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Biogeography of *Aphodiinae* from the Phytogeographic Orocantabrica Province, Cantabrian Range, Spain (*Col. Scarabaeoidea*)

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Abstract. A faunistic composition of *Aphodiinae* caught in the Phytogeographic Orocantabrica Province (Cantabrian Mountains, North of Spain) is presented. Results are based on three years (1986-1988) of systematic sampling in 53 localities selected according to phytogeographic characteristics. A total of 45 species have been studied, including three species collected outside of the area in question. The results show the high species richness (about 40% of *Aphodiinae* of the Iberian fauna) with a significant share of eurocaucasic biogeographical elements and Iberian endemics. As a whole the Orocantabrica Province supports a high biodiversity. The specific richness of *Aphodiinae* (Shannon index H', E and Margalef index D_{Mg}) remains high throughout the whole territory. The highest *Aphodiinae* diversity corresponds to the eastern phytogeographic subsectors (Altocarriones, Picoeuropeano and Ubiñense subsectors) and the highest specific richness of *Aphodiinae* species was found in the June/July period. With respect to the altitudinal distribution, 76% of species occurred in the 1000-1500 m altitude range and the endemic species appeared above 1000 m altitude. The necessity of protecting areas and habitats in this region is indicated.

Key words: Diversity, *Aphodiinae, Scarabaeoidea,* Cantabrian Mountains, Iberian Peninsula.

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I. INTRODUCTION

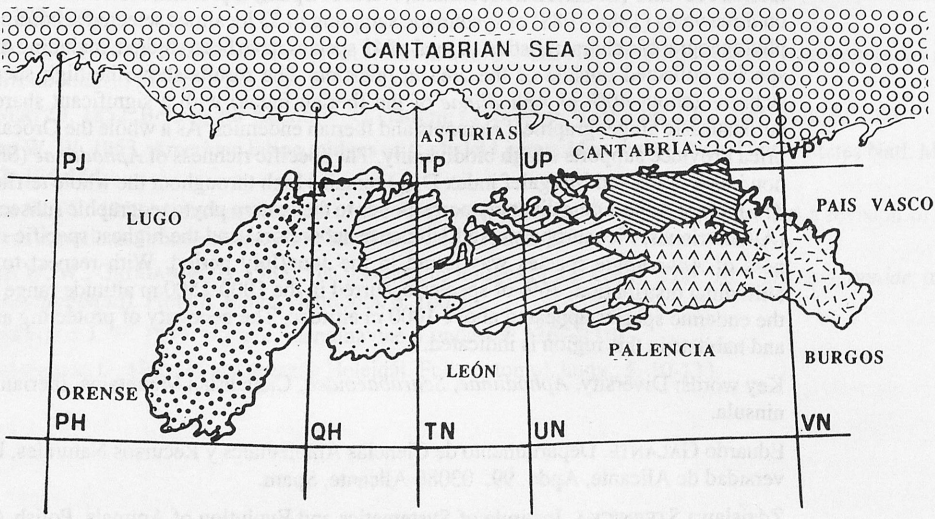
The Cantabrian Mountains are situated in the Eurosiberian Subregion of the north of Spain on the border of the Mediterranean Subregion. This area offers a high geological and pedological diversity with a decrease in rainfall and increase in temperatures from the east to the west.

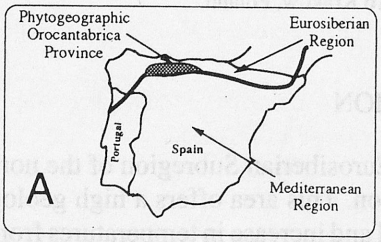
The landscape and ecosystems vary greatly in the study area, being shown by the vegetation (RIVAS-MARTINEZ et al. 1984). Likewise different vegetation composition also

depends on the orientation of valleys and mountains that bring about the appearance of local climates. As a result the areas flora and fauna are exceptionally rich owing to the great variety of environments and ecological refuges available in the region.

Most mountain ecosystems of the Iberian Peninsula have been altered by man introducing cattle and creating new open pastures, similar to the other European ecosystems. The availability of large mammal dung has increased historically in many areas and they have been used by the dung beetles, particularly by the *Aphodiinae* species (HANSKI 1991). At the same time, in wooded area habitats, wild herbivores are often important dung producers which can be exploited by the *Aphodiinae* fauna and other dung beetles. This anthropic activity has led to an increase in the species composition and diversity of the dung beetle fauna in these mountainous ecosystems.

This paper is focussed on the study of *Aphodiinae* biogeography in the Cantabrian Range as a result of sampling during three years (1986-1989) in the Orocantabrica phytogeographic province (RIVAS-MARTINEZ et al. 1984) and of complementary captures at some sites outside this phytogeographic area in 1988. The first results of dung beetle fauna in this area belonged to *Scarabaeidae* (GALANTE & RODRIGUEZ-MENENDEZ 1989). The objectives of the present paper are to ascertain the diversity of *Aphodiinae* fauna in





SECTOR	SUBSECTOR	
Laciano-Ancarense	Naviano-Ancarense (NA) Laciano-Narcense (LN)	
Ubiñense-Picoeuropeano	Ubiñense (U) Picoeuropeano (P)	
Campurriano-Carrionés	Altocarrionés (A) Altocampurriano	

B

Fig. 1. Map of the Phytogeographic Orocantabrica Province: A – Situation in the Iberian Peninsula; B – Phytogeographic Sectors and Subsectors.

this Iberian region and to analyse their distribution in relation to the phytogeographic divisions.

The voucher specimens of *Aphodiinae* species were deposited in the collection of E. GALANTE, at present in the Department of Ciencias Ambientales y Recursos Naturales, University of Alicante, Spain.

II. STUDY AREA

The Phytogeographic Orocantabrica Province (RIVAS MARTINEZ et al. 1984), situated in the central Cantabrian Mountains, was chosen as the principal study area (Fig. 1). The Orocantabrica lies at altitudes ranging from 100 to 2648 m. Human influence is high and during summer sheep and cattle graze in the montane and subalpine meadows, specially from 1000 to 1900 m.

RIVAS MARTINEZ et al. (1984) distinguished several phytogeographic sectors:

1) LACIANO-ANCARENSE – Situated in the extreme west, with montane and subalpine levels. Siliceous soils predominate and in this area summer precipitation reaches its lowest levels. Two subsectors can be seen: NAVIANO-ANCARENSE (NA) and LACIANO-NARCENSE (LN).

2) UBIÑENSE-PICOEUROPEANO – Situated in the central area. Calcicolous soils predominate and all levels are present. Two subsectors can be seen: UBIÑENSE (U) and PICOEUROPEANO (P).

3) CAMPURRIANO-CARRIONÉS – Situated in the extreme east and characterized by its continental climate, fundamentally siliceous soils and high average altitude. It is formed by two very similar subsectors: ALTOCARRIONÉS (A) and ALTOCAMPURRIANO ; for this reason analyse have only been carried out in the Altocarrionés, although a few isolated samples were taken in sites in the Altocampurriano.

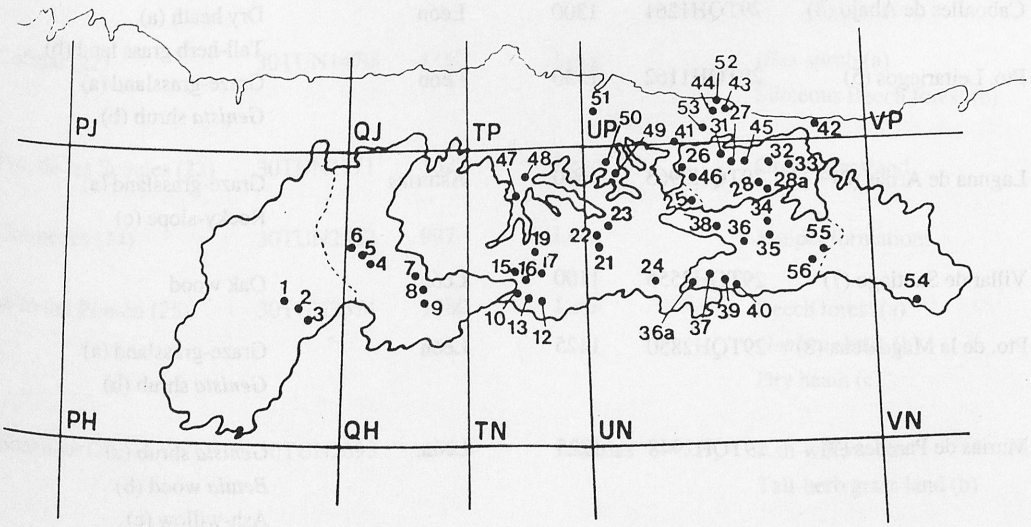


Fig. 2. Sampling sites in the Phytogeographic Orocantabrica Province.

III. METHODS

Forty two main sites ranging in altitude from 150 m (Arenas de Cabrales and Santillan) to 1834 m (Aliva) of the Phytogeographic Orocantabrica Province were selected according to the vegetation of each sector and subsector (Table I). As a result of the specific vegetation of each area, the number and distribution of sample sites in the phytogeographic divisions were not equal (Fig. 2). In the Naviano-Ancarense Subsector three sites included all the types of subsector vegetation, whereas in other subsectors numerous sampling sites were necessary to include all vegetational formations of the subsector. Because the phytogeographical characteristics of the Altocarriones were similar to those of the Alto-campurriano, this subsector was not sampled periodically.

Table I

Sampling sites : geographic coordinates U.T.M., altitude, administrative provinces and plant formations (landscape) are indicated

Locality (No)	U.T.M.	Altitude	Adm. Province	Landscape
		LACIANO-ANCARENSE Sector		
Pto Ancares (1)	29TPH7949	1648	León	*Betula* wood (a) Dry heath (b)
Pereda de Ancares (2)	29TPH8443	900	León	Chesnutgrove
Candín (3)	29TPH8642	875	León	*Genista* shrub (a) Ash-willow (b) Tall-herb grass land (c) Oak wood (d)
Caboalles de Abajo (4)	29TQH1261	1300	León	Dry heath (a) Tall-herb grass land (b)
Pto. Leitariegos (5)	29TQH1162	1550	León	Graze-grassland (a) *Genista* shrub (b)
Laguna de Arbás (6)	29TQH0963	1690	Asturias	Graze-grassland (a) Rocky-slope (c)
Villar de Santiago (7)	29TQH2555	1100	León	Oak wood
Pto. de la Magdalena (8)	29TQH2850	1425	León	Graze-grassland (a) *Genista* shrub (b)
Murias de Paredes (9)	29TQH2948	1225	León.	*Genista* shrub (a) *Betula* wood (b) Ash-willow (c) Tall-herb grass land (d)

UBIÑENSE-PICOEUROPEANO Sector

Mirantes de Luna (10)	30TTN6751	1150	León	Juniper formations
Beberinos (12)	30TTN8150	1000	León.	Tall-herb grass land (a) Ash-willow (b) Rocky slope (c)
Geras (13)	30TTN7451	1100	León	Beech forest
Alto de Aralla (15)	30TTN7054	1536	León	Graze-grassland
Aralla (16)	30TTN7055	1400.	León	Siliceous Dry heath (a) Calciolous *Ulex* shrub (b)
Valle de Casares (17)	30TTN7658	1310	León	Tall-herb grass land (a) Hazelnut-grove (b)
Pto. Pajares (18)	30TTN7563	1379	León	Graze-grassland
Brañillín (19)	30TTN7563	1379	León	Brezal-Tojal (a) *Betula* wood (b)
Cofiñal (21)	30TUN1468	1250	León	*Erica-Ulex* shrub (a) *Genista* shrub (b) *Pinus-Betula* wood (c) Peat bog (d) Calcicolous Beech forest (e) Graze-grassland (f)
Cofiñal (22)	30TUN1470	1450	León	*Ulex* shrub (a) Siliceous Beech forest (b)
Pto. de las Señales (23)	30TUN1771	1625	León	Graze-grassland
Crémenes (24)	30TUN2552	997	León	Juniper formations
Alto del Pontón (25)	30TUN3574	1280	León	Beech forest (a) *Genista* shrub (b) Dry heath (c)
Santillán (26)	30TUN2693	150	Asturias	Ash-willow (a) Tall-herb grass land (b)
Poncebos (27)	30TUN5291	300	Asturias	Holm-oak

Tresviso (27a)	30TUN6490	950	Cantabria	Graze-grassland (a) Tall-herb grass land (b) Ash-willow (c)
Aliva (28)	30TUN5379	1834	Cantabria.	Nardus grassland Rocky-slope
Fuente Dé (28a)	30TUN5278	1100	Cantabria	Beech forest (a) Graze-grassland (b)
Tielve (45)	30TUN5691	600	Asturias	Graze-grassland
Amieva (46)	30TUN2893	300	Asturias	Chesnutgrove
Arenas de Cabrales (31)	30TUN5395	150	Asturias	Chesnutgrove
Desf. de la Hermida (32)	30TUN6090	250	Cantabria	Rocky slope (a) Ash-willow (b) Tall-herb grass land (c)
Lebeña (33)	30TUN7185	300	Cantabria	Holm-oak (a) *Ulex* shrub (b)
CAMPURRIANO-CARRIONES Sector				
Vada (34)	30TUN6472	600	Cantabria	Oak forest
Vejo (35)	30TUN6072	1000	Cantabria	Beech forest
Pto. San Glorio (36)	30TUN5669	1609	León	Subalpine grassland (d) *Genista* shrub (b)
Pto. de Pandetrave (36a)	30TUN4874	1562	León	Beech forest
Predosa del Rey (37)	30TUN3956	1100	León	*Pinus* wood (a) Graze-grassland (b)
Pto. del Pando (38)	30TUN4054	1432	León	Dry heath (a) *Genista* shrub (b) Beech forest (c)
Prioro (39)	30TUN3951	1123	León	*Pinus* wood (a) Ash-willow (b)
Morgovejo (40)	30TUN3838	1050	León	Oak forest

Sta. María de Redondo (55)	30TUN8361	1150	Palencia	Graze-grassland (a) Beech forest (b)
Tremaya (56)	30TUN8059	1300	Palencia	Graze-grassland (a) Beech forest (b)

OTHERS

(Phytogeographic Cantabroatlántica Province -RIVAS-MARTINEZ et al., 1984-)

Locality (No)	U.T.M.	Altitude	Adm. Province	Phytogeogr. Sector (Phytogeogr. Subsect.)
Corao (41)	30TUP3200	100	Asturias	Galaico-Asturiano (Ovetense)
Unquera (42)	29TUP7902	50	Cantabria	Galaico-Asturiano (Ovetense)
La Pereda (43)	30TUP5607	150	Asturias	Galaico-Asturiano (Ovetense)
Alto de Tornería (44)	30TUP5205	500	Asturias	Galaico-Asturiano (Ovetense)
Misiegos (47)	30TTN8083	475	Asturias	Galaico-Asturiano (Ovetense)
La Colladona (48)	30TTN8884	800	Asturias	Galaico-Asturiano (Ovetense)
Bueres (49)	30TUN0986	700	Asturias	Galaico-Asturiano (Ovetense)
Collado de Arnicio (50)	30TUN0888	908	Asturias	Galaico-Asturiano (Ovetense)
Villamayor (51)	30TUP1303	100	Asturias	Galaico-Asturiano (Ovetense)
Llanes (52)	30TUP5708	25	Asturias	Galaico-Asturiano (Ovetense)
Meré (53)	30TUP4106	150	Asturias	Galaico-Asturiano (Ovetense)

The 42 localities were sampled monthly from mid spring (early June) to the middle of autumn (November). The very low temperatures and snow prevented the presence of cattle in the region during the rest of the year. As a result the activity of the dung beetles was in practice limited to the indicated period.

Moreover, in some sites outside of the Phytogeographic Orocantabrica Province, a complementary monthly sampling was conducted in 1988. These localities were designated as "Others" and located in the area between the Orocantabrica Province and the coastline (Phytogeographic Cantabroatlantica Province, Ovetense Subsector).

A total of 643 samples were carried out in the study area (588 in the Orocantabrica Province and 55 in the Ovetense Subsector), but only 131 samples were successful: 1 in the Naviano-Ancarense; 22 in the Laciano-Narcense; 47 in the Ubiñense; 14 in the Picoeuropeano; 37 in the Altocarriones; 21 in the Ovetense ("Others"). This is a result of the absence of large mammals in some sampling sites for various reasons: at the end of spring the cattle were not present at high altitudes; generally the cattle leave these mountainous areas in September; on some occasions the presence of cattle was sporadic during the whole period of this study.

The coprophagous species were captured directly in the dung and also in the soil examined under it. The specimens were kept in alcohol 70^{o} as a preserving fluid.

In order to study other groups of soil beetles, some baited pitfall traps were placed in the study localities. The bait consisted of wine, beer or liver. During 1986 and 1987 the traps were used from May to October. Although the traps were not placed specially to catch *Aphodiinae*, nevertheless the data obtained from this group are included in the present paper.

The chorological and biogeographical interpretation is according to HORION's (1958), PAWŁOWSKI's (1967) and STEBNICKA's (1976a; 1976b) nomenclature:

Cosmopolitan.– World wide distribution.

Holarctic.– Species distributed throughout the Palaearctic Region and North America.

Western-Palaearctic.– Species living in Europe, North Africa, Central Asia and Western Siberia.

Eurasian.– Species distributed throughout Europe reaching the Pacific Ocean from the Atlantic Ocean across the Siberian Region. Likewise are present in Japan and North China.

Eurosiberian.– Species distributed throughout Europe reaching the Central Region of Siberia.

Eurocaucasian.– Species distributed throughout Europe and Asia Minor to the Caucasian Mountains.

Ponto-Mediterranean.– Species living around the Black Sea and the Mediterranean basin.

European.– Species exclusively present in Europe.

Alpine (s.str.).– Mountain species living at over 1000 m of altitude.

Boreo-Montane.– Isolated species in the European mountains and the north of Europe (tundra).

Iberian.– Species exclusively known at present in the Iberian Peninsula.

Aphodiinae found in the Cantabrian Mountains. The numbers refer to the localities studied (see Table VI) and the capital letters to the Phytogeographic Subsectors (RIVAS-MARTINEZ et al. 1984): N-A (Naviano-Ancarense), L-N (Laciano-Narcense), U (Ubiñense), P (Picoeuropeano), A (Altocarrionés). "Others" include the neighbouring localities also investigated (Phytogeographic Cantabroatlantica Province). **ni** : number of specimens of each species collected in the subsectors. **nt** : total numbers of specimens collected in the Phytogeographic Orocantabrica Province. **Alt. r.** : Altitudinal range. *: Species new for the Cantabrian Mountains. **?**: Species previously cited from the area studied, but not captured during the period of sampling.

Species	N-A	ni	L-N	ni	U	ni	P	ni	A	ni	nt	Others	ni	Alt.r.
Aphodius ILLIGER, 1798														
A. erraticus (LINNAEUS,1758)	1,2,3	90	4,5,6,8.9	110	10,12,15,16,17,18, 19,21,22,23,24,25	283	26,28,28a,33	13	34,36,36a,37, 38,39,40,56	253	749	41,42,43,47 50,51,53	216	50-1834
A. scrutator (HERBST, 1789)	1,2	12	6,8,9	30	12,15,17,18,19, 21,22,23,24,25	53	33	1	34,36,36a,37 38,40	73	169	–	–	600-1690
A. subterraneus (LINNAEUS, 1758)	–	–	9	2	16	1	–	–	39,56	9	12	–	–	1050-1400
A. haemorrhoidalis (LINNAEUS, 1758)	1,2,3	31	4,5,6,8,9	120	12,13,15,16,17,18 19,21,22,23,24,25	207	26,28,28a,33	27	34,36,36a, 38,40,56	30	415	42,43,47,48 50,51	26	50-1834
A. fossor (LINNAEUS, 1758)	1,2	10	4,5,6,8	10	15,17,18,19,21,22 23,24,25	101	26,28,28a,33	34	36,36a,45	44	199	41,42,43,44,47 48,50,51,52	50	50-1834
A. frigidus BRISOUT, 1886	1	1	4,5,6,9	27	13,15,17,23,25	17	28,28a	3	34,36,36a,39	5	53	–	–	600-1690
A. lusitanicus ERICHSON, 1848	2	1	–	–	–	–	–	–	–	–	1	–	–	900
A. rufipes (LINNAEUS, 1758)	1,3	26	4,5,6,8,9	70	12,15,17,18,19 21,22,23,25	473	27a,28,28a,33	22	34,35,36,36a, 37,38,40	86	678	41,42,43,44,48 49,50,52,53	91	50-1690
A. carpetanus GRAELLS, 1847	–	–	8,9	48	–	–	–	–	39,40,55	5	53	–	–	1050-1425
A. luridus (FABRICIUS, 1775)	–	–	–	–	–	–	27a	4	–	–	4			950
A. depressus (KUGELANN, 1792)	1	9	5,6,9	10	13,18,19,21, 22,23,25	142	28,33	5	35,36,36a 37,38,39	26	192	43,44,47, 48,50	69	150-1690
A. heydeni HAROLD, 1871	–	–	5,6,9	36	19,21,23	11	–	–	–	–	47	–	–	1225-1690

Table II ctd.

Species	N-A	ni	L-N	ni	U	ni	P	ni	A	ni	nt	Others	ni	Alt.r.
A. mixtus VILLA, 1833	–	–	–	–	23	6	28	1	–	–	7	–	–	1625-1834
A. bonvouloiri cantabricus PITTINO, 1981	1	21	5,6,8	791	13,15,17,18 21,23	31	28	5	36	1	849	–	–	1310-1834
A. coenosus (PANZER, 1798)	–	–	–	–	–	–	–	–	–	–	–	41	1	100
**A. paracoenosus* BALTHASAR & HRUBANT, 1960	–	–	–	–	–	–	27,33	7	39	1	8	41,47,48,50	20	100-1123
A. pusillus (HERBST, 1789)	–	–	5,8,9	20	12,13,15,17, 21,23	20	26,27a,31	7	36,37,45	6	50	41,47,50	21	100-1625
A. quadrimaculatus (LINNAEUS, 1761)	–	–	–	–	13	1	–	–	–	1	–	–	–	1100
A. contaminatus (HERBST, 1783)	3	1	4,5,7,8,9	284	12,13,15,17,18 19,21,22,23,25	1068	28,28a,31,33	94	34,35,36,36a 37,39,40	350	1797	47,49,50	55	150-1625
A. affinis PANZER, 1823	3	138	7,8	21	12,13,15,17, 19,21	50	31,33	36	34,35,36,37, 39,40,45	163	408	41,47,48,49,50	200	100-1609
* *A. pictus* STURM, 1805	-	-	7	1	13	2	-	-	36a	1	4	-	-	1100-1562
A. conspurcatus (LINNAEUS, 1758)	-	-	4	2	15,17	4	-	-	36,37	5	11	-	-	1100-1609
A. tessulatus (PAYKULL, 1798)	-	-	-	-	17,21	13	-	-	-	-	13	-	-	1250-1310
A. distinctus (MÜLLER, 1776)	-	-	-	-	-	-	-	-	36	1	1	-	-	1.609
A. sticticus (PANZER,1798)	-	-	-	-	-	-	31	5	-	-	5	47	1	150-475
* *A. melanostictus* SCHMIDT, 1840	-	-	-	-	12	3	-	-	-	-	3	-	-	1000
A. prodromus (BRAHM, 1790)	3	1	8,9	110	12,13,21	5	31,33	3	39,40,45	40	159	41,51	22	100-1425
A. sphacelatus (PANZER, 1798)	3	3	5,8,9	206	12,15,17	8	28,31	3	36,36a,37,39	43	263	47,49,50	4	150-1425
A. consputus CREUTZER, 1799	-	-	-	-	12,13,15,17	171	33	125	34,35,39,40	151	447	-	-	300-1310
A. obscurus (FABRICIUS, 1792)	1	1	-	-	12,13,15,16 21,23,24	142	27a,28,28a	239	36,36a,39	31	369	50	11	950-1834
A. thermicola STURM, 1800	-	-	-	-	12,15	8	-	-	-	-	8	-	-	1000-1563
A. porcus (FABRICIUS, 1792)	-	-	-	-	-	-	--	-	-	-	-	49,50	2	
* *A. annamariae* BARAUD, 1982	-	-	9	1	12	1	-	-	40	1	3	-	-	
A. merdarius (FABRICIUS, 1775)	-	-	8	3	-	-	-	-	55	1	4	-	-	1150-1425

Species	N-A	ni	L-N	ni	U	ni	P	ni	A	ni	nt	Others	ni	Alt.r.
A. fimetarius (LINNAEUS, 1758)	1,2,3	153	4,5,6, 7,8,9	214	12,13,15,16, 17,18,21,22, 23,24,25	239	26,28,28a, 31,33	84	34,35,36,36a, 37,38,39,40, 45,55,56	290	980	41,42,43,44 47,48,49,50 51,52,53	255	150-1834
A. foetens (FABRICIUS, 1787)	-	-	8,9	9	18,19,21, 22,23,25	49	-	-	36a	1	59	49,50	22	700-1625
* *A. foetidus* (HERBST, 1783)	-	-	-	-	16	1	33	1	34,40	2	4	-	-	300-1400
A. ater (DE GEER, 1774)	-	-	5	1	25	1	27,27a,28	97	-	-	9	43,44,50	14	150-1550
A. borealis GYLLENHAL, 1827	-	-	9	1	13	1	28,31	26	55	2	30	-	-	150-1834
* *A. fasciatus* (OLIVIER, 1789)	-	-	-	-	-	-	-	-	35	5	5	-	-	1000
A. alpinus (SCOPOLI, 1763)	-	-	-	-	18,23	19	-	-	36	2	21	-	-	1379-1625
A. corvinus ERICHSON, 1848	-	-	-	-	13,15,23	3	-	-	35,39,40	8	11	57	1	1000-1625
A. rufus (MOLL, 1782)	1,3	79	4,5,6,8,9	69	12,13,15,17,18, 19,21,22,25	584	28,28a	54	34,35,36,36a, 37,38,39,40, 55,56	171	957	44,47,50	29	600-1834
A. granarius (LINNAEUS, 1767)	1,2,3	39	5,6,8,9	9	12,13,15, 16,17,21	40	28,33	4	34,36,40,45	15	107	41,42,50,51	10	50-1834
Oxyomus STEPHENS, 1839														
O. silvestris (SCOPOLI, 1763)	-	-	-	-	-	-	32	1	-	-	1	-	-	250
TOTAL		**616**		**2205**		**3758**		**902**		**1822**	**9303**		**1220**	

? *A.nitidulus* (FABRICIUS, 1792) : Cantabria, Asturias, León
? *A. constans* DUFTSCHMITD, 1805: León (Puerto de Tarna, Villanueva de laTercia)
? *A. satellitius* (HERBST, 1789) León (Soto y Amío)
? *A. quadriguttatus* (HERBST, 1783) León (Ribota de Sajambre)
? *A. elevatus* (OLIVIER, 1789) León (Soto y Amío)
? *A. reyi* REITTER, 1892 León (Vega de Gordón)

IV. RESULTS AND DISCUSSION

Recorded species

10,423 specimens belonging to 45 species were studied (Table II). They represent approximately 40% of the *Aphodiinae* fauna known at present in the Iberian Peninsula (BARAUD 1977; 1982; 1992). Most of them are eurytopic with a wide geographic distribution occasionally indicated in the Cantabrian Mountains (BAGUENA 1967; COLLADO 1975; 1977; BARAUD 1977; SALGADO & DELGADO-VELAYOS 1979; SALGADO & GALANTE 1987).

As a result of this study two species infrequently found in the Iberian Peninsula (BAGUENA 1967; BARAUD 1977; 1992) were caught: *Aphodius pictus* STURM, 1805 and *A. paracoenosus* BALTHASAR & HRUBANT, 1960.

A. pictus pointed out by LA FUENTE (1907), was rejected from his catalogue of *Coleoptera* (LA FUENTE 1918). This species is restricted to a few sites in middle and southern Europe, occurring in the humid and cold valleys. In the Cantabrian Mountains *A. pictus* occurs in autumn at three sites of humid forest above 1100 m (Table II).

The *A. paracoenosus* chorology is not yet properly known since, in the middle of this century, it was separated from *A. coenosus* (PANZER, 1798) (BALTHASAR & HRUBANT 1960). Recently recorded in the French Pyrenees (BARAUD 1977) and the Iberian Peninsula (VEIGA & MARTIN-PIERA 1988), *A. paracoenosus* occurs in the studied region in the early summer in open pastures from 100 to 1123 m (Table II).

Table III

List of the species captured with traps. The number of specimens obtained in cattle and sheep dung and in the different types of traps used is indicated. **Nt** : Total numbers of specimens of each species captured with traps. **Ni** : Total number of individuals studied. **%T** : Percentage of specimens captured with traps

	PITFALL TRAPS						
SPECIES	DUNG	Vine	Beer	Liver	Nt	Ni	%T
A.erraticus (L.)	748	-	1	-	1	749	0,13
A. haemorrhoidalis (L.)	414	-	1	-	1	415	0,24
A. frigidus BRIS.	47	3	3	-	6	53	11,3
A. lusitanicus ERICH.	-	-	1	-	1	1	100
A.rufipes (L.)	674	1	1	-	2	676	0,29
A. depresssus (KUG.)	191	-	1	-	1	192	0,52
A. heydeni HAR.	-	10	35	2	47	47	100
A. bonvouloiri cantabricus PITT.	815	13	21	-	34	849	4
A.obscurus (F.)	348	8	13	-	21	369	5,69
A. borealis GYLL.	29	-	1	-	1	30	3,33
A. granarius (L.)	106	-	1	-	1	107	0,16

Likewise four species were recorded for the first time in the Cantabrian Mountains: *Aphodius melanostictus* SCHMIDT, 1840, recorded in a few localities of the province of León (SALGADO & DELGADO-VELAYOS 1979), *Aphodius annamariae* BARAUD, 1982, *Aphodius foetidus* (HERBST, 1783) and *Aphodius fasciatus* (OLIVIER, 1789) (Table II). They were captured exclusively in the Phytogeographic Orocantabrica Province, with autumnal adult activity.

At the end of Table II, six species recorded from the Cantabrian Mountains are included (BAGUENA-CORELLA 1967; SALGADO & DELGADO-VELAYOS 1979). These species were not found in the study area.

Pitfall traps baited with wine, beer or liver were not very effective in the capture of *Aphodiinae* (Table III). Nevertheless two species: *A. heydeni* HAROLD, 1871 and *A. lusitanicus* ERICHSON, 1848, were collected exclusively with these traps.

Table IV

Values of indexes for localities in the Phytogeographic Orocantabrica Province. No = number of the site in the map of figure 2; H' = Shannon diversity index; E = Shannon equitability index; D_{Mg} = Margalef diversity index

No	Studied localities	H'	D_{Mg}	E
1	Pto Ancares	3.003	2.870	0.837
2	Pereda de Ancares	1.991	1.849	0.709
3	Candín	1.884	1.805	0.567
4	Caboalles de Abajo	2.504	2.306	0.790
5	Pto. Leitariegos	2.240	2.136	0.573
6	Laguna de Arbás	2.837	2.658.	0.791
7	Villar de Santiago	2.022	1.877	0.782
8	Pto. de la Magdalena	2.085	2.055	0.510
9	Murias de Paredes	3.150	3.039	0.741
12	Beberinos	2.873	2.734	0.702
13	Geras	2.715	2.451	0.664
15	Alto de Aralla	2.873	2.790	0.689
16	Aralla	2.169	1.832	0.772
17	Valle de Casares	3.367	3.214	0.823
18	Pto. Pajares	2.911	2.746	0.841
19	Brañillín	2.622	2.437	0.758
21	Cofiñal	2.635	2.559	0.658
22	Cofiñal	2.236	2.159	0.705
23	Pto. de las Señales	2.572	2.513	0.629
24	Crémenes	2.202	1.790	0.852
25	Alto del Pontón	2.792	2.710	0.807
26	Santillán	1.829	1.522	0.787
28	Aliva	2.297	2.198	0.574
28a	Fuente Dé	2.852	2.536	0.899
31	Arenas de Cabrales	2.337	2.041	0.703
32	Desf. de la Hermida	1.000	0.500	1.000
33	Lebeña	2.215	2.098	0.581
45	Tielve	2.010	1.724	0.777
34	Vada	2.286	2.195	0.660
35	Vejo	2.151	2.007	0.678
36	Pto. San Glorio	3.045	2.924	0.716
36a	Pto. de Pandetrave	3.182	2.968	0.835
37	Predosa del Rey	2.434	2.306	0.703
38	Pto. del Pando	2.775	2.532	0.988
39	Prioro	2.855	2.690	0.750
40	Morgovejo	3.183	3.029	0.795

Table V

Comparison among the Phytogeographic Subsectors in the Orocantabrica Province. H' = Shannon diversity index; E = Shannon equitability index; D_{Mg} = Margalef diversity index

Phytogeographic Subsector	H'	D_{Mg}	E
NAVIANO-ANCARENSE	3.004	2.929	0.735
LACIANO-ANCARENSE	3.043	2.929	0.735
UBIÑENSE	3.382	3.353	0.670
PICOEUROPEANO	3.464	3.375	0.746
ALTOCARRIONES	3.569	3.516	0.727

Diversity and richness

The richness of *Aphodiinae* species in the Cantabrian Region is supported by the range of phytoclimatic conditions and its special geographic situation in the Iberian Peninsula.

Specific diversity expressed by the Shannon index H', the Margalef index D_{Mg} and the equitability index E (MAGURRAN 1989), gives a good idea of the structure and organization of the dung beetle communities and the stability of environmental conditions (DAGET 1976).

In the study area, during the whole of the beetle activity period, the highest values of H' and E (H' ranging from 3.37 to 3.00; E from 0.84 to 0.72) correspond to communities occurring at the eight highest sites (exceeding 1000 m) (Table IV). The diversity index H' is high in 84% of the studied localities (32 sites; H' from 3.37 to 2.02). They correspond

Table VI

Number of species and specimens of *Aphodiinae* captured in the Sectors and Subsectors of the Phytogeographic Orocantabrica Province. % spp. : percentage of species. % indiv.: percentage of specimens

OROCANTABRICA	No species	% spp.	No individuals	% indiv.
LACIANO-ANCARENSE	28	66,7	2821	30,5
Naviano Ancarense	17	40,4	616	6,7
Laciano Narcense	26	61,9	2205	23,8
UBIÑENSE-PICOEUROPEANO	36	85,7	4517	48,8
Ubiñense	34	80,9	3758	40,6
Picoeuropeano	25	59,5	759	8,2
CAMPURRIANO-CARRIONES	32	76,1	1822	19,9
Altocarrionés	32	76,1	1822	19,9
TOTAL	42	100	9.160	100

to stable environments for *Aphodiinae* taxocoenosis, with a large mammalian fauna living here from spring to autumn. The lowest values of H' (from 1.99 to 1.0) correspond to disturbed sites where large mammals occur occasionally.

The equitability index (E) is generally high in the Cantabrian Mountains sites (E ranging from 0.99 to 0.51). The specific richness expressed by Margalef index D_{Mg} varied according to the sites but remained high throughout the whole territory (D_{Mg} from 3.04 to 1.52, with only one exception where D_{Mg} was 0.50) (Table IV).

The Cantabrian Mountains support a high biodiversity. Table V shows the values of H' and E in the five phytogeographic subsectors. When these phytogeographic divisions are considered individually, the highest biodiversity was found in the eastern part: Altocarriones (H' 3.57; D_{Mg} 3.52), Picoeuropeano (H' 3.46; D_{Mg} 3.38) and Ubiñense (H' 3.38; D_{Mg} 3.35). These subsectors include ecosystems ranging from high sites in the Picos de Europa to localities on the border of the Mediterranean region and also ways of communication between the northern and southern slopes of the mountains with "corridor" dispersion effects. All these special features induce the richness of ecological niches and the *Aphodiinae* taxocoenosis.

The highest specific richness corresponds to the Ubiñense Subsector where 80.9% of the *Aphodiinae* (34 species) found in the Cantabrian Mountains were present (Table VI). This results from the variety of the environment, with typical high mountain species found together with low altitudinal species and endemics.

The Laciano-Ancarense sector was the poorest for the *Aphodiinae* species (Table VI). Situated in the west part of the Cantabrian Mountains, it was the driest sector and the vegetation reflects this particularity. However this area supports the higher rate of endemism concerning Iberian *Aphodiinae* (Table VIII).

Phenology

The highest specific richness of *Aphodiinae* was found in the June/July period (Table VII). The activity of some species reached a maximum in the late spring (June): *A. erraticus, A. frigidus, A. depressus, A. heydeni, A. paracoenosus* and *A. pusillus.* Another group of species was mostly active in the early summer (July)*: A. haemorrhoidalis, A. fossor, A. carpetanus, A. mixtus, A. bonvouloiri cantabricus, A. obscurus, A. foetens, A. borealis* and *A. alpinus.*

Three species, *A. scrutator, A. rufipes* and *A. rufus* begin to be active in the late spring, but with a maximun in the late summer (September).

Likewise autumn corresponds to another period of activity for *Aphodiinae* species. Some species emerge at the end of summer (September-October) : *A. contaminatus, A. affinis, A. pictus, A. prodromus, A. sphacelatus* and *A. consputus.* In autumn two species living above 1000 m, reached their maximum activity : *A. contaminatus* and *A. prodromus.* Later, in the middle of autumn (November), when cattle and sheep had left most of the area, *A. sphacelatus, A. affinis* and *A. consputus* were at their maximum activity. Also in November, *A. conspurcatus* and *A. tessulatus* initiated their activity.

Table VII

Number of specimens of each species monthly captured during the study. Orocantabrica: Phytogeographic Orocantabrica Province; Others: neighbouring localities (Phytogeographic Cantabroatlantica Province)

	OROCANTABRICA							OTHERS						
SPECIES / MONTH	V	VI	VII	VIII	IX	X	XI	V	VI	VII	VIII	IX	X	XI
Aphodius ILLIGER, 1798														
A. erraticus (LINNAEUS,1758)	-	329	281	109	27	3	-	-	3	83	42	8	91	-
A. scrutator (HERBST, 1789)	-	7	37	45	79	1	-	-	-	19	-	-	-	-
A. subterraneus (LINNAEUS, 1758)	-	5	4	3	-	-	-	-	-	-	-	-	-	-
A. haemorrhoidalis (LINNAEUS, 1758)	-	87	208	56	64	-	-	-	-	36	4	2	-	-
A. fossor (LINNAEUS, 1758)	-	75	114	8	5	-	-	-	-	45	9	-	-	-
A. frigidus BRISOUT, 1886	-	37	9	4	3	-	-		-	-	-	-	-	-
A. lusitanicus ERICHSON, 1848	-	-	-	1	-	-	-	-	-	-	-	-	-	-
A. rufipes (LINNAEUS, 1758)	-	10	92	91	481	-	2	-	-	22	50	11	10	-
A. carpetanus GRAELLS, 1847	-	1	52	-	-	-	-	-	-	-	-	-	-	-
A. luridus (FABRICIUS, 1775)	-	-	-	-	-	-	-	-	-	4	-	-	-	-
A. depressus (KUGELANN, 1792)	-	94	31	15	49	-	3	-	-	60	9	-	-	-
A. heydeni HAROLD, 1871	-	43	4	-	-	-	-	-	-	-	-	-	-	-
A. mixtus VILLA, 1833	-	1	6	-	-	-	-	-	-	-	-	-	-	-
A. bonvouloiri cantabricus PITTINO, 1981	-	236	604	9	-	-	-	-	-	-	--	-	-	-
A. coenosus (PANZER, 1798)	-	-	-	-	-	-	-	-	-	1	-	-	-	-
A. paracoenosus BALTHASAR & HRUBANT, 1960	-	6	2	-	-	-	-	-	12	8	-	-	-	-
A. pusillus (HERBST, 1789)	-	42	8	-	-	-	-	-	13	11	-	-	1	-
A. quadrimaculatus (LINNAEUS, 1761)	-	1	-	-	-	-	-	-	-	-	-	-	-	-
A. contaminatus (HERBST, 1783)	-	-	-	4	1056	365	372	-	-	-	-	37	10	8
A. affinis PANZER, 1823	-	-	-	1	2	180	225	-	-	-	-	111	78	11
A. pictus STURM, 1805	-	-	-	-	1	-	3	-	-	-	-	-	-	-
A. conspurcatus (LINNAEUS, 1758)	-	-	-	-	-	-	11	-	-	-	-	-	-	-
A. tessulatus (PAYKULL, 1798)	-	-	-	-	-	1	12	-	-	-	-	-	-	-
A. distinctus (MÜLLER, 1776)	-	-	-	-	-	-	1	-	-	-	-	-	-	-
A. sticticus (PANZER,1798)	-	-	5	-	-	-	-	-	-	-	1	-	-	-
A. melanostictus SCHMIDT, 1840	-	-	-	-	-	3	-	-	-	-	-	-	-	-
A. prodromus (BRAHM, 1790)	1	94	21	-	-	38	5	-	4	-	-	-	16	2
A. sphacelatus (PANZER, 1798)	3	55	2	-	2	52	149	-	-	-	-	-	3	1
A. consputus CREUTZER, 1799	-	-	-	-	-	52	395	-	-	-	-	-	-	-
A. obscurus (FABRICIUS, 1792)	9	94	181	38	46	-	1	-	-	44	11	-	-	-
A. thermicola STURM, 1800	-	-	-	-	-	7	1	-	-	-	-	-	-	-
A. porcus (FABRICIUS, 1792)	-	-	-	-	-	-	-	-	-	-	-	1	1	-
A. annamariae BARAUD, 1982	-	-	-	-	3	-	-	-	-	-	-	-	-	-
A. merdarius (FABRICIUS, 1775)	-	2	2	-	-	-	-	-	-	-	-	-	-	-
A. fimetarius (LINNAEUS, 1758)	2	331	265	132	124	60	66	-	20	215	33	1	4	6
A. foetens (FABRICIUS, 1787)	-	2	45	11	1	-	-	-	-	20	1	1	-	-
A. foetidus (HERBST, 1783)	-	-	1	-	-	3	-	-	-	-	-	-	-	-
A. ater (DE GEER, 1774)	-	4	5	-	-	-	-	-	2	102	-	-	-	-
A. borealis GYLLENHAL, 1827	-	2	28	-	-	-	-	-	-	-	-	-	-	-
A. fasciatus (OLIVIER, 1789)	-	-	-	-	-	5	-	-	-	-	-	-	-	-
A. alpinus (SCOPOLI, 1763)	-	3	13	4	1	-	-	-	-	-	-	-	-	-
A. corvinus ERICHSON, 1848	-	-	5	1	2	2	1	-	-	1	-	-	-	-
A. rufus (MOLL, 1782)	-	11	81	160	701	2	2	-	-	17	14	-	-	-
A. granarius (LINNAEUS, 1767)	-	78	29	-	-	-	-	-	-	10	-	-	-	-
Oxyomus STEPHENS, 1839														
O. silvestris (SCOPOLI, 1763)	-	1	-	-	-	-	-	-	-	-	-	-	-	-
TOTAL SPECIMENS	**15**	**1651**	**2132**	**692**	**2647**	**774**	**1249**	**-**	**54**	**698**	**174**	**172**	**214**	**28**
TOTAL SPECIES	**4**	**27**	**28**	**18**	**18**	**15**	**14**	**-**	**6**	**17**	**10**	**8**	**8**	**5**

Table VIII

Origin and composition of the biogeographic elements in each of the Phytogeographic Subsectors studied and the whole (Total) Orocantabrica Province

BIOGEOGRAPHIC ELEMENTS	Phytogeographic Subsectors					TOTAL	Altitude ranges (metres)				SPECIES
	Nav. Anc.	Lac. Narc.	Ubiñ.	Pico europ.	Altoc.	PROV. OROC.	<500	500-1000	1000-1500	>1500	
Cosmopolitan	1	1	1	1	1	1	1	1	1	1	*A. granarius*
Holartic	6	7	7	6	7	7	5	5	6	3	*A. erraticus, A. subterraneus, A. haemorrhoidalis, A. fossor, A. rufipes, A. prodromus, A. fimetarius*
Western-Palearctic	-	2	3	2	3	5	2	2	3	1	*A. pictus, A. melanostictus, A. consputus, A. merdarius, Oxyomus sylvestris*
Eurasian	-	2	2	2	2	3	3	2	2	2	*A. pusillus, A. ater, A. fasciatus*
Eurosiberian	2	3	3	3	4	4	3	3	3	3	*A. depressus, A. distinctus, A. borealis A. rufus*
Eurocaucasian	4	4	7	6	6	9	4	6	6	4	*A. scrutator, A. paracoenosus, A. contaminatus, A. tessulatus, A. sticticus, A. sphacelatus, A. obscurus, A. thermicola, A. foetens*
Ponto-Mediterranean	1	1	3	2	2	3	2	2	3	1	*A. foetidus, A. quadrimaculatus, A. affinis*
European	-	1	2	-	2	2	-	1	2	2	*A. conspurcatus, A. corvinus*
Alpine (s.str.)	-	-	1	1	-	1	-	-	-	1	*A. mixtus*
Boreo-Montane	-	-	1	-	1	1	-	-	1	1	*A. alpinus*
Iberian	3	5	4	2	4	6	-	1	5	3	*A. frigidus, A. lusitanicus, A. carpetanus, A. heydeni, A. bonvouloiri cantabricus, A. annamariae*
TOTAL SPECIES	**17**	**26**	**34**	**25**	**32**	**42**	**20**	**23**	**32**	**22**	

Biogeography considerations

Most of the species found in the Cantabrian Mountains were ubiquitous, with a wide distribution area (Table VIII). Eurocaucasian elements dominated (21.4%), followed by Holartic (16.7%), Iberian (14.2%), Western Palaeartic (11.8%) and Eurosiberian elements (9.5%). The presence of Mediterranean elements was low, as was that of European species "sensu lato" (European, Alpine and Boreo-Montane) which comprised only 9.5% of the total.

With respect to their altitudinal distribution in the Orocantabrica Province, 76% of species occurred in the 1000-1500 m altitude range (Table I). In this altitude range most of the whole biogeographic elements (excepting Alpine) were found. Above 1500 m the number of species decreased (57% of total were present) belonging to Holartic (50%), Western-Palaearctic (65%), Eurocaucasian (65%) and Iberian elements (60%).

Endemic Iberian species appeared above 1000 m, except *A. frigidus* which was found from 600 m altitude to 1690 m.

The historical changing of the structure and landscape, together with the diversity of the present ecosystems, are factors which determine a montane entomofaunal distribution, like that of an insular fauna (HALFFTER 1987; LUMARET & STIERNET 1992).The temperate regions of Europe were drastically affected by the Pleistocene glaciations with the vegetation zones contracting and expanding according to the changing climate (HOWDEN 1985). The fossil material shows that in Europe most insects migrated with changing climate and their populations were restricted to small and located areas with their environmental requirements (COOPE 1970; 1977; 1978).

The Cantabrians are the oldest mountains in Europe. They arose in the Carboniferous period with the Herzinian Orogenesis and they constituted the first emerged territory of the Iberian Peninsula (Macizo Hesperico). In the Eocene-Oligocene period (50-40 millions years) these mountains suffered the Alpine Orogenesis but it was not too important in this Iberian area. The Pleistocene glaciations also affected this region and in the Iberian Peninsula the end of the last Pleistocene glaciation took place at 14,000 years ago (TURNER & HANNON, 1988).

The first true coprophagous *Aphodius* are not known before the Lower Oligocene period in Baltic amber (CAMBEFORT 1991). From historical viewpoint, the composition of the *Aphodiinae* taxocoenosis from the Cantabrian Mountains can be considered as the result of post-glacial immigration with the exception of some endemic species. Probably these endemic species represent the remaining relic species of the Tertiary or Plio-Pleistocene period which have taken refuge in the Cantabrian Mountains and at present are considered as orophilus endemics. The mountain systems constitute both centres of differentiation and refuges for dung beetles (LUMARET & STIERNET 1991). An example is *Aphodius bonvouloiri,* a species now known only from the mountains of the Iberian Peninsula (Iberian Central System *A.bonvouloiri bonvouloiri* HAROLD, 1860 and the Cantabrian Mountains *A. bonvouloiri cantabricus* PITTINO, 1981), but which was an abundant dung beetle in the British Isles, 45,000 years old during the interglaciation Upton Warren (COOPE 1979; COOPE & ANGUS, 1975; PAULIAN 1988). Probably the subspeciation took place after the last glaciation, since studies on some beetle groups have shown

that an isolation period of 5,000 years may be long enough for the development of genetically isolated taxa (NAGEL 1986).

Some previous studies have shown the entomofaunistic richness of this Iberic region (GALANTE & RODRIGUEZ-MENENDEZ 1989; MARCOS-GARCIA 1990a; 1990b; NIETO-NAFRIA et al. 1990; 1991; NUEZ et al. 1990). The present study shows that the *Aphodiinae* diversity of the Cantabrian Range is probably one of the richest in the Iberian Peninsula. In this way we can conclude the necessity of establishing specific programmes to preserve areas and some habitats in this region, particularly in the Picos de Europa (Altocarrionés and Picoeuropeano Phytogeographic Subsectors) where the highest diversity was found.

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