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The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

15. Carnivore Guild Structure

by

Doris Nagel[1] & George D. Koufos[2]

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Abstract

The carnivore community of previous collections from the Upper Miocene of Samos contained 16 taxa, and most of them were found during recent field works in the Mytilinii Basin, as well. The new material added one taxon, *Protictitherium*, as well as new information concerning the already known taxa (see chapter 5, this volume). Three parameters are used to classify the carnivoran guild from Samos – diet class, locomotion pattern and body size. The results are given together with the taxon list. The same analyses were done on the fossil carnivore material from Pikermi for comparison. Both results are visualised in a three dimensional graph. Evaluations of palaeo-guilds can be used as proxies for palaeoecological interpretations of former habitats. These are the first guild structure analyses from the Mediterranean area.

Keywords: Late Miocene, Samos, Greece, Mammalia, Carnivora, Guild Structure.

Zusammenfassung

Aus früheren Aufsammlungen aus dem Obermiozän von Samos konnten insgesamt 16 Raubtier-Taxa identifiziert werden. Die meisten wurden durch neuere Funde aus dem Mytilinii-Becken bestätigt. Eine weitere Art kam hinzu, *Protictitherium*, sowie neue Informationen zu den bereits bekannten Formen (siehe Kapitel 5, dieser Band). Drei Parameter werden für die Klassifizierung der Raubtier-Guild verwendet – Nahrungspräferenz, Lokomotionstyp und Gewichtsklasse. Die Ergebnisse sind gemeinsam mit der Artenliste aufgeführt. Dieselbe Analyse wurde zu Vergleichszwecken am Raubtiermaterial von Pikermi durchgeführt. Beide Resultate sind in Form von 3D-Grafiken dargestellt. Evaluierungen von Paläoguilds können als Proxies für paläoökologische Interpretationen von ehemaligen Habitaten verwendet werden. Dies sind die ersten Guild-Untersuchungen des mediterranen Raumes.

Schlüsselworte: Oberes Miozän, Samos, Griechenland, Säugetiere, Carnivora, Paläoguilds.

1. Introduction

The late Miocene carnivoran assemblage of Samos has been studied by several authors (Pilgrim, 1931; Solounias, 1981; Koufos & Melentis, 1982; Koufos, this volume-a). The old collections from Samos, housed at various museums include a great number of carnivore's taxa (Solounias, 1981; Bernor et al., 1996). In our new collection the carnivores are relatively few and they mainly come from the fossiliferous sites of the locality Mytilinii-1 (MTL), situated in the Adrianos ravine (Koufos, this volume-b; Kostopoulos et al., this volume). The faunal list in the NOW database (Neogene Old World database) is based on the determination of Bernor et al. (1996) and preliminary ecomorphological assignments are already indicated.

The present guild analysis is based on the list of the NOW database and on the list of the new collection. The list of NOW is based on the old collections from Samos which come from various fossiliferous sites of different age; most of them are without locality indications and the material is mixed (Koufos, this volume-b). Thus, the authors give the guild structure based on the NOW faunal list (old col-

[1] Prof. Doris Nagel, University of Vienna, Department of Palaeontology, Althanstrasse 14, A-1090 Wien, Austria, e-mail: doris.nagel@univie.ac.at

[2] Prof. George D. Koufos, Aristotle University of Thessaloniki. Department of Geology, Laboratory of Geology and Palaeontology, GR-54124 Thessaloniki, Greece, e-mail: koufos@geo.auth.gr

Corresponding Author: Department of Palaeontology, University of Vienna, Althanstrasse 14, A-1090 Wien, Austria, e-mail: doris.nagel@univie.ac.at

lection) and on the new collection. The carnivores of the new collection originate mainly from the locality MTL which is dated to middle Turolian (MN 12) and more precisely to 7.1-7.0 Ma by magnetostratigraphy (KOUFOS et al., this volume-b).

Several studies concerning carnivorous guilds are known combining two parameters, usually body mass and either locomotor pattern or food preferences (VAN VALKENBURGH, 1992, 1999; WERDELIN, 1996; VAN VALKENBURGH et al., 2004; WESLEY-HUNT, 2005). New approaches combine all three paramenters MORLO, 1999; NAGEL & MORLO, 2000, 2003; MORLO & GUNNELL, 2005, 2006; MORLO & NAGEL, 2007; NAGEL et al., 2005; STEFEN et al., 2005; GUNNELL & MORLO, 2006; MORLO et al. in press). Three parameters are used to evaluate the ecomorphological space of the different taxa: body mass, diet type, and locomotor pattern.

Body Mass. Several studies have documented the quantitative relationship between body mass and carnassial tooth size (THACKERAY & KIESER, 1992; VIRANTA & ANDREWS, 1995; LEGENDRE & ROTH, 1988; VAN VALKENBURGH, 1990). Another approach is to take limb bone measurements to estimate the body mass of carnivores (GINGERICH, 1990; ANYONGE, 1993; HEINRICH & BIKNEVICIUS, 1998; CHRISTIANSEN, 1999). Since no limb bones are described from the new carnivore collection from Samos (KOUFOS, this volume-a), we chose to use carnassial tooth size as a proxy for body mass in both the new taxa, as well as for taxa not described in this volume. In previous studies, the use of body mass classes proved to be more reliable as an ecomorphological indicator, instead of absolute body mass data, since there are always an individual species variation as well as methodological differences. Therefore we used following body mass classes: 0–1 kg, 1–3 kg, 3–10 kg, 10–30 kg, 30–100 kg, >100 kg (MORLO, 1999).

Diet. In general, four diet classes can be distinguished in carnivorans: bone/meat, hypercarnivorous, carnivorous and hypocarnivorous (VALKENBURGH, 1988). The hypocarnivores are a quite diverse group since they include omnivores as well as durophagous taxa. Although insectivorous carnivores could be seen as hypocarnivorous, FRISCIA et al. (2007) defined them by their pointed teeth and so "insectivorous" can be added to the diet class system.

Locomotor Pattern. No new information is given for the carnivores from Samos in this volume, but the taxa are all known from earlier descriptions (WERDELIN, 1996; GINSBURG, 1961; GINSBURG, 1999) and from other sites as well. Therefore it is possible to assign them to different locomotor patterns. Qualitative characters were described by following authors: BARNET & NAPIER (1953), GINSBURG (1961), HEINRICH & ROSE (1997), JENKINS & CAMAZINE (1977), LABORDE (1987), TAYLOR (1974, 1976, 1989), BERTRAM & BIEWIENER (1990) and ANDERSSON (2004). Different postcranial features were used to define locomotion preference including: scapular outline, shape and size of humeral head, size of distal humeral epicondyle, length and orientation of olecranon, shape and size of humeral and radial notches and size of distal radioulnar articular process at the ulna, hand posture, shape of astragalus and calcaneum, and foot posture. We separate arboreal, scansorial, cursorial, generalized terrestrial, semifossorial, and semiaquatic taxa. The results are given in 3-D visualizations of guild structure.

2. The Carnivore Guild from Samos MN 12

The following taxa have been recognized in the new collection from Samos: *Parataxidea maraghana*, *Plioviverrops orbignyi*, *Hyaenictitherium wongii*, *Adcrocuta eximia*, *Metailurus parvulus* and *Machairodus giganteus* (KOUFOS, this volume-a). Additionally SOLOUNIAS (1981), BERNOR et al. (1996) and the NOW database listed: *Ursavus* cf. *depereti*, *Indarctos atticus*, *Promeles palaeattica*, *Promephitis*

No.	Colour	Family	Genus	Species	Body Mass	Locomotor Class	Diet Class
1		Ursidae	*Ursavus*	cf. *depereti*	30-100 kg	ambulatorial terrestrial	hypocarnivorous
2		Ursidae	*Indarctos*	*atticus*	> 100kg	generalized terrestrial	carnivorous
3		Mustelidae	*Promeles*	*palaeattica*	3 - 10 kg	ambulatorial terrestrial	carnivorous
4		Mustelidae	*Promephitis*	*larteti*	3 - 10 kg	unknown	hypocarnivorous
5		Mustelidae	*Parataxidea*	*maraghana*	3 - 10 kg	unknown	hypocarnivorous
6		Hyaenidae	*Plioviverrops*	*orbignyi*	3 - 10 kg	generalized terrestrial	insectivorous
7		Hyaenidae	*Protictitherium*	*crassum*	3 - 10 kg	scansorial	insectivorous
8		Hyaenidae	*Ictitherium*	*viverrinum*	10-30 kg	cursorial	carnivorous
9		Hyaenidae	*Hyaenictitherium*	*wongi*	30-100 kg	generalized terrestrial	carnivorous
10		Hyaenidae	*Lycyaena*	*chaeretis*	30-100 kg	cursorial	meat/bone
11		Hyaenidae	*Belbus*	*beaumonti*	30-100 kg	cursorial	carnivorous
12		Hyaenidae	*Adcrocuta*	*eximia*	30-100 kg	generalized terrestrial	meat/bone
13		Felidae	*Felis*	*attica*	3 - 10 kg	scansorial	hypercarnivorous
14		Felidae	*Metailurus*	*major*	30-100 kg	scansorial	hypercarnivorous
15		Felidae	*Metailurus*	*parvulus*	30-100 kg	scansorial	hypercarnivorous
16		Felidae	*Machairodus*	*giganteus*	> 100 kg	generalized terrestrial	hypercarnivorous

Table 1: Assignment of the carnivorous taxa from Samos, Late Miocene (MN 12) to body mass, diet and locomotion class.

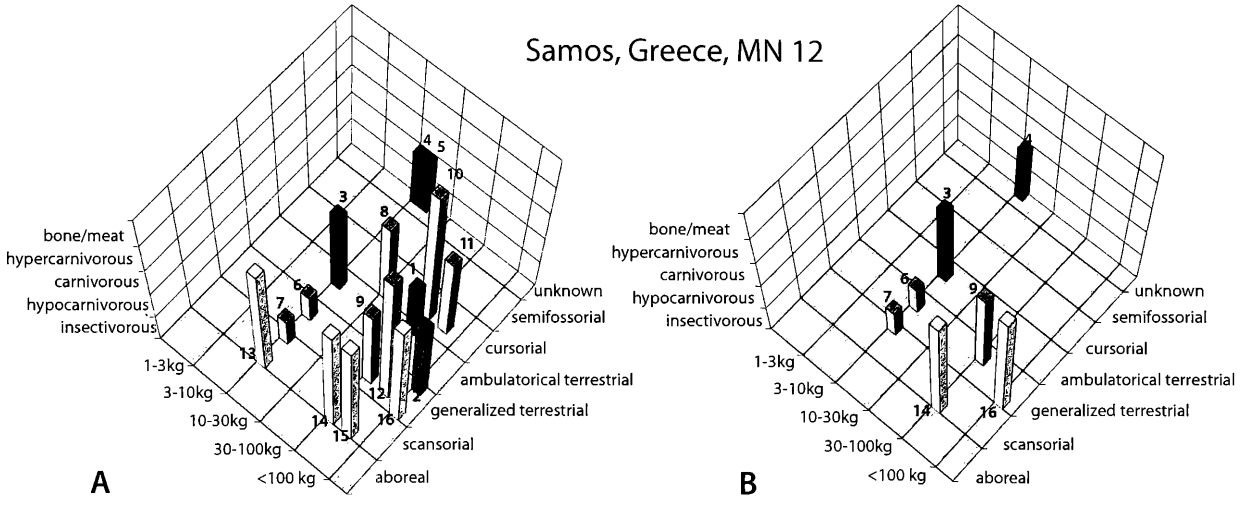

Figure 1: 1 - *Ursavus* cf. *depereti*; 2 - *Indarctos atticus*; **3** - *Promeles palaeattica*; **4** - *Promephitis larteti*; 5 - *Parataxidea maraghana*; **6** - *Plioviverrops orbignyi*; **7** - *Protictitherium crassum*; 8 - *Ictitherium viverrinum*; **9** - *Hyaenictitherium wongi*; 10 - *Lycyaena chaeretis*; 11 - *Belbus beaumonti*; 12 - *Adcrocuta eximia*; 13 - *Felis attica*; **14** - *Metailurus parvulus*; 15 - *Metailurus major*; **16** - *Machairodus giganteus*. A - graph with all known carnivores from Samos ; B - only carnivores from recent excavation from Samos published by KOUFOS (this volume), **in bold**.

larteti, *Ictitherium viverrinum*, *Lycyaena chaeretis*, *Belbus beaumonti*, *Felis attica*, *Metailurus major*.

The characterization of all mentioned taxa is given in Tab. 1, but the authors are well aware that the material was not collected from one but from several sites on Samos and their stratigraphic position is questionable. Thus, for comparative reasons, in one graph the result for the recent carnivore list following KOUFOS (this volume) is depicted, and in the other the result for all carnivores known from Samos (Fig. 1).

The hyaenids were characterized by WERDELIN & SOLOUNIAS (1996) and according to their work: *Protictitherium* is insectivorous and scansorial (semi-aboreal), *Plioviverrops* is evaluated as insectivorous and generalized terrestrial, *Hyaenictitherium* and *Ictitherium* as carnivorous and generalized terrestrial, although the latter was described from Lothagam, at least partly, as a cursorial species (WERDELIN, 2003). *Belbus* and *Lycaena* are seen as cursorial meat eaters, the latter as a meat/bone eater and *Adcrocuta* as a specialized bone cracker with stout limbs (= generalized terrestrial).

The feline forms are all hypercarnivores, very easily identified by the sectorial shape with a highly reduced talonid on the carnassial. All have limb proportions close to the extant felids, but maybe *Metailurus* is not as digitigrade (GINSBURG, 1999).

While *Indarctos* has almost identical limb proportions as modern *Ursus*, *Ursavus* (PILGRIM, 1931; GINSBURG 1999) is at least close to the same form of locomotion and both are considered as ambulatorial terrestrial. The low crown height as well as the elongated teeth with reduced shearing function are typical for hypocarnivorous forms.

Promeles palaeattica (WEITHOFER, 1888) was found on Samos, in Perivolaki, Pikermi (Greece) and Dorn-Dürkheim, Germany (WEITHOFER, 1888; MORLO, 1999; KOUFOS, 2006), probably in Maragha (BERNOR et al., 1996), and the smaller *P. macedonicus* (SCHMIDT-KITTLER, 1995) in Maramena, Greece. This medium-sized mustelid had a carnivorous tendency, with the trigonid and talonid of almost equal size and a short M1. The postcranial elements, described in more detail by ROUSSIAKIS (2002) from Pikermi, indicate a plantigrade animal; it is therefore assigned to the ambulatorial terrestrial locomotion type.

The genus *Promephitis* is known from Europe to Asia with several species. The dental morphology is rather primitive in some aspects, such as a subequal paracone and metacone on M1, or extra roots on m1 (WANG & QUI, 2004). The latter is often seen in aquatic mammals as well. There is no indication that *Promephitis* was in any way a semi-aquatic form, but it probably preferred a wider range of food and is therefore judged as hypocarnivorous. *Promephitis larteti* from Samos was medium-sized compared to other *Promephitis* species. *Parataxidea* was first described by ZDANSKY (1924) from China and is of Eurasian distribution. Its dental structure is enforced by cingula, the first upper molar is broad, the P4 is low and broad, as well; a detailed description is given in KOUFOS (this volume-a). The morphology of the skull of the type genus induced ZDANSKY (1924) to speculate about a semi-aquatic lifestyle for *Parataxidea* but unfortunately no evaluation of postcranial material is known so far. The teeth confirm the preference of a larger variety of food, even including molluscs or crabs (ZDANSKY, 1924).

3. Discussion and Comparison

The carnivore guild from Samos, all described species taken together, consisted of 16 taxa. Compared to recent assemblages, this is a very good record, since extant car-

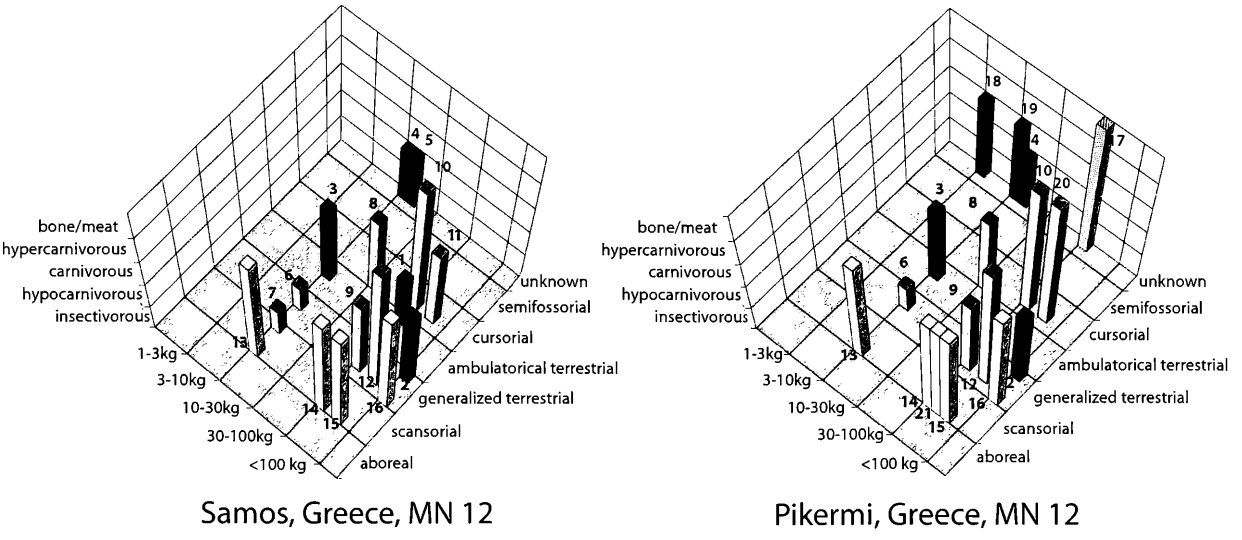

Figure 2: Carnivores from Samos. 1 *Ursavus* cf. *depereti*; 2 - *Indarctos atticus*; 3 - *Promeles palaeattica*; 4 – *Promephitis larteti*; 5 - *Parataxidea maraghana*; 6 - *Plioviverrops orbignyi*; 7 – *Protictitherium crassum*; 8 - *Ictitherium viverrinum*; 9 - *Hyaenictitherium wongi*; 10 - *Lycyaena chaeretis*; 11 - *Belbus beaumonti*; 12 - *Adcrocuta eximia*; 13 - *Felis attica*; 14 - *Metailurus parvulus*; 15 - *Metailurus major*; 16 - *Machairodus giganteus*.

Additional elements in the Pikermi fauna: 17 - *Simocyon primigenius*; 18 - *Sinictis pentelici*; 19 - *Martes woodwardi*; 20 - *Hyaenictis graeca*; 21 - *Paramachairodus orientalis*.

nivore communities tend to have between 15 and 25 taxa. Judging from the locomotor type, the carnivore guild from Samos contained no semifossorial or arboreal taxa. To answer the question if any of the smaller taxa were adapted to a semi-aquatic lifestyle, further investigation is necessary, it and cannot be answered in this paper. Concerning the locomotion, the main part of the carnivoran community belongs to the generalists, to the scansorial and cursorial forms. Smaller forms, the ones below three kilograms, are missing in the body mass evaluation. It seems possible that some were not preserved or are difficult to identify, if only fragmentary material was found. However, carnivores over 100 kilograms were present (*Indarctos* and *Machairodus*). All diet classes are represented in the Samos guild. Insectivorous forms (*Proticitherium* and *Ictitherium*) were found, as well as taxa with a mixed diet, with a more carnivorous tendency, and the hypercarnivorous class, filled by the felids *Felis attica*, *Metailurus major* and *M. parvulus* and by *Machairodus*. One large bone/meat eater was present, *Adcrocuta eximia*.

We compared the carnivoran guild from Samos with the one from Pikermi. Again, the analysis is based on material from several collections, summarized in the NOW database. Samos holds sixteen well defined taxa and Pikermi has twenty taxa, but three are questionable and only identified at genus level. Since no further information about food preferences, locomotion or body size was available, these three taxa were omitted from the evaluation (? *Enhydriodon* sp., ?*Plesiogulo* sp., *Felis* sp.). Although the two carnivore communities are similar in size, the taxa are not the same. Known from Samos, but not from Pikermi are: *Ursavus* cf. *depereti*, *Parataxidea maraghana*, *Protictitherium crassum* and *Belbus beaumonti*. Known from Pikermi but not from Samos are: *Simocyon primigenius*, *Sinictis pentelici*, *Martes woodwardi*, *Hyaenictis graeca* and *Paramachairodus orientalis*.

The Pikermi guild results are similar to the Samos guild (Fig. 2). Again the smaller forms < 10kg are missing. No arboreal or semi-fossorial forms are known and all diet classes are occupied. In Pikermi, three bone/meat eater and three larger (30-100 kg) hypercarnivorous taxa were present, while in Samos only one bone/meat eater and two larger hypercarnivorous taxa were found.

Wooded environments seem to favour larger carnivores from three kilograms up, but no extreme forms over 100 kg. It comes as no surprise that these environments hold many scansorial forms, but also a lot of hypercarnivorous taxa. Savannah-like habitats are characterized by carnivores with a larger variety in different body mass classes (below 1 kg and over 100 kg) and a larger variety in food preferences (insectivorous and bone/meat eater).

4. Results

The carnivore guild from Samos presents a very good record of Late Miocene predators in the Mediterranean area. Although information about locomotor assignment in some taxa is still missing, a general interpretation is possible. The carnivore community from Samos neither fits a heavily wooded environment like an equatorial tropical rain forest (e.g. Guyana), nor a typical savannah like equatorial Serengeti today. The larger taxa, as well as the few cursorial forms, indicate areas with open habitats

but, at the same time, the generalists indicate the presence of wooded environments as well. These environmental conditions fit in quite well with the proposed open bushland with a thick grass floor landscape for the Turolian of Samos (KOUFOS et al., this volume-a). The Pikermi carnivoran community is quite similar and mirrors the results from Samos.

These are the first guild investigations for the Mediterranean area of the Late Miocene. It will be interesting to compare these in future with other sites in this very special ecological area.

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