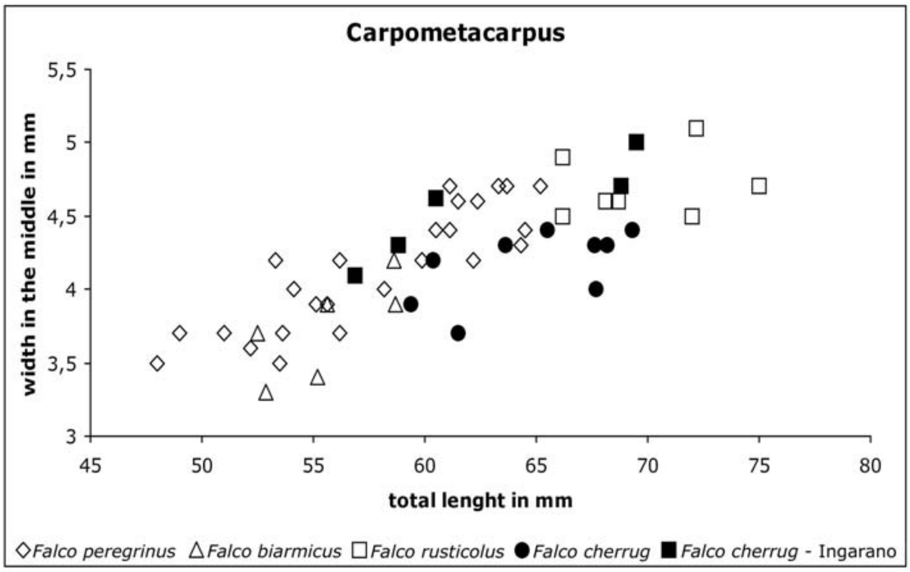

Fig. 5 - Scatter diagrams of the measurements of carpometacarpus of recent *Falco peregrinus*, *F. biarmicus*, *F. rusticolus*, *F. cherrug* and the fossil *F. cherrug* from the Late Pleistocene of Ingarano (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

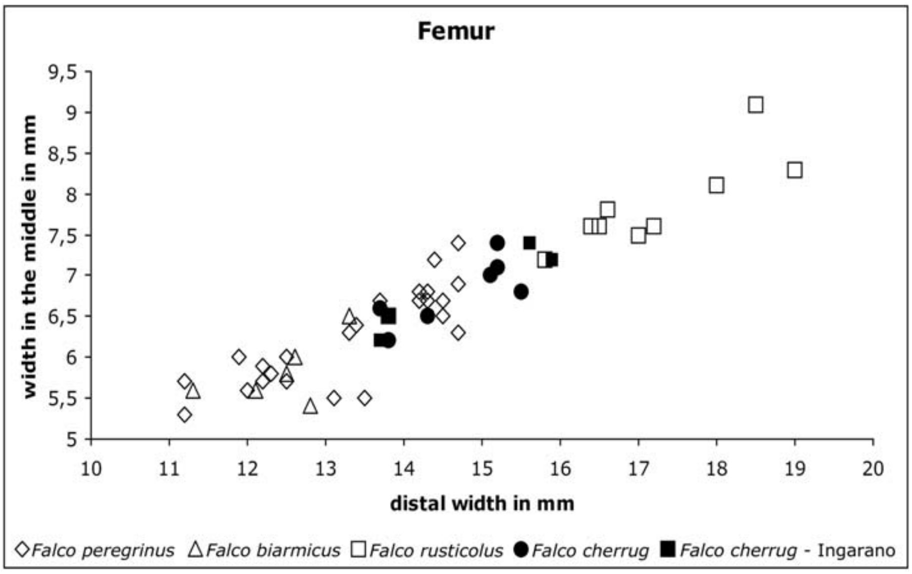

Fig. 6 - Scatter diagrams of the measurements of femur of recent *Falco peregrinus*, *F. biarmicus*, *F. rusticolus*, *F. cherrug* and the fossil *F. cherrug* from the Late Pleistocene of Ingarano (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

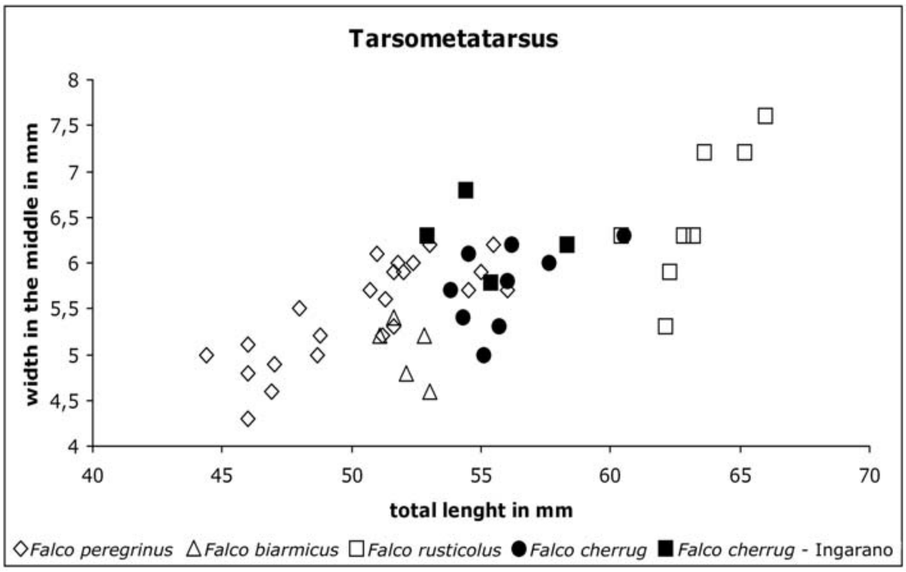

Fig. 7 - Scatter diagrams of the measurements of tarsometatarsus of recent *Falco peregrinus*, *F. biarmicus*, *F. rusticolus*, *F. cherrug* and the fossil *F. cherrug* from the Late Pleistocene of Ingarano (data from Solti 1980, 1981a, 1981b and courtesy C. Mourer-Chauviré).

	Falco cherrug - Ingarano		*Falco cherrug*		*Falco peregrinus*	
	min. - max.	$\bar{x}$	min. - max.	$\bar{x}$	min. - max.	$\bar{x}$
Humerus						
Total length / distal width	5.10 - 5.43	5.23	5.12 - 5.34	5.25	4.86 - 5.08	4.96
Carpometacarpus						
Total length / proximal width	3.80 - 4.00	3.89	3.82 - 4.13	3.94	3.61 - 3.376	3.69
Tibiotarsus						
Total length / distal width	6.41 - 6.47	6.44	6.31 - 6.78	6.48	6.39 - 7.15	6.69
Tarsometatarsus						
Total length / proximal width	3.99 - 4.12	4.04	3.62 - 4.04	3.86	3.71 - 3.90	3.78

Tab. 3 - Ratios between different measurements of various long bones of Late Pleistocene *Falco cherrug* from Ingarano, compared with those of recent *F. cherrug* and *F. peregrinus* (data from Solti 1981b).

which is shorter than in *F. rusticolus* and stouter than in *F. cherrug*. The Ingarano material best fits *F. cherrug*.

Biochronological and ecological remarks. *Falco cherrug* is dubiously reported from the Early Pleistocene and Middle Pleistocene of Romania and Czech Republic respectively (Tyrberg 1998, 2006) and is recorded with certainty only in few Late Pleistocene localities of the Balkan area and Ukraine. The Ingarano remains represent the first Italian record of this species and the westernmost in the Palearctic so far.

This species currently breeds in the plains and steppe areas of Eastern Europe and winters in the eastern Mediterranean region, North Africa and Middle East, feeding on middle-sized mammals and birds (Cramp & Simmons 1980); the presence of *Falco cherrug* in the lower layer of the Ingarano succession indicates the presence of open environments with low vegetation.

Order **Galliformes** Temminck, 1820
Family Phasianidae Vigors, 1825
Genus *Alectoris* Kaup, 1829

Alectoris graeca (Meisner, 1804)
Pl. 2, fig. D

1992 *Alectoris graeca* - Capasso Barbato et al., p. 325.
1996 *Alectoris graeca* - Petronio et al., p. 334.
1998 *Alectoris graeca* - Petronio & Sardella, p. 289.

Material. 17 bones coming from layers B and C. In detail: one sternum (Layer C), four coracoids (1 layer B, 3 layer C), two humeri (Layer C), two ulnae (Layer C), one femur (Layer C), two tibiotarsi (Layer C), five tarsometatarsi (1 layer B, 4 layer C).

Description and comparisons. The genus *Alectoris* is definitively larger than the genus *Perdix* in each post-cranial element and can also be separated from the latter for some morphological characteristics in the long bones (Kraft 1972). *Alectoris graeca* is little bigger than the other European species *Alectoris rufa*, with some differences in the long bones, as also stated by Kraft (1972), like the shape of the facies articularis sternalis of the distal coracoid not rounded as in *Alectoris rufa*; in the distal humerus a larger fossa musculi brachialis is present in *Alectoris graeca*; and in the proximal tarsometatarsus the cristae medialis hypotarsi are more developed than in *Alectoris rufa*. The other Palaearctic species of the genus, *Alectoris chukar*, can be excluded for its oriental geographical distribution, clearly separated from that of *A. graeca* (del Hoyo et al. 1994).

Biochronological and ecological remarks. *Alectoris graeca* is known since the Middle Pleistocene in various European and Italian localities and became very common in the Late Pleistocene (Tyrberg 1998, 2006). Two extinct subspecies, *A. g. martelensis* and *A. g. mediterranea*, have been described from the Middle Pleistocene of France (Mourer-Chauviré 1975b) and later reported also from Greece (Kretzoi & Poulianos 1982) and for the Early Pleistocene of Monte Argentario, Italy (Cassoli 1980). The latter records need to be reconsidered, because they are too poorly circumstantiated (see Cassoli 1980, p. 173) and a recent revision of the material reveals that the fossil remains of *Alectoris graeca* found in the Monte Argentario are too fragmented to allow an identification at subspecific level (Bedetti 2003). In conclusion, at present we prefer to identify the Ingarano material at the specific level, waiting for a complete revision of the data in the literature.

Alectoris graeca is currently breed in the open environments of the mountain regions of the Mediterranean area (Cramp & Simmons 1980), so it can confirm the presence of open rocky areas surroundings the Ingarano locality during the Late Pleistocene.

Genus *Perdix* Brisson, 1760

Perdix perdix (Linnaeus, 1758)

Pl. 2, fig. C

1992 *Perdix perdix* - Capasso Barbato et al., p. 326.
1996 *Perdix perdix* - Petronio et al., p. 334.
1998 *Perdix perdix* - Petronio & Sardella, p. 289.

Material. 10 bones coming from layer D. In detail: three coracoids, two humeri, two ulnae, one carpometacarpus, one femur, one tarsometatarsus.

Description and comparisons. *Perdix perdix* is a small-sized Phasianidae clearly separable from the similar-sized *Alectoris* species by some differences in the long bones (Kraft 1972). In particular the coracoid is small and shows the distal outline of the facies articularis sternalis narrow, different from *Alectoris* where it is broad; in the distal humerus the condylus ventralis is not very pronounced unlike in *Alectoris*.

In the Middle Pleistocene of France Mourer-Chauviré (1975b) described the extinct *Perdix palaeoperdix*, considered the direct ancestor of the extant *P. perdix*. The extinct species can be separated from the extant one in having smaller dimensions of the long bones and for this reason it can be excluded when considering the Ingarano remains, that are to be referred to *Perdix perdix*.

Biochronological and ecological remarks. *Perdix perdix* is reported in the Palearctic since the Early Pleistocene and became very abundant in the Late Pleistocene of Europe including Italy, even if most of the Early and Middle Pleistocene data are probably better referred to *P. palaeoperdix* (Tyrberg 1998, 2006).

Perdix perdix is a widespread species in Europe at present and lives in open cultivated areas in the plains (Cramp & Simmons 1980). It has similar ecological adaptations as *Alectoris graeca*, but it lives at warmer temperatures and low altitude, so it indicates a change in the environmental conditions of the Ingarano area between the lower and the upper layers.

Order **Columbiformes** Latham, 1790

Family Columbidae Illiger, 1811

Genus *Columba* Linnaeus, 1758

Columba livia Gmelin, 1789

Pl. 2, fig. E

1992 *Columba oenas* - Capasso Barbato et al., p. 326.
1996 *Columba livia* - Petronio et al., p. 334.
1998 *Columba livia* - Petronio & Sardella, p. 288-289.

Material. 82 bones coming from layers C and D. In detail: nineteen coracoids (12 layer C, 7 layer D), six scapulae (5 layer C, 1 layer D), twenty-two humeri (15 layer C, 7 layer D), nine ulnae (5 layer C, 4 layer D), sixteen carpometacarpi (12 layer C, 4 layer D), two femurs (Layer C), one tibiotarsus (layer C), seven tarsometatarsi (5 layer C, 2 layer D).

Description and comparisons. The morphological features of the Ingarano remains are concordant with the genus *Columba*, in particular with the smaller species of the genus found in the Western Palearctic: *C. livia* and *C. oenas*. According to the indications listed by Fick (1974), the morphological features of the Ingarano fossil remains, particularly in the proximal ulna and tarsometatarsus, allow us to determine them as *Columba livia*.

Biochronological and ecological remarks. This species is known since the Early Pleistocene and some extinct subspecies have been described, especially from the Middle Pleistocene of France (Mourer-Chauviré 1975b; Tyrberg 1998); in the Late Pleistocene it is commonly reported from almost all the fossil localities of Europe including Italy (Tyrberg 1998, 2006).

Columba livia lives in areas with cliffs, even of small dimensions, where it builds the nests, and open areas where feeds on seeds and small invertebrates (Cramp 1985).

Order **Strigiformes** Wagler, 1830

Family Strigidae Vigors, 1825

Genus *Otus* Pennant, 1769

Otus scops (Linnaeus, 1758)

Material. One humerus coming from layer E.

Description and comparisons. The size of the fossil is similar to those of *Otus scops*, as it is smaller than any other member of the Strigidae, except for *Glaucidium passerinum* which is even smaller. It also differs from *Athene noctua* by the poorly developed crista deltopectoralis and the external outline of the crista bicipitalis, which is not square as in *Athene noctua*, but more rounded as in *Otus scops*.

Biochronological and ecological remarks. This small strigiform bird is known since the Early Pleistocene and is recorded more frequently from the Late Pleistocene (Tyrberg 1998, 2006).

The genus *Otus* is widespread in the World with 63 species, mainly in tropical latitudes (del Hoyo et al. 1999); the Euopean species *Otus scops* is typical of the Mediterranean region and is the only European strigiform bird that migrates annualy to central and southern Africa (Cramp 1985). Even in the fossil record this species is always found together with temperate-warm climate species, as is the case at the Ingarano deposit, in which it is found together with *Perdix perdix* and *Dama dama dama* in layer E. This confirms the presence of warmer conditions at the top of the succession compared to the lower layers.

Genus *Nyctea* Stephens, 1826

Nyctea scandiaca (Linnaeus, 1758)

Pl. 2, figs A, B, G, L, N

1992 *Nyctea scandiaca* - Capasso Barbato et al., p. 326.
1996 *Nyctea scandiaca* - Petronio et al., p. 334.
1998 *Nyctea scandiaca* - Petronio & Sardella, p. 289-290.

Material. 295 bones coming from layers B and C. Most of the bones come from layer C, except those indicated as coming from layer B. In detail: three skulls, two maxillae, nine mandibulae, two sterni, one furcula, twenty-one coracoids (2 layer B), nine scapulae (1 layer B), twelve humeri, (2 layer B), twenty-five ulnae (3 layer B), sixteen carpometacarpi (2 layer B), ten wing phalanges (2 layer B), thirteen synsacri (3 layer B), forty-three femora (9 layer B), fifty-four tibiotarsi (6 layer B), forty-eight tarsometatarsi (7 layer B), twenty-seven posterior phalanges (8 layer B).

Description and comparisons. This species is one of the largest members of the family Strigidae in the Western Palearctic. It is easily separated from the similar-sized *Strix nebulosa*, a species rarely reported from the Late Pleistocene (Tyrberg 1998, 2006), because the latter shows the morphological characteristics of the genus *Strix*, clearly different from *Nyctea* in all osteological elements. *Nyctea scandiaca* can possibly be confused with *Bubo bubo*, which is morphologically similar and only slightly larger. Some morphological characteristics useful in identifying these two species have been found in all the major long bones. In the coracoid the facies articularis clavicularis is more developed laterally in *Bubo bubo* than in *Nyctea scandiaca*. In the proximal part of the humerus the caput humeri is more protruding in *Nyctea scandiaca*, while in the distal part the epicondylus ventralis is more developed ventrally in *Bubo bubo*, giving a wider shape to the whole diaphysis; additionally in the distal part the sulcus humerotricipitalis is deeper in *Nyctea scandiaca*. In the proximal part of the ulna the tuberculum ligamenti collateralis ventralis is less evident and closer to the cotyla ventralis in *Nyctea scandiaca* than in *Bubo bubo*, and in the distal part the tuberculum carpale is more pronounced distally in *Nyctea scandiaca*. On the caudal side of the proximal part of the femur of *Bubo bubo* there is a low area under the facies articularis antitrochanterica, which is very reduced or even absent in *Nyctea scandiaca*, also the crista trochanteris is much more developed in *Bubo bubo*; in the distal part of the bone the condylus medialis is more prominent in *Nyctea scandiaca* than in *Bubo bubo*, and the fossa poplitea is deeper. The tibiotarsus, in distal view, shows a different shape of both condylus lateralis and medialis, the latter being more protruding laterally. The tarsometatarsus is the most characteristic bone of *Nyctea scandiaca*; it is clearly stouter than that of *Bubo bubo*, and in the proximal part the crista medialis hypotarsi is clearly squared in the latter species, with a square angle distalward between this process and the diaphysis, while in *Nyctea scandiaca* it is jointed at a more obtuse angle.

Mourer-Chauviré (1975b) described the extinct subspecies *Nyctea scandiaca gallica* from the Middle Pleistocene of France, with the females being larger than in the nominate subspecies. The Ingarano material was compared with recent skeletons and bones of the extinct subspecies and the results are not clear enough for subspecific identification.

Biochronological and ecological remarks. This species is known since the Early Pleistocene of France and became very abundant in the Late Pleistocene of Europe (Tyrberg 1998, 2006). Although currently it lives exclusively in the tundra region of the Northern Hemisphere (Cramp 1985), during the glacial phases of the Middle and Late Pleistocene it had a different distribution, probably due to glacial pressure, and reached southern Europe (mainly in the Late Pleistocene) with records from Gibraltar, southern Italy and southern France (Tyrberg 1998, 2006).

Pleistocene records of *Nyctea scandiaca* are normally from caves, whereas now it lives in open tundra environments; this fact could be interpreted as a change in the ecology or habits of this species and its strict relationship with cold climates in the present time could be a secondary adaptation that arose after these changes. In light of this assumption, care should be taken in using *Nyctea scandiaca* as a strong indicator of cold climates with tundra-like environments; the same can be said for several other bird species that are also often used for the same purpose (Bedetti & Pavia 2001). This species is very abundant in the lower part of the Ingarano succession, together with a vertebrate association which does not indicate cold climate and, as we stated above, the presence of *Nyctea scandiaca* does not necessarily refer the association to an extremely cold stage of the last glacial, contra Petronio & Sardella (1998).

Nyctea scandiaca (Linnaeus, 1758) vel **Bubo bubo** (Linnaeus, 1758)

Material. 8 bones coming from layer C. In detail: one furcula, one coracoid, one scapula, two humeri, three wing phalanges.

Remarks. Some bones clearly referable to the Strigidae are slightly larger than those referred to *Nyctea scandiaca* found in the Ingarano deposit and they may suggest the presence of *Bubo bubo*; unfortunately they are too fragmentary to allow a determination to a specific level. The two species *Nyctea scandiaca* and *Bubo bubo* are now living in different habitat: the first one is extremely specialized to live in the arctic tundra, while the other one is recorded in a wide range of habitats from the northern taiga forest to the semi-desertic areas of the Middle East and North Africa (Cramp 1985). The coexistence of the two species is not commonly recorded in the Pleistocene of Europe (Tyrberg 1998, 2006); this seems to be related to the fact that, even in the same area, they tend to separate one to each other probably because of different ecological needs or intraspecific competition.

Genus *Athene* Boie, 1822

Athene noctua noctua (Scopoli, 1769)

Material. 3 bones coming from layer C of the Ingarano succession were studied. In detail: one left ulna, one right ulna, one left tarsometatarsus.

Description and comparisons. The remains show the typical characteristics of the small Strigiformes, in particular the tarsometatarsus with the well developed arcus extensorius and the prominent crista mediali hypotarsi. All the fossil remains are clearly larger than *Glaucidium passerinum* and *Otus scops* and smaller than any other Strigidae except for *Athene noctua* and *Aegolius funereus*. They can be attributed to the former thanks to certain morphological features; in the ulna of *Aegolius funereus* the condilus ventralis ulnaris is more developed laterally, as is the tuberculum ligamenti collateralis ventralis. The tarsometatarsus from Ingarano is slender, as is that of *Athene noctua,* and it is not as stout as in *Aegolius funereus*.

The extinct subspecies *Athene noctua lunellensis* was described from the Middle Pleistocene of France (Mourer-Chauviré 1975b). It differs from the nominate in its larger body size. This subspecies can be excluded here because the mean dimensions of the Ingarano material fit well with those of the extant *Athene noctua noctua*.

Biochronological and ecological remarks. This Strigiform is known since the Early Pleistocene, with the nominal subspecies and with the extinct subspecies *Athene noctua lunellensis* (Tyrberg 1998). Currently this species is widespread in Central and Southern Europe, as far north as central England (Cramp 1985).

This species has been found in layer C at Ingarano, associated with *Nyctea scandiaca* and *Falco cherrug*; this fact confirms that this layer was not deposited in very cold climatic conditions, as previously suggested, but more probably in a temperate-cold climate.

Order **Passeriformes** Linnaeus, 1758
Family Corvidae Vigors, 1825
Genus *Pyrrhocorax* Tunstall, 1771

Pyrrhocorax graculus (Linnaeus, 1766)

Pl. 2, figs K, M

1992 *Pyrrhocorax graculus* - Capasso Barbato et al., p. 326.
1996 *Pyrrhocorax graculus* - Petronio et al., p. 334.
1998 *Pyrrhocorax graculus* - Petronio & Sardella, p. 288-289.

Material. 1314 bones coming from layers B, C and D. Most of the bones come from layer C, except the ones indicated as coming from layers B and D. In detail: three cranii (1 layer B), one maxilla, five mandibulae (1 layer B), nine sterni, six furculae, 195 coracoids (21 layer B, 3 layer D), fifty-one scapulae (3 layer B, 1 layer D), 283 humeri (21 layer B, 5 layer D), 279 ulnae (30 layer B, 3 layer D), 173 carpometacarpi (11 layer B, 1 layer D), ninety-six femora (11 layer B, 3 layer D), seventy-one tibiotarsi (3 layer B), 141 tarsometatarsi (19 layer B, 4 layer D).

Description and comparisons. The morphological characteristics of all the bones examined clearly demonstrate their relationships with the family Corvidae, as indicated by Tomek & Bochenski (2000). Within the family Corvidae, the genus *Pyrrhocorax* shows thinner bills and stouter proportions in all the long bones; these characteristics allow us to refer the material to the genus *Pyrrhocorax*, in particular to *P. graculus*. Only two species of the genus have been described, both living and fossils, and they can be easily separated by size, *Pyrrhocorax graculus* being clearly smaller than *Pyrrhocorax pyrrhocorax*, with almost no overlap in the ratio between total length and shaft diameter of the long bones (Tomek & Bochenski 2000).

In the Middle Pleistocene of Europe (Tyrberg 1998, 2006) some authors reported the presence of the extinct subspecies *Pyrrhocorax graculus vetus* Mourer-Chauviré, 1975b, with slight differences in the proportions of the long bones compared to extant birds. Louchart (2002) described the extinct subspecies *P. graculus castiglionis,* endemic to the Late Pleistocene/Holocene of northern Corsica. This taxon differs from the nominal subspecies in certain measurments, in particular the larger cranial elements. We did not undertake a population analysis to identify the Ingarano material to subspecies, so we leave them as *Pyrrhocorax graculus* s.l.

Biochronological and ecological remarks. This species is known since the Early Pleistocene and is extremely common in Late Pleistocene localities throughout Europe (Tyrberg 1998, 2006).

This species now lives in rocky environment, especially near cliffs in the southern Western Palearctic, particularly in mountainous areas; it nests in cliffs holes and feeds in grasslands and other open areas near its breeding sites (Cramp & Perrins 1994). It is extremely common in layers B and C of Ingarano succession, including young individuals, which indicates the presence of a large colony of this species in the area during the Late Pleistocene, as suggested by the huge deposit of phosphatic elements, likely guano, forming layer B. A very small number of bones has also been found in layer D, which indicates the persistence of the species in the area. The decrease amount of remains from layer C to layer D demonstrates a change in the environmental conditions between the first level and the upper ones of the Ingarano succession.

Pyrrhocorax pyrrhocorax (Linnaeus, 1758)

Pl. 2, fig. F

1996 *Pyrrhocorax* sp. - Petronio et al., p. 334.
1996 *Corvus monedula* - Petronio et al., p. 334.
1998 *Pyrrhocorax* sp. - Petronio & Sardella, p. 289.
1998 *Corvus monedula* - Petronio & Sardella, p. 289.

Material. 28 bones coming from layer C. In detail: nine humeri, four ulnae, three carpometacarpi, twelve tibiotarsi.

Description and comparisons. Some of the specimens here described were previously determined as *Corvus monedula*, but their morphological characteristics and their stoutness allow us to place these remains in the genus *Pyrrhocorax*, (see Tomek & Bochenski 2000). The dimensions of the bones here identified as *Pyrrhocorax pyrrhocorax* fit exactly those indicated in the literature for the species (Mourer-Chauviré 1975b; Tomek & Bochenski 2000; Louchart 2002).

Biochronological and ecological remarks. *Pyrrhocorax pyrrhocorax* is dubiously reported as a fossil since the Early Pleistocene and became common in the Palearctic in the Middle and Late Pleistocene, albeit not as much as the congeneric *P. graculus* (Tyrberg 1998, 2003).

This species has ecological characteristics similar to those of *Pyrrhocorax graculus,* with which it forms mixed flocks although *P. pyrrhocorax* is more frequently encountered at low altitudes and along the coastal cliffs (Cramp & Perrins 1994). This information indicates the presence of cliffs supporting a colony of *Pyrrhocorax* spp. along with the presence of open areas used as foraging areas by very large groups of *Pyrrhocorax* in the Ingarano area at the time of the deposition of the lower layers.

Genus *Corvus* Linnaeus, 1758

Corvus corone Linnaeus, 1758

Material. 12 bones coming from layers C and D. In detail: two coracoids (1 layer C, 1 layer D) one humerus (Layer C), two ulnae (Layer C), one carpometacarpus (Layer C), one synsacrum (Layer C), one femur (Layer C), one tibiotarsus (Layer C), three tarsometatarsi (2 layer C, 1 layer D).

Description and comparisons. The dimensions of the Ingarano remains fit those indicated by Tomek & Bochenski (2000) for both *Corvus corone* and *C. frugilegus*. Our morphological analysis of the fossil remains, and comparisons with recent specimens of both species allow us to identify the Ingarano remains as *Corvus corone*. In particular in the proximal humerus the edge of the crista bicipitalis is narrow and not broad as in *Corvus frugilegus*, and the fossa pneumatica is relatively broad. In the proximal part of the carpometacarpus there is a saddle between the processus pisiformis and the processus alularis, as in *Corvus corone*. In the distal part of the carpometacarpus the fossil remain shows the deep depression typical of *Corvus corone*, as indicated by Tomek & Bochenski (2000). The pelvis shows a distinct, relatively large bulge in the caudal part of the crista dorsolaterali ilii, very reduced in *Corvus frugilegus*. A very visible depression is present under the edge of the articular part of the femur, as shown only by *Corvus corone*. In the tarsometatarsus the groove in the plantar side of the trochlea metatarsi III is narrow and not as broad as in *Corvus frugilegus* (Tomek & Bochenski 2000).

Biochronological and ecological remarks. This species is recorded as early as the Early Pleistocene of Israel and is commonly reported in most Late Pleistocene fossil localities in Europe (Tyrberg 1998, 2003).

Corvus corone is now widespread in the Western Palearctic in a wide range of habitats (Cramp & Perrins 1994). It is thus is not very useful as a climatic and environmental indicator; in fact it has been found in two layers of the Ingarano succession that show great differences, as indicated by the other vertebrate associations.

Corvus corone Linnaeus, 1758 vel **Corvus frugilegus** Linnaeus, 1758

Material. 2 tarsometatarsi coming from layers D and E.

Remarks. Both remains of tarsometatarsus show dimensions comparable to both *Corvus corone* and *C. frugilegus*, but they are too much encrusted to see any morphological detail and so they are identified as *Corvus corone* vel *C. frugilegus*.

Corvus corax Linnaeus, 1758

1996 *Corvus corax* - Petronio et al., p. 334.
1998 *Corvus corax* - Petronio & Sardella, p. 289.

Material. 4 bones coming from layer D. In detail: one ulna, two femurs, one tarsometatarsus.

Description and comparisons. The Ingarano remains show the typical features of the family Corvidae (Tomek & Bochenski 2000); the dimensions of the fossil remains allow us to identify them as *Corvus corax*, the largest species in the family Corvidae living in the Western Palearctic (Mourer-Chauviré 1975b; Tomek & Bochenski 2000).

Biochronological and ecological remarks. *Corvus corax* is known with few records since the Early Pleistocene in the Palearctic and became more and more common from the Middle Pleistocene to the Late Pleistocene (Tyrberg 1998, 2006).

One distal femur found at Ingarano shows a granulose infilling the diaphysis, that can be interpreted as the medullary bone. This accumulation is necessary to store minerals useful for the production of the egg shells (Driver 1982); for this reason it appears only in females, some weeks before the egg laying, and disappears a few days later. The medullary bone, already recorded in fossils (e. g. Ballmann 1979; Mattiesen 1990; Pavia 2000), informs that the species bred near the fossil locality at the time of its deposition. In most cases the presence of breeding birds allows to improve the palaeoenvironmental reconstruction, because we can know precisely the ecological requirements of the different bird species during the breeding season, especially the extant ones. *Corvus corax* is a species widespread in Europe, from the North to the South, and lives in the rocky and cliff environments (Cramp & Perrins 1994), even in the mountains and along the sea shore. Its presence as a breeding species at Ingarano testifies the presence of a cliff nearby the deposit.

Discussion

Taphonomic indications

The detailed stratigraphical observations carried out during this work provided some useful information for understanding the depositional events of the Late Pleistocene Ingarano succession, in particular with regards to layers B and C. The lower layer B, constituted by phosphatic material, is probably the result of the decomposition of the guano deposit produced by a bird colony inhabiting the cave, likely formed by *Pyrrhocorax* species; it encrusts some bones of birds and mammals accumulated in the ancient floor of the cave. Layer C is constituted by small rounded calcareous pebbles and was accumulated in the cave by a single flood event, as the layer does not show any sedimentary structure and the sediment fills in all the free gaps between the stalagmites and collapsed stalactites accumulated on the floor of the cave. The fossils found in layers B and C are well preserved with no traces of transportation, and some anatomical connections have been found in both mammal (Petronio & Sardella, 1998) and bird remains (Pl. 2, figs. M-N); such biostratinomic data indicate the biogenic production of the fossil bones very close to the deposition place. The upper layers, D and E, are characterized by different episodes within each layer, as shown by differences in granulometry of clasts and by size-classes of the fossil remains, with local concentrations of small mammal bones, which are absent in most of the rest of the layers D and E. Actually the various lenticular bodies observed in layers D and E reflect different depositional phases, which were developed after gravitative processes, possibly in a relatively short time, so that no differences are observed in their species composition. The bones in layers D and E are more fragmented and abraded and never found in anatomical connection, which indicates longer transport than in layers B and C.

Some bird bones of lower layers, mainly *Pyrrhocorax graculus*, and middle-sized mammal bones show predation marks. In particular, these marks involve the two epiphyses of the long bones and less frequently the shaft of the bones. The bones affected by these modifications were analysed to recognize the predator responsible for their accumulation. The bones are complete, except for the breakage of the two epiphyses, and do not show any trace of digestive processes. This preservation seems to indicate that the bones correspond to food remains of birds of prey, such as Accipitriformes and Strigiformes. Taphonomical analyses of recent bird bones found in food remains of both *Nyctea scandiaca* and *Falco rusticolus* have recently been carried out (Bochenski 1997; Bochenski et al. 1998); we compare these results with the Ingarano fossil remains, in which *Nyctea scandiaca* and *Falco cherrug*, the latter similar in size to *F. rusticolus*, are the most common birds of prey of the assemblage and could be responsible for the bone accumulation. These two raptors tend to produce heavy modification on the bones, with a great percentage of breakage and digestive processes, more pronounced in *Falco rusticolus* (Bochenski et al. 1998) than in *Nyctea scandiaca* (Bochenski 1997); based on this we can exclude these birds of prey as the accumulators of the Ingarano remains since our bones are rarely broken and do not show any signs of digestive processes. Other possibilities include mammalian predators. The pattern of modification shown by the Ingarano remains are comparable to those observed on large bones eaten by wolves and lions (Haynes 1980, 1983). In fact the bones analysed from Ingarano are too big to be ingested by medium-sized carnivores, such as foxes and martens, and they also do not show the digestive effects that would be expected from these species (Andrews & Nesbit Evans 1983; Andrews 1990). Thus we are led to suggest that the bones of Ingarano were gnawed by large-sized carnivores, like *Lynx lynx* and *Canis lupus*, which are very abundant in the lower layers of the Ingarano deposit (D'Aguanno 1998; Massari 1999), as suggested as well by some teeth marks on the shaft of *Falco cherrug* and *Nyctea scandiaca* bones. To strengthen this hypothesis, a complete ulna of *Corvus corax* with a similar modification pattern has been recently described from the Late Pleistocene of Grotta dei Fiori (Pavia & Bedetti 2003), probably gnawed by *Cynotherium sardous*, a canid which represents the top of the food chain of the Late Pleistocene of Sardinia (Sondaar & van der Geer 2002).

In conclusion the fossil bird and mammal bones found in the lower layers B and C of the Ingarano cave deposit were probably accumulated close to the cave after natural death, while some were brought in by mammalian predators. Subsequently, they were carried deeper into the cave by a single flood event.

The fossil bones found in the upper levels D and E, which were transported over long distances, possibly more than once, do not show modifications that help clarify their taphonomic origin. We can only propose that these remains were produced far from the final place of burial.

Palaeoecological indications

The different layers recognized in the Ingarano succession contain characteristic fossil bird assemblages, useful to determine the palaeoenvironment and, secondarily, the palaeoclimate of the western part of the Gargano peninsula through the Late Pleistocene. In particular the assemblages of layers B and C are similar to each other, while those of layers D and E show a different species composition. In other words two different taxonomic assemblages, with different ecological requirements, characterize the Ingarano succession (Tab. 4).

In the lower layers, B and C, diurnal and nocturnal birds of prey are very common, although the most common taxon is *Pyrrhocorax graculus*. The species composition of these two layers indicates open environments with humid areas and some woods, as also indicated by *Lynx lynx* and *Felis silvestris*. In the upper layers, D and E, the environmental indications are similar to those of the lower ones, but open areas had to be dryer as indicated by the abundance of *Columba livia* and the presence of *Perdix perdix* and *Otus scops*.

PLATE 1

Bird remains from the Late Pleistocene of Ingarano. A) *Aquila chrysaëtos*, left ulna (IGF, uncatalogued) cranial view; B) *Aquila chrysaëtos*, left tibiotarsus (Ing. A. 44), cranial view; C) *Aquila chrysaëtos*, left femur (Ing. A. 1105), caudal view; D) *Falco cherrug*, left humerus (Ing. A. 1135), caudal view; F) *Falco cherrug*, left coracoid (Ing. A. 23), caudal view; H) *Aquila chrysaëtos*, first phalanx of the left first digit (Ing. A. 1115), cranial view; I) *Falco cherrug*, right tibiotarsus (Ing. A. 43), cranial view; J) *Falco cherrug*, distal left tarsometatarsus (Ing. A. 1124), dorsal view; K) *Falco cherrug*, left tarsometatarsus (Ing. A. 1126) dorsal view; L) *Falco cherrug*, left humerus (Ing. A. 76), caudal view.

Recent *Falco cherrug* (NHM 5/1981.5.2). E) left humerus, caudal view; G) left coracoid, caudal view. The scale bars represent 1 centimetre. Specimens coated with ammonium chloride to enhance details.

PLATE 1

	Layers B + C	**Layers D + E**
Recognized taxa	*Circus aeruginosus*	*Buteo rufinus*
	Buteo rufinus	*Perdix perdix*
	Aquila chrysaëtos	*Columba livia*
	Falco columbarius	*Otus scops*
	Falco cherrug	*Pyrrhocorax graculus*
	Alectoris graeca	*Corvus corone*
	Columba livia	*Corvus corax*
	Athene noctua noctua	
	Nyctea scandiaca	
	Pyrrhocorax graculus	
	Pyrrhocorax pyrrhocorax	
	Corvus corone	

Tab. 4 - Bird taxa recorded in the lower part (Layers B + C) and in the upper part (Layers D + E) of the Late Pleistocene Ingarano succession.

An environmental characteristic shared by all the fossil assemblages of Ingarano is the development of a rocky wall or cliff where colonies of *Pyrrhocorax* spp. were probably located during the first phase of taphonomical deposition within the cave. On the other hand the presence of cliffs or at least rocky ground throughout the period of activity of the Ingarano cave is indicated by the presence of other species, such as *Falco cherrug*, *Columba livia* and *Corvus corax*.

The different bird assemblages provide us with some interesting indications on climate; in fact, although in the paragraphs above we carefully considered the climatic clues provided by single species, taken as a whole, the bird species association of the lower layers indicates a colder climate than the ones of the upper layers. This is confirmed by the presence of *Nyctea scandiaca* together with *Falco cherrug* and *Alectoris graeca* and by the great abundance of *Pyrrhocorax graculus*; the mammal association of layers B and C also contains some species associated with cold climates, including some, such as *Lynx lynx* and *Gulo gulo*, which are present in great numbers (Petronio & Sardella 1998; Sardella 2000). In the upper layers some species, such as *Nyctea scandiaca* and *Alectoris graeca*, disappear, while others appear, including *Otus scops* and *Perdix perdix*, and *Columba livia* becomes the most common bird species; these faunal changes reflect the warmer climatic conditions of the upper layers. Similar changes are observed in mammal assemblages, with the disappearance of *Lynx lynx* and *Gulo gulo* and the presence of *Equus hydruntinus* and *Bos primigenius* (Petronio & Sardella 1998).

The climatic indications suggested by the fossil birds of Ingarano seem to rule out Petronio & Sardella's (1998) suggestion that the lower layers were deposited during a strong glacial period of the Late Pleistocene. Indeed the Ingarano deposits lack some taxa present in other Southern Italy localities dated to the Last Glacial, such as *Falco rusticolus* and *Lagopus mutus*. These species now live in arctic regions and in the Alps and Pyrenees above tree line (Cramp & Simmons 1980); they have been recorded at Cardamone and at Grotta della Madonna (Tyrberg 1998), both localities being dated to the Last Glacial period (Tyrberg 1998; Rustioni et al. 2003).

In conclusion, the lower layers of the Ingarano succession represent a cold phase of the Late Pleistocene, in particular during the MIS 3, while the upper layers reflect a warmer oscillation within the same Marine Isotopic Stage.

Chronological indications

Previous papers (Petronio et al. 1996; Petronio & Sardella 1998) reported some chronological data based on geochemical analyses and on the study of some lithic artefacts. In particular, the dating of the phosphatic material of the layer B, made with $^{239}\text{Th}/^{234}\text{U}$ method, revealed an age of 40.000 ± 2000 year BP; while the analysis of some Mousterian lithic artefacts found at the transition between the layer D and E made by Mussi (in Petronio et al. 1996) indicates an age of no less than 37-35.000 years BP. These two dates, according to the climatic indications above, allow us to refer the whole Ingarano succession, layers B to E, to the MIS 3, the lower two layers indicating a colder phase and the upper two a warmer phase of the same Isotopic stage. Compared to the analysis made by Petronio & Sardella (1998), we do not consider as valid the existence of a layer (Layer G) with fossil vertebrates, mainly birds, referable to the MIS 2.

In conclusion we can state that the Late Pleistocene Ingarano cave succession was deposited in a short time span during the MIS 3, as supported by the two datings already made at the base and near the top of the succession.

PLATE 2

Bird remains from the Late Pleistocene of Ingarano. A) *Nyctea scandiaca*, left tibiotarsus (Ing. A. 49), cranial view; B) *Nyctea scandiaca*, left humerus (Ing. A. 82), caudal view; C) *Perdix perdix*, right coracoid (Ing. A. 1378), caudal view; D) *Alectoris graeca*, left tarsometatarsus (Ing. A. 58), dorsal view; E) *Columba livia*, right humerus (Ing. A. 1381), caudal view; F) *Pyrrhocorax pyrrhocorax*, left ulna (Ing. A. 1484), cranial view; G) *Nyctea scandiaca*, left tarsometatarsus (Ing. A. 27); H) *Buteo rufinus*, proximal right tarsometatarsus (Ing. A. 1318), dorsal view; I) *Falco columbarius*, distal left humerus (Ing. A. 70), cranial view; J) *Circus aeruginosus*, distal right humerus (Ing. A. 81), cranial view; K) *Pyrrhocorax graculus*, right humerus (Ing. A. 1385), caudal view; L) *Nyctea scandiaca*, fragmented mandible (PU 102623), cranial view; M) *Pyrrhocorax graculus*, articulated left wing (PU 102625); N) *Nyctea scandiaca*, articulated synsacrum and left femur (PU 102624). The scale bars represent 1 centimetre. Specimens coated with ammonium chloride to enhance details, except for fig. M and fig. N.

PLATE 2

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