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A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae)

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We test whether there is a significant correspondence between the morphology of ground beetles and their life traits, as measured with phylogenetic independent contrasts. Seven life traits of known functional importance, and the morphospace defined by 87 species of ground beetles occurring in Scottish agricultural land were investigated using two different systematic arrangements as an approximation to the phylogeny of the group. The morphospace was previously defined with the first three multivariate ordination axes of 13 quantitative measures of the shape of the body, hind legs, eyes and antennae, plus total length as a surrogate measurement of size. Results were found to be largely coherent irrespective of the classification used, demonstrating the robustness of the associations despite possible changes in the knowledge of the detailed phylogeny of the group. The first ordination axis of the morphospace was significantly related to diet, and the second to diel activity. When individual morphological measures were compared, diet of the adult was most significantly related with length of the hind legs. The variable most related with diel activity was the length of the antennae. Species with overwintering larvae and species with two year cycles were larger than species which either overwinter solely as adults or which always complete their development in one year.

1. Introduction

The functional relationship between the morphology of the species and their ecological or physiological characteristics has been a major subject in comparative biology (e.g., Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Wainwright & Reilly 1994). The recognition of the functional diversity in addition to the taxonomic or ecological diversity contributes to the understanding of ecosystem functions and processes, which may depend more on the functional diversity, or the presence of key functional groups or species, than on taxonomic diversity (Grime 1997, Tilman *et al.* 1997). The presence or absence of particular functional groups, and the factors controlling their distribution are also important from an agricultural change perspective, where farmland management policies for the future can be modified to enhance functional diversity once their relationships with the wider environment are identified. In this sense, the identification of possible functional associations between morphological and life trait characteristics, as measured with phylogenetic methods, is a significant step towards the understanding of the functional diversity of a monophyletic group of organisms (Harvey & Pagel 1991, Reilly & Wainwright 1994, Koehl 1996).

Previous studies of carabids deal with a limited set of morphological characters in a few species, selected *a priori* for their supposed strong adaptive value. For example, the relationship between feeding behaviour and the morphology of the feeding apparatus (e.g., Forsythe 1983a, Evans & Forsythe 1985, Bauer 1985a, Forsythe 1991), or the morphology of the eyes (Bauer 1981, 1985b, Bauer & Kredler 1993, Morwinsky & Bauer 1997). More general relationships, based on a larger number of species, deal basically with the morphology of the hind legs in relation with the biomechanics of running and pushing (Evans 1977, 1986, Forsythe 1981, 1983b, 1987, Evans & Forsythe 1984, Evans 1994), with no or little discussion of the implications for the wider biology of the species. In addition, none of these comparative studies used a phylogenetic approach to avoid the possible bias introduced by the non-independence of characters in closely related species (Harvey & Pagel 1991).

The aim of this paper is to study the relationships between selected life traits of the ground beetle species of family Carabidae found in Scottish agricultural land and their morphological diversity, with the use of phylogenetic independent contrasts. The morphological diversity of the same species set was described by Ribera *et al.* (1999) with the scores of the ordination axes of 13 quantitative morphological variables, which are used here (together with a measure of size and five qualitative variables) to characterise their morphology. Carabids are an important component of the ground-dwelling fauna of most areas of the world, and provide a suitable model system for investigation of wider ecological or evolutionary problems (*see* e.g., Lövei & Sunderland 1996 or Niemelä 1996 for recent reviews).

2. Material and methods

2. 1. Material

The species included in the study were collected between 1995 and 1996 using pitfall traps in habitats ranging from intensive cereal fields to upland moorland in 63 localities around Scotland (*see* Abernethy *et al.* 1996 for more details). Sites were representative of the range of agricultural habitats in Scotland, and the species studied constitute the great majority of the carabids living in them (as estimated with rarefaction methods, Downie *et al.* 1998). The British, and in particular the Scottish fauna of ground beetles is clearly impoverished, but constitutes a good representation of the wider family, with species in all major taxonomic groups represented in the western Palaearctic fauna. Our study gives a general framework in which other species with similar morphologies can be easily accommodated. Species with deviating morphologies living in particular habitats (e.g., arboricolous species, such as *Dromius*) were not included in the study, to avoid the strong bias they would introduce in the comparative analysis. Although carabids do not form a community in the ecological sense because of their wide range of resource use, they form a well defined evolutionary unit with a similar body plan, suitable for comparative studies (Lövei & Sunderland 1996).

2.2. Description of the morphospace defined by the studied species

The morphological space defined by the species included in the analysis was described by Ribera *et al.* (1999) using thirteen linear measurements of the 87 species included in the study (Tables 1 and 2), which represents almost half the Scottish fauna of Carabids, and a much wider proportion of

Table 1. List of the species included in the analysis, with the values of the life trait variables and the scores of the first three ordination axes of the morphospace (*see* Ribera *et al*. 1999). Nomenclature follows Kryzhanovskij *et al.* (1995) and Lindroth (1985, 1986); names of common use in UK are given in brackets; unknown traits marked with '?'. See Table 3 for the codes of the variables. Life trait data obtained from Lindroth (1945, 1974), Huizen (1977), Thiele (1977), Luff (1978), Jones (1979), Hengeveld (1980), Houston (1981), Desender (1982, 1983), Desender *et al.* (1984), Desender and Pollet (1985), Pollet and Desender (1987), Pollet *et al.* (1987), Brandmayr (1990), Den Boer and Den Boer-Daanje (1990), Desender and Alderweirldt (1990), Kegel (1990), Bauer and Kredler (1993), Sydmonson *et al.* (1996), Luff (1998), and Martin Luff (personal communication 1997).

No.	Species	Total size mm/10	Factor 1	Factor 2	Factor 3	OVE	CYC	FOA	DAY	BRE	EME	ACT
1	*Cicindela campestris* Linnaeus, 1758	108.0	2.39	1.86	1.44	2	1	2	1	1	2	1
2	*Cychrus caraboides* (Linnaeus, 1758)	138.1	1.22	–1.22	1.53	2	2	2	3	3	2	2
3	*Carabus granulatus* Linnaeus, 1758	154.5	0.68	–0.27	0.64	1	1	2	3	1	2	2
4	*Carabus nitens* Linnaeus, 1758	133.6	–0.45	0.09	0.00	1	1	2	1	2	2	5
5	*Carabus nemoralis* O. Müller, 1764	184.5	0.05	0.52	–0.05	2	1	2	3	1	2	2
6	*Carabus problematicus* Herbst, 1786	193.9	0.53	–0.04	1.03	2	2	2	3	2	1	2
7	*Carabus arvensis* Herbst, 1784	150.4	0.31	0.08	0.20	1	1	2	1	1	2	2
8	*Carabus violaceus* Linnaeus, 1758	208.1	–0.41	–0.64	1.57	2	1	2	3	3	2	2
9	*Carabus glabratus* Paykull, 1790	201.8	–0.33	–0.35	0.89	2	2	2	2	2	3	2
10	*Leistus fulvibarbis* Dejean, 1826	63.0	1.39	–0.07	0.67	2	1	1	3	3	1	2
11	*Leistus terminatus* (Hellwig in Panzer, 1793) (= *L. rufescens*)	52.8	1.71	–0.34	0.63	2	1	1	3	3	2	2
12	*Nebria brevicollis* (Fabricius, 1792)	98.9	0.69	0.50	0.81	2	1	2	3	3	1	5
13	*Nebria salina* Fairmaire & Laboulbène, 1854	93.9	0.87	0.41	0.76	2	1	2	3	3	1	2
14	*Notiophilus palustris* (Duftschmid, 1812)	45.1	0.34	2.50	1.11	2	1	1	1	3	2	2
15	*Notiophilus substriatus* Waterhouse, 1833	42.1	0.25	2.18	1.09	1	1	1	1	1	3	2
16	*Notiophilus biguttatus* (Fabricius, 1779)	42.7	0.33	2.49	1.06	2	1	1	1	2	2	2
17	*Notiophilus aquaticus* (Linnaeus, 1758)	45.6	0.21	2.00	1.21	?	1	1	1	1	2	?
18	*Notiophilus germinyi* Fauvel, 1863	43.1	0.87	3.15	0.52	1	1	1	1	1	2	2
19	*Elaphrus lapponicus* Gyllenhal, 1810	79.7	0.28	1.05	1.95	1	1	2	1	2	2	1
20	*Elaphrus uliginosus* Fabricius, 1775	77.2	0.10	1.67	1.42	1	1	2	1	1	2	2
21	*Elaphrus cupreus* Duftschmid, 1812	72.9	0.41	1.54	1.39	1	1	2	1	1	2	2
22	*Loricera pilicornis* (Fabricius, 1775)	62.8	0.79	–1.09	0.39	1	1	1	2	2	3	2
23	*Dyschiroides globosus* (Herbst, 1783) (= *Dyschirius globosus)*	22.7	–2.63	0.26	2.30	1	1	2	1	1	2	4
24	*Clivina fossor* (Linnaeus, 1758)	50.3	–3.61	–1.44	2.16	2	1	2	2	1	3	2
25	*Miscodera arctica* (Paykull, 1798)	44.8	–2.32	–0.42	2.38	2	1	2	?	3	2	1
26	*Patrobus atrorufus* (Ström, 1768)	65.3	0.13	–0.54	0.39	2	2	2	3	3	2	2
27	*Patrobus assimilis* Chaudoir, 1844	62.7	–0.53	–1.03	0.15	2	2	2	?	2	2	2
28	*Trechoblemus micros* (Herbst, 1784) (= *Trechus micros*)	32.9	1.00	–1.83	–0.30	2	1	1	?	2	2	4
29	*Trechus rubens* (Fabricius, 1792)	44.0	1.01	–1.39	–0.44	1	1	2	3	3	2	5
30	*Trechus quadristriatus* (Schrank, 1781)	32.5	0.49	–0.88	–0.97	2	1	1	3	3	2	4
31	*Trechus obtusus* (Erichson, 1837)	30.7	0.88	–0.46	–1.55	2	1	1	3	3	1	2
32	*Asaphidion flavipes* (Linnaeus, 1761)	36.9	1.16	0.75	0.78	1	1	1	1	1	2	2
33	*Bembidion lampros* (Herbst, 1784)	30.6	0.74	0.59	0.12	1	1	1	1	1	2	1
34	*Bembidion obtusum* Serville, 1821	24.9	0.37	0.19	–0.38	1	1	2	2	4	2	1
35	*Bembidion aeneum* Germar, 1824	35.6	0.52	–0.11	–0.30	2	1	2	?	1	2	1
36	*Bembidion guttula* (Fabricius, 1792)	28.2	0.53	–0.03	–0.14	1	1	2	3	1	2	1
37	*Bembidion mannerheimi* C.R. Sahlberg, 1834	25.9	0.86	0.69	–0.85	1	1	2	?	1	2	1
38	*Bembidion tetracolum* Say, 1823	57.9	0.43	–0.78	–0.05	1	1	2	3	1	2	1
39	*Bembidion bruxellense* Wesmael, 1835	40.3	0.24	–0.86	0.45	1	1	2	1	1	2	1
40	*Stomis pumicatus* (Panzer, 1796)	57.2	–0.60	–1.34	0.43	1	1	2	3	1	2	1
41	*Poecilus versicolor* (Sturm, 1824) (= *Pterostichus versicolor*)	94.5	–0.29	0.01	–1.05	1	1	2	1	2	3	1

Continued

Table 1. Continued.

No.	Species	Total size mm/10	Factor 1	Factor 2	Factor 3	OVE	CYC	FOA	DAY	BRE	EME	ACT
42	*Pterostichus aethiops* (Panzer, 1797)	99.3	0.23	0.30	–1.55	2	1	2	3	2	3	4
43	*Pterostichus madidus* (Fabricius, 1775)	117.5	–0.41	0.39	–1.05	2	2	3	3	3	2	2
44	*Pterostichus cristatus* (Dufour, 1820)	119.1	0.75	–0.19	–1.07	2	1	2	3	3	2	2
45	*Pterostichus vernalis* (Panzer, 1796)	55.6	–0.10	–0.41	–0.71	1	1	2	3	1	3	1
46	*Pterostichus melanarius* (Illiger, 1798)	125.1	–0.88	0.24	–0.78	2	2	2	2	3	1	2
47	*Pterostichus niger* (Schaller, 1783)	151.9	–0.10	–0.87	–0.29	2	1	2	3	3	1	2
48	*Pterostichus nigrita* (Paykull, 1790)	87.8	–0.45	–0.30	–0.80	2	1	2	3	1	2	2
49	*Pterostichus rhaeticus* Heer, 1838	77.0	–0.38	0.16	–1.02	2	1	2	3	1	2	?
50	*Pterostichus adstrictus* Eschscholtz, 1823	96.1	–0.46	–0.10	0.21	2	1	2	3	2	2	2
51	*Pterostichus strenuus* (Panzer, 1797)	52.3	–0.56	–0.52	–0.11	1	1	2	3	1	2	1
52	*Pterostichus diligens* (Sturm, 1824)	49.1	–0.86	–0.52	–0.11	2	1	2	3	1	3	1
53	*Calathus rotundicollis* Dejean, 1828 (= *C. piceus*)	77.8	0.78	–0.52	–0.29	2	1	2	3	3	1	2
54	*Calathus fuscipes* (Goeze, 1777)	97.4	0.05	–0.38	–0.31	2	2	2	3	3	2	2
55	*Calathus melanocephalus* (Linnaeus, 1758)	65.2	0.00	–0.80	–0.29	2	1	2	3	3	2	5
56	*Calathus micropterus* (Duftschmid, 1812)	63.9	0.41	–1.05	–0.28	2	1	2	3	3	2	2
57	*Laemostenus terricola* (Herbst, 1783)	114.7	0.30	–0.99	0.70	2	1	2	3	3	2	2
58	*Synuchus vivalis* (Illiger, 1798) (= *S. nivalis*)	56.1	–0.10	–0.84	–0.61	2	1	4	3	3	2	2
59	*Olisthopus rotundatus* (Paykull, 1790)	56.5	0.17	–0.70	–0.74	2	1	2	?	3	2	2
60	*Anchomenus dorsalis* (Pontoppidan, 1763) (= *Agonum dorsale*)	55.5	1.87	–0.85	0.53	1	1	2	3	1	2	2
61	*Platynus assimile* (Paykull, 1790) (= *Agonum assimile*)	89.2	0.92	–1.25	0.30	1	1	2	3	1	2	2
62	*Agonum marginatum* (Linnaeus, 1758)	82.5	0.55	–0.80	0.34	1	1	2	1	1	2	2
63	*Agonum muelleri* (Herbst, 1784)	65.0	0.38	–0.58	–0.46	1	1	2	2	1	2	2
64	*Agonum viduum* (Panzer, 1797)	67.2	0.58	–0.50	–0.28	1	1	2	?	1	2	2
65	*Agonum dolens* (C.R. Sahlberg, 1827) (= *A. moestum*)	67.6	0.73	–0.51	–0.37	1	1	2	?	1	2	2
66	*Agonum fuliginosum* (Panzer, 1809)	50.9	1.05	–0.68	–0.28	1	1	2	?	1	3	1
67	*Agonum gracile* (Sturm, 1824)	48.8	0.56	–1.43	0.55	1	1	2	?	1	2	1
68	*Amara plebeja* (Gyllenhal, 1810)	62.8	–0.62	0.77	–0.65	1	1	4	1	1	2	2
69	*Amara eurynota* (Panzer, 1797)	90.5	–0.73	1.16	–1.70	2	1	4	1	4	2	3
70	*Amara ovata* (Fabricius, 1792)	79.5	–0.95	0.72	–1.40	1	1	4	?	1	2	1
71	*Amara apricaria* (Paykull, 1790)	68.5	–1.55	0.79	–0.76	2	1	4	3	3	2	2
72	*Amara bifrons* (Gyllenhal, 1810)	54.4	–1.00	0.47	–1.16	2	1	4	3	3	2	2
73	*Amara familiaris* (Duftschmid, 1812)	58.6	–1.10	0.57	–1.02	1	1	4	1	1	2	1
74	*Amara aenea* (De Geer, 1794)	62.5	–1.07	0.93	–1.27	1	1	4	1	1	2	2
75	*Amara communis* (Panzer, 1797)	63.2	–1.27	1.04	–1.16	2	1	4	1	1	2	1
76	*Amara lunicollis* Schiödte, 1837	69.7	–1.43	0.30	–1.00	1	1	4	1	1	2	2
77	*Curtonotus aulicus* (Panzer, 1797) (= *Amara aulica*)	102.3	–0.66	1.15	–1.18	2	1	4	3	3	2	2
78	*Harpalus rufipes* (De Geer, 1774)	114.7	–0.81	0.50	–0.95	2	2	3	3	3	2	2
79	*Harpalus affinis* (Schrank, 1781)	78.7	–0.96	0.60	–1.59	2	1	4	3	1	2	1
80	*Harpalus latus* (Linnaeus, 1758)	75.8	–0.85	0.86	–1.95	1	1	4	3	2	2	4
81	*Dicheirotrichus* (= *Trichocellus*) *cognatus* (Gyllenhal, 1827)	37.3	–0.64	–0.65	0.57	1	1	3	?	4	2	1
82	*Dicheirotrichus* (= *Trichocellus*) *placidus* (Gyllenhal, 1827)	38.8	–0.32	–0.64	0.52	1	1	3	?	4	2	4
83	*Bradycellus ruficollis* (Stephens, 1828)	28.8	–1.18	–0.57	0.61	1	1	4	?	3	2	3
84	*Bradycellus verbasci* (Duftschmid, 1812)	42.3	–1.17	–0.41	0.65	2	1	4	3	3	1	2
85	*Bradycellus harpalinus* (Serville, 1821)	37.8	–0.98	–0.38	0.48	2	1	4	?	3	2	2
86	*Badister bullatus* (Schrank, 1798) (= *B. bipustulatus*)	49.2	0.58	–0.83	–0.98	2	1	2	1	1	2	1
87	*Cymindis vaporariorum* (Linnaeus, 1758)	62.2	0.94	–0.49	–0.10	2	1	2	?	2	2	2

the specific fauna of non-forested habitats. All species found were included in the analysis with the exception of eight which lacked replicate specimens, for which very similar species of the same genus or subgenus were already measured. The morphological space was described with a Factor Analysis of the standardised residuals of the regressions of all variables with total length, considered to be a good measure of general size (*see* Ribera *et al.* 1999 for additional details). Main trends in the ordination scatter plots were that species with long hind legs and antennae had high scores for the first axis, species with wide heads, large eyes, short antennae and deep pronotum had high scores for the second axis, and species with wide pronotum, long meta-trochanters and wide meta-femora had lower scores for the third axis. The basic correlations defining the three ordination axes were significant when compared with phylogenetic independent contrasts, demonstrating their independent occurrence in several phyletic lines (Ribera *et al.* 1999).

In addtion to the scores of the first three ordination axes of the morphospace, total size and five qualitative morphological variables were also used (Table 2, *see* Ribera *et al.* 1999 for the values of the qualitative variables in each species).

2.3. Life traits

Seven life traits of the species studied were codified according to published information (Table 3). Traits were chosen with the aim of characterising possible differences in life and/or ecological strategies, rather than autecological differences in habitat requirements. For species displaying polymorphism for some of the variables, information relating to Scottish or northern England populations was used whenever possible. When contradictory information was found, the most recent source was used, in particular that included in Luff (1998).

Overwintering (OVE): Species were divided into those which overwinter only as adults, and those which overwinter as larvae. The latter include species overwintering only as larvae and species overwintering as larvae and adult, as some adults of species are known to be able to survive occasionally more than one season even if they do not reproduce in the second year (Luff 1998).

Life cycle (CYC): Species were divided into those having a one year cycle, and those having a two year cycle, either obligate or facultative. Although all species with a two year cycle had overwintering larvae, a number of species overwintering as larvae had one year cycles (Table 1).

Food of the adults (FOA): Species were ordered as a gradient from the most specialised predators (preying mostly on Collembola), which are generally considered to have the most derived morphologies (*see* e.g., Bauer 1982, 1985a), generalised predators, species with a mixed diet (animal and vegetal), and those with a diet almost exclusively composed of plant material. Preliminary results showed that the values of this multistate variable were ordered in a coherent linear gradient, and thus it was not necessary to construct multiple dichotomous variables (*see* below).

Diel activity (DAY): Species were considered to be one

Table 2. Morphological variables used in the analysis (from Ribera *et al.* 1999).

Code	Variable
Quantitative	
HW	Width of the head, measured behind the eyes
YW	Diameter of the eye, measured from above
AL	Length of the antenna
PL	Length of the pronotum in the medial line
PW	Maximum width of the pronotum
PH	Maximum deepth of the pronotum
EL	Length of the elytra, from the medial ridge of the scutellum to the apex
EW	Maximum width of the elytra
FL	Length of the metafemur (with the articulation segments), from the coxa to the apex
TR	Length of the metatrochanter
BL	Length of the metatibia
RL	Length of the metatarsi
FW	Maximum width of the metafemur
TL	Total length (PL + EL)
Qualitative	
CLG	Colour of the legs (1 pale, 2 black, 3 metallic)
CLB	Colour of the body (1 pale, 2 black, 3 metallic)
WIN	Wing development (1 apterous or brachipterous, 2 dimorphic, 3 macropterous)
PRS	Shape of the pronotum (1 oval, 2 cordiform, 3 trapezoidal)
PUB	Pubescence (1 glabrous, 2 pubescent)

of three states; diurnal, with activity not restricted to either day or night, or nocturnal. As was the case with the diet of the adult, the different values of the variable were ordered in a coherent linear gradient. For sixteen species it was not possible to find data on their diel activity, and they were not included in the comparison of this trait.

Breeding season (BRE): species were divided into those breeding in spring, in summer, in autumn, and in winter. In this case the variable did not have a clear coherent linear gradient, and thus an alternative dichotomous variable, BREd, (contrasting species which reproduce in spring and summer with species which reproduce in autumn and winter) was also included in the analysis.

Emergence (EME): period of emergence of the adults. Species were placed into groups where adults emerge in spring, in summer, or in autumn (there were no species emerging in winter). As was the case with BRE, a dichotomous variable (EMEd) was constructed pooling species that emerge in spring and summer.

Activity (ACT): main period of activity of the adults. Species were placed into groups where adults are active in spring, in summer, in autumn, or the whole year (there were no species active only in winter). A special category was made for species that aestivate. Species active in spring and summer only, and species active in autumn (irrespective or their possible activity in other seasons) were respectively pooled to construct a dichotomous variable (ACTd), contrasting the two most generalised patterns (Lövei & Sunderland 1996). No published data were found for two of the species, which were excluded from the analysis.

2.4. Relationship between morphology and life traits

Correlations between morphological characters and life traits cannot be directly interpreted as significant, because of the non-independence of the values of phylogenetically related species (Harvey & Pagel 1991, Miles & Dunham 1993, Harvey 1996). The CAIC package (Purvis & Rambaut 1995), with a procedure based on Felsenstein's (1985) comparative method, was used to construct phylogenetically independent contrasts, which provide an independent set of points in which to base the comparisons. The CAIC package allows the use of not fully resolved phylogenies (using a modification of the method described by Pagel 1992), as well as the analysis between quantitative variables and one categorical variable. Procedures in CAIC were designed for the comparison of dichotomous variables, but it is possible to use multistate categorical variables when their values form a coherent gradient (Purvis & Rambaut 1995), which was the case for Food of adults and Diel activity.

There is not an agreed phylogeny of the family Carabidae (Lövei & Sunderland 1996), although the different taxonomic classifications presently in use were all constructed under a general phylogenetic perspective, and taking into account the detailed phylogenetic studies of some taxa. Two general arrangements of the family have been proposed, a more conservative one by Kryzhanovskij *et al.* (1995), and a more deviating one by Erwin and Sims (1984) (also included in Lindroth 1985). Both classifications are coincident at the lower taxonomic levels, with most differences largely restricted to the arrangement of the categories above genus level. Although classifications are not substitutes for phylogenies constructed using cladistic methods (e.g., Miles & Dunham 1993), the use of two contrasting arrangements increases the robustness of the results.

The length of the branches of the phylogeny was considered to be equal in all cases because only the species found in the sampled habitats were included in the analysis. This is equivalent to assuming equal rates of evolutionary change per unit branch length in all branches of the phylogeny, a conservative assumption necessary also when there are numerous polytomous branching in the phylogeny (Purvis & Rambaut 1995, Díaz-Uriarte & Garland 1996). Both morphological and ecological characters used in the analysis are of little systematic use because of their strong plasticity. They are therefore not used in the construction of phylogenies, nor in the arrangement of taxa in the classifications, avoiding in this way the possible circularity when these characters are compared with independent contrasts (de Queiroz 1996).

To determine the significance of the relationship be-

Table 3. Life traits of the species included in the analysis.

Code	Variable
OVE	overwintering (1 adult, 2 adult and larvae or only larvae)
CYC	Duration of the life cycle (1 one year, 2 two years).
FOA	food of the adult (1 mostly collembola, 2 generalist predator, 3 mixed diet, 4 mostly plant material)
DAY	daily activity (1 diurnal, 2 diurnal and nocturnal, 3 nocturnal)
BRE	breeding season (1 spring, 2 summer, 3 autumn, 4 winter)
BREd	breeding season (dichotomous) (1 spring + summer, 2 autumn + winter)
EME	main period of emergence of the adults (1 spring, 2 summer, 3 autumn)
EMEd	main period of emergence of the adults (dichotomous) (1 spring + summer, 2 autumn)
ACT	main period of adult activity (1 spring, 2 summer, 3 autumn, 4 whole year, 5 aestivate)
ACTd	main period of adult activity (dichotomous) (1 summer only, 2 autumn)

tween two variables the 95% confidence interval of the mean value of the contrasts was computed, and when the whole interval was positive or negative the dependent (quantitative) variable was considered to respectively increase or decrease with an increase of the predictor (qualitative) variable (Purvis & Rambaut 1995).

3. Results

3.1. Relationships between life traits and size

There were significant differences in the logarithm of the total length (LTL) between species for two of the life traits, when measured with phylogenetic independent contrasts: overwintering (OVE), and duration of the life cycle (CYC). Independent contrasts were significantly different from zero ($p < 0.05$) for both the classifications of Kryzhanovskij *et al.* (1995) and Erwin and Sims (1984) (Table 4).

Species overwintering as larvae were larger than species that overwinter only as adults. Differences were also significant when the measures were directly compared with ANOVA ($p < 0.01$). Species with a one year cycle were smaller than species with a two year life cycle, either obligatory or facultative. Differences were also significant when compared directly with ANOVA ($p < 0.01$).

When the contrasts for total size were significant, contrasts of individual raw measurements (not the residuals of the regression with log total size) were in general also significant, but with a few exceptions. The diameter of the eye (LYW) was significantly different between species with one or two year cycles only in the classification by Kryzhanovskij *et al.* (1995), and not significantly different between species which overwinter as larvae or only as adults. The length of the antennae (LAL), the femur (LFL), the tarsi (LRL), and the elytra (LEL), were significantly different between species overwintering as larvae or only as adults for the classification by Erwin and Sims (1984), but not for that of Kryzhanovskij *et al.* (1995). Differences in absolute length of the trochanter (LTR) were not significant in any of the comparisons studied.

3.2. Relationships between life traits and the ordination axes of the morphospace

Phylogenetic independent contrasts were highly significant when the scores of the first ordination axis of the morphospace were compared among species with different adult diet (FOA), using both classifications. Species feeding on Collembola had the highest scores, and species feeding exclusively on plant material the lowest (Table 1; Figs. 1A and 2). Differences between scores of the ordination axes were also highly significant when measured directly with ANOVA ($p < 0.001$). Among

Table 4. Relationships between life traits, total size, and ordination axes of the morphospace, as compared with phylogenetic independent contrasts. Only values with significant relationships ($p < 0.05$) for at least one of the classifications are given. LTL = log total size; n = number of contrasts. *See* Tables 2 and 3 for the codes of the variables.

		Kryzhanovskij *et al.* (1995)			Erwin & Sims (1984)		
Morphological variable	Life trait	Mean	conf. interval	*n*	Mean	conf. interval	*n*
LTL	OVE	8.92	95%	15	12.90	95%	15
	CYC	20.66	95%	6	20.88	95%	7
Factor 1	FOA	–0.27	95%	9	–0.21	95%	11
Factor 2	DAY	–0.27	95%	10	–0.36	90%	12
LAL	DAY	0.019	95%	10	0.020	88%	12
LEW	CYC	–0.007	95%	6	–0.007	95%	7
LFL	FOA	–0.014	95%	9	–0.010	90%	11
LTR	EME	0.014	95%	13	0.015	95%	14
	EMEd	0.019	95%	9	0.0023	95%	9
LRL	FOA	–0.018	95%	9	–0.018	95%	11

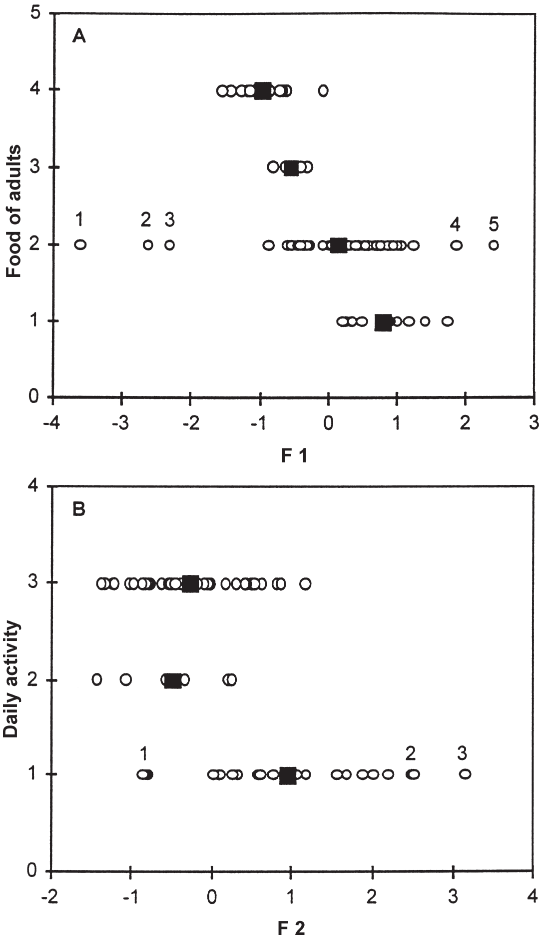

Fig. 1. Plot of (A) the scores of the species in the first ordination axis (F1) on the food of the adult (FOA), and (B) the scores of the species in the second ordination axis (F2) on the daily activity (DAY). Squares: average score per value of the categorical variable. (A) 1: *Clivina fossor*, 2: *Dyschiroides globosus*, 3: *Miscodera arctica*, 4: *Anchomenus dorsalis*, 5: *Cicindela campestris*; (B) 1: *Bembidion bruxellense*, *Badister bullatus* and *Agonum marginatum*, 2: *Notiophilus palustris* and *N. biguttatus*, 3: *N. germinyi.*

generalist predators, *Clivina fossor*, *Dyschiroides globosus*, and *Miscodera arctica* had the most deviating morphology, with extreme values on the ordination axes, due to their short and thin hindlegs, and short trochanters and antennae (Table 1; Figs. 1A and 2). This particular combination was not found in any other species (Ribera *et al.* 1999). At the other extreme of the axis, *Cicindela campestris* and *Anchomenus dorsalis*, although considered to be generalist predators, had morphologies more like those species exclusively feeding on Collembola (Fig. 1A).

No significant relationships were found between the second and third ordination axes and adult diet when measured with phylogenetic independent contrasts, although differences were highly significant when the raw scores were directly compared with ANOVA ($p < 0.001$). Species were clearly ordered in the second axis, with Collembola predators having the highest values, species with mostly plant material in their diets having intermediate scores, and generalist predators the lowest (Fig. 2A). Individual differences (as measured with a Bonferroni test) were significant between all groups with the exception of the comparisons with species with a mixed diet. In the third axis individual differences were significant between species feeding mostly on plant material (with extreme negative values, Fig. 2B) and predators, both generalist and Collembola specialists.

Contrasts for diel activity (DAY) were significant at $p < 0.05$ only when the classification by Kryzhanovskij *et al.* (1995) was used. When the classification of Erwin & Sims (1984) was used, results were significant at $p < 0.1$ (i.e., using 90% confidence intervals for the mean value of the contrasts). Diurnal species had higher scores than nocturnal species for the second ordination axis (Figs. 1B and 2). Species which can be active both day and night had scores more similar to that of nocturnal species, with an average value slightly lower. Overall differences between scores were highly significant (ANOVA; $p < 0.001$), individual differences were significant between diurnal and nocturnal species, and between diurnal and day and night active species, but not between nocturnal species and day and night active species (as measured with a Bonferroni test for individual t-Student comparisons).

With both classifications most of the contrasts for diel activity were negative (8 out of 10 with Kryzhanovskij *et al.* 1995, and 9 out of 12 with Erwin & Sims 1984). Two of the positive contrasts, in which the overall trend of the family (negative values of the second axis for nocturnal species) was reversed, were the same in both cases: *Bembidion bruxellense* vs. *B. tetracolum*, and the multiple contrast of the polytomy formed by *Agonum marginatum*, *A. muelleri*, *A. viduum* and

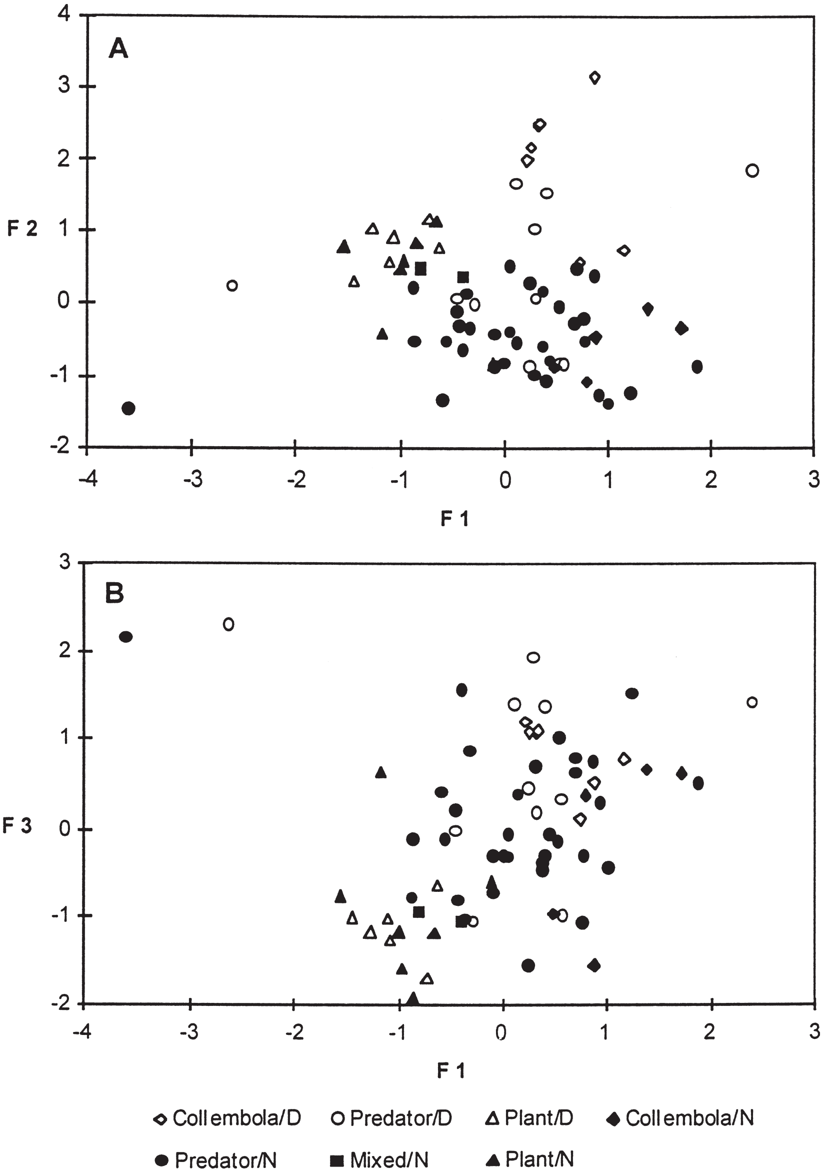

Fig. 2. Plots of the scores of the species grouped by food of the adult (FOA) and daily activity (DAY) (D, diurnal, N, nocturnal) in the Factorial Analysis with the residuals of the regression of the log measures with log Total length. (A) First and second ordination axes, (B) first and third ordination axes. Species active during the whole day are grouped with nocturnal (*see* text).

A. dolens. Differences between the two classifications were largely due to the inclusion of a third positive contrast when using Erwin and Sims (1984), comparing the four supertribes of Harpalinae. Positive contrasts were due to the effect of *Bembidion bruxellense*, *Agonum marginatum*, and *Badister bullatus*, which although diurnal, had morphologies more typical of nocturnal species (Fig. 1B). *Bembidion bruxellense* and *A. marginatum* belong to genus which are predominantly nocturnal, being however particular in that both species had a variegated colour, with metallic and pale areas, while most of the species of *Bembidion* and *Agonum* are black or brown (Table 1). The only other variegated species of *Bembidion* included in the analysis is *B. tetracolum*, which is of a similar size, though nocturnal (Luff 1978). *Bembidion bruxellense*, a diurnal species, had relatively smaller antennae, larger eyes, and smaller trochanter when compared with *B. tetracolum* (Ribera *et al.* 1999). *Badister bullatus* also had a variegated elytral design, but in this case other species of the genus (not included in the analysis) had similar colour patterns (Lindroth 1974). *Ba-*

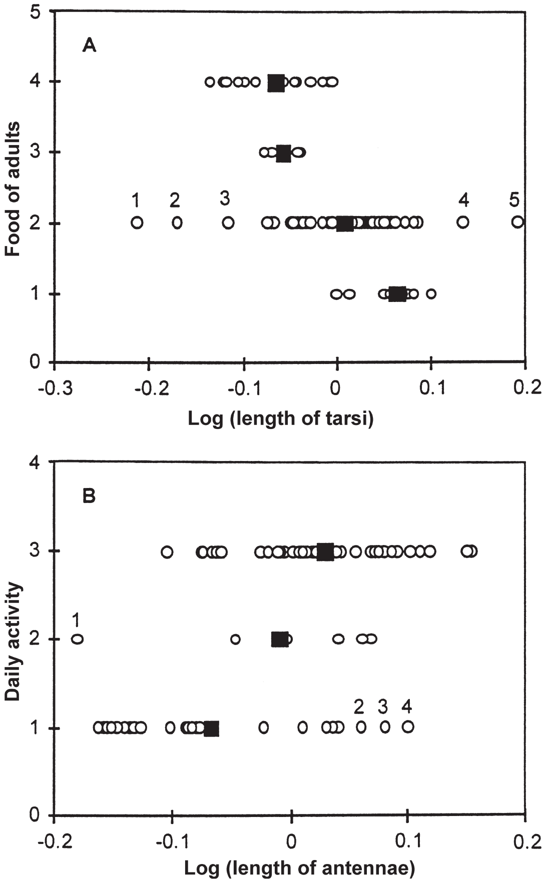

Fig. 3. Plot of (A) the log length of the tarsi (LRL) on the food of the adult (FOA), and (B) the log length of the antennae (LAL) on the daily activity of the adults (DAY). Squares: average score per value of the categorical variable. (A) 1: *Clivina fossor*, 2: *Dyschiroides globosus*, 3: *Miscodera arctica*, 4: *Anchomenus dorsalis*, 5: *Cicindela campestris*; (B) 1: *Clivina fossor*, 2: *Bembidion bruxellense*, 3: *Cicindela campestris*, 4: *Badister bullatus.*

dister bullatus was the only member of supertribe Callistitae in both classifications, but while in Erwin and Sims (1984) it is included in subfamily Harpalinae and contrasted with only three other supertribes of Harpalinae, in Kryzhanovskij *et al.* (1995) it has the same taxonomic range as Harpalitae, and included together with another 11 supertribes of Carabinae in a major contrast including all species but one (*Cicindela campestris*), in which its effects were less noticable owing to the large number of averaged species.

Phylogenetic independent contrasts comparing overwintering stage, breeding season (BRE), emergence period (EME), or period of activity of the adults (ACT) were not significantly different from zero, or had very low significance ($p > 0.2$) for at least one of the two classifications used.

3.3. Relationships between life traits and individual morphological measurements

Differences in the length of the tarsi between species with different adult diet were significant when measured with phylogenetic independent contrasts for the two classifications used (Table 4). Species feeding on Collembola had the longer tarsi, and species with plant diet the shortest (Fig. 3A). Differences were also highly significant when the residuals were compared with ANOVA ($p < 0.001$). Individual comparisons (as measured with Bonferroni multiple t-Student comparisons) were all significant, except between species with a mixed diet vs. predators, and species with a mixed diet vs. phytophages. The highest variability in the tarsi length was found among generalist predators. The tarsi of *Anchomenus dorsalis* and *Cicindela campestris* were relatively longer than those of any of the species feeding on Collembola (Fig. 3A). The shortest were that of *Clivina fossor*, *Dyschiroides globosus* and *Miscodera arctica*, the first two the shortest of all species (Fig. 3A). Contrasts comparing the length of the femur with the diet of the adult were significantly different from zero at a $p < 0.05$ level only when Kryzhanovskij *et al.* (1995) classification was used (Table 4). When Erwin and Sims (1984) classification was used the significance level dropped to $p < 0.1$ (confidence interval level of 90%).

Contrasts comparing the width of the elytra (LEW) with the duration of the life cycle were significantly different from zero for the two classifications (Table 4). Species with a two year cycle were narrower than species with a one year cycle. Differences using the raw residuals were also significant (ANOVA; $p = 0.05$).

Contrasts comparing the length of the trochanter with the period of emergence of the adults were significantly different from zero for the two classifications (Table 4), both when the variable with three categories (EME) and the dichotomised variable (EMEd) were used. Species which preferentially emerge late in the year as adults had longer trochanters, although differences were not significant when the raw residuals were directly compared with ANOVA.

Contrasts comparing the length of the antennae with the daily activity of the adults were significantly different from zero at a $p < 0.05$ level only when the classification by Kryzhanovskij *et al.* (1995) was used (Table 4). Differences were also significant when the residuals were compared with ANOVA ($p < 0.001$). Individual *t*-Student comparisons were significant only between nocturnal and diurnal species (Bonferroni test) (Fig. 3B). When the Erwin and Sims (1984) classification was used, significance level dropped to $p = 0.12$ (confidence interval of 88%). In both cases most of the contrasts were positive (9 out of 10 with Kryzhanovskij *et al.* 1995, and 10 out of 12 with Erwin and Sims 1984). The contrast comparing *Clivina fossor* and *Dyschiroides globosus* was negative in the two classifications, i.e., *C. fossor*, despite being active both night and day, had relatively shorter antennae than *D. globosus* (diurnal), and shorter than most of the species of its group (Table 1 and Fig. 3B). Similarly to what happened with the comparison of the scores of the second ordination axis, differences between both classifications were largely due to the inclusion of an additional negative contrasts when using Erwin and Sims (1984), that compared the supertribes of subfamily Harpalinae (see above). This contrast included *Badister bullatus*, which despite being diurnal had long antennae, with lengths well in the range of nocturnal species (Fig. 3B). *Cicindela campestris* was another diurnal species with antennae longer than that of other species of its group (Fig. 3B).

Phylogenetic independent contrasts comparing other variables were not significantly different from zero, or had very low significance ($p > 0.2$) for at least one of the classifications used.

4. Discussion

Clear relationships were found between some of the life traits investigated and the morphology of the species, irrespective of the systematic arrangement used in the comparative methods. This can be taken as evidence of the independent origin of the morphological traits measured, suggesting their possible functional significance (Harvey & Pagel 1991, Koehl 1996).

Relationships with the scores of the ordination axis of the morphospace, which summarise the main morphological trends within the group, were highly significant for two of the life traits studied, diel activity and diet of the adults. Species feeding on Collembola had the highest average scores for the first axis, although the highest individual scores corresponded to two species considered being generalist predators, *Anchomenus dorsalis* and *Cicindela campestris*. *Anchomenus dorsalis* was considered to be a generalist predator because it preys regularly on aphids (Basedow 1994, Luff 1998), but it is known to feed mostly on Collembola in certain habitats (Basedow 1994). *Cicindela campestris* is a typical visual hunter that uses visual clues to locate its prey (Gilbert 1986). It is a speed runner (with a mean speed of 156 mm/s, and a maximum recorded speed of 362 mm/s, i.e., more than three times its body length per second, Gilbert 1986), which feeds on a wide range of prey (Larochelle 1974).

In contrast, other Collembola feeders with high scores for the first axis, such as the species of *Leistus* and *Loricera pilicornis*, are able to hunt in total darkness using tactile and chemical clues detected with the antennae, as demonstrated with experimental manipulations by Bauer (1982, 1985a). Species of *Leistus* are nocturnal, and have a complex setal trap to overcome the escape reaction of springtails (Bauer 1985a). *Loricera pilicornis* is active during both day and night, but there is no overlap in the frontal vision field, such as the case in *Asaphidion flavipes* or species of the genus *Notiophilus*, and thus it seems to be less adapted to the use of visual clues for the detection of its prey.

The relationship between the first ordination axis of the morphospace and diet was mainly due to the high correlations between the length of the antennae and the hind leg with adult diet. These correlations were highly significant despite the relative shorter antennae of some diurnal visual hunters, such as the species of *Notiophilus* or *Elaphrus* (which however had lower scores for the first ordination axis). The length of the tarsi was the individual variable most significant in distinguishing diet, although these differences are difficult to interpret because of the high correlation between the length of leg segments (Table 4).

The second ordination axis was significantly correlated with diel activity when compared with phylogenetic independent contrast. If the scores of this second ordination axis are directly compared with ANOVA both adult diet and diel activity are highly significant, but differences in diet do not retain their significance when compared with CAIC. Differences in adult diet (which were significantly associated to the first ordination axis, as seen above) were also partially associated to differences in diel activity, i.e., diurnal species with the highest scores were all Collembola predators, and most generalist predators were nocturnal (Fig. 2).

Nocturnal species had lower values of the second ordination axis of the morphospace, with longer antennae, smaller eyes, and narrower pronota than diurnal species (Ribera *et al.* 1999). The most significant individual variable to distinguish diurnal and nocturnal species was the length of the antennae, shorter in diurnal species except *Cicindela campestris* and *Badister bullatus*. The same characters were noted in Bauer and Kredler (1993), which added a large binocular overlap in diurnal species, and antennae inserted more in front of the eyes in nocturnal ones. Species with high scores in the second axis, mostly diurnal, were also predominantly metallic, while species with lower values, mostly nocturnal, had pale or black colour (Ribera *et al.* 1999). In contrast to the suggestion by Lövei and Sunderland (1996), there was no significant difference between the size of diurnal and nocturnal species included in this study, either when compared with independent contrasts or with the raw data

Three species, *Bembidion bruxellense*, *Badister bullatus* and *Agonum marginatum*, had morphologies closer to the nocturnal species, despite being diurnal. All of them belong to predominantly nocturnal genera, and a change from nocturnal to diurnal habit, with the likely shift in resource use, was associated only with some minor (if at all) morphological modification of the quantitative characters included in this study. All three species are variegated, with more or less extended metallic patches, something not directly reflected in the morphospace defined by the ordination axes (which were based only on quantitative characters). *Badister bullatus* is the most widespread species of the genus in the UK, with a more eurytopic character (it is the only species not necessarily linked with the presence of water) (Luff 1998). The case is similar to that of *Dyschiroides globosus*, which still retains a very specialised morphology typical of its genus, considered to be an adaptation to dig, but has diurnal habits and can be found on the soil surface (Lindroth 1945, Luff 1998). In both cases, the change in habit may also be the cause of their great ecological success, being the most eurytopic, abundant, and frequent species of their respective genus in the UK (Luff 1998).

The above mentioned examples of small morphological changes associated with major habit shifts demonstrates that even when there are clear limitations of the habitat to which the morphology of the species is constrained (a template in the sense of Southwood 1988), such as the subterranean environment for digger specialists, changes in mode of life may lead to successful innovations that obscure the functional interpretation of the morphological characters. Changes in habit within the same type of physical environment, such as those of nocturnal species becoming diurnal, or in the proportion of the plant and animal material in the diet, are still more difficult to analyse without a detailed knowledge of the phylogeny and the autecology of the species involved.

The ecological success of species likely to have experimented a recent shift in some life trait, but still retaining the plesiomorphic morphology of the related species of the genus, is of interest in that it suggests that the constraints that the morphological specialisation could impose can be overcomed by a shift in habits. The decoupling of morphological and life traits in these cases is not an impediment for the success of the species, something that points to a possible mechanism for the origin of diversification to new adaptive zones.

Relationships with the third ordination axis were not significant when measured with phylogenetic independent contrasts, despite the high significance in the differences among the scores of species with different diet when compared directly with ANOVA. The third axis was mainly a reflection of the positive correlation between trochanter length and femora width, with the diameter of the eye having also a relatively high correlation (Ribera *et al.* 1999). Species with long metatrochanter, wide metafemora and smaller eyes had the lowest scores, and species with small metatrochanters, narrow metafemora and larger eyes had the highest scores. The former were mainly species feeding on plant material, while the latter were all predators, both generalist and specialised Collembola hunters. The lack of significance when phylogenetic independent contrasts were used suggests that these relationships may be a product of a phylogenetic effect: all but one of the species feeding mostly on plant material belong to three genera, *Amara*, *Harpalus* and *Bradycellus*, which did not contain species with a different diet, with the exception of *Harpalus rufipes* (mixed, Table 1). However, in neither of the classifications used do these genera (or combinations of two) form a monophyletic group, implying at least three independent acquisitions of a diet based on plant material, with all the associated morphological adaptations. In this particular case, the lack of significance could also be attributed to the low number of contrasts that could be constructed.

The importance of the variability of the length of the trochanter and the diameter of the eye within the studied species was also evidenced by the fact that they were the only individual variables that were not significant in contrasts in which differences in total size were significant (the length of the trochanter in all cases, and the diameter of the eye in all but for life cycle with the classification of Kryzhanovskij *et al.* 1995). This means that absolute variability in the length of the trochanter and in eye diameter within each size group were important enough to conceal the large relative differences in size across the whole species data set. The fact that the association between diet and the third ordination axis was not significant as measured with comparative methods has to be interpreted as lack of evidence, not as an evidence of the absence of a relationship. Phylogenetic independent contrasts may not be able to detect adaptive autapomorphies evolved only once in the evolution of the clade, or to discriminate between alternative hypotheses when a character association is found to be significant (Frumhoff & Reeve 1994, Leroi *et al.* 1994, Doughty 1996).

Among the most significant relationships were size differences in species overwintering as larvae and species which overwinter only as adults, and in species with one or two year cycles. All species with a two-year life cycle had overwintering larvae, but some species with overwintering larvae completed development in one year. There were also large species with a one year life cycle (e.g., some species of *Carabus*, Table 1). This excludes the hypothesis that large species need two years to achieve full development, and suggests a direct causal relationship between size of the adult and overwintering stage. The larger size of species overwintering as larvae may be a consequence of the need to store resources for overwintering, a costly process that depletes the energy reserves of the larvae (Leather *et al.* 1993). In this case, the need for large larvae to survive winter would be the underlying reason producing larger adults. Physiological studies are necessary to further investigate the relationship between size and overwintering stage, and the capacity of the larvae to store resources (e.g., Luff 1994).

Some necessary cautionary notes have to be made in what refers to the data set used in the study. In extensive comparisons between a large number of taxa, such as the case in this paper, an inevitable drawback is the need for a clear understanding of the life traits of each individual species. This has two main inconveniences. Firstly, species are to some extent variable in their life traits, depending on genetic or environmental differences. In ground beetles there is strong variability in the breeding period and duration in different geographical areas (Leyk *et al.* 1986, Paarman 1990), altitude (Sparks *et al.* 1995, Butterfield 1996), temperature (Paarman 1994), or food availability (Ernsting *et al.* 1992). Diel activity of the same species may vary in habitats with different degrees of human disturbance (Desender & Alderweireldt 1990), and phenology of species living in agricultural fields may depend on different management intensity (Basedow 1994). In broad studies it is impossible to take into account all variability, but if more specific functional problems were addressed it would be important to consider this within species variation, as measurements of fitness are only valid in the populations in which the rest of measurements are taken (Reilly & Wainwright 1994).

The second difficulty is the use of categorical variables, which in some cases may lead to a loss of information. It is impossible to summarise all possible patterns of breeding season in a few categories (*see* e.g., Den Boer & Den Boer-Daanje 1990, Makarov 1994). It would be necessary to quantify reproductive periods (but they are also dependent on local conditions, as noted above), something that would require comprehensive autecological studies of all the species in the analysis.

The lack of an agreed phylogeny for the group may also create difficulties in comparative studies, despite agreement in the ordination of the lower rank taxa in most taxonomic classifications presently in use (genera and subgenra). The general agreement of the results irrespective of the classification used can, however, be taken as evidence of their robustness. Thus, with the exception of the comparison of some characters in diurnal and nocturnal species, and that of the length of the femur in species with different diet, all results were significant at the usual $p < 0.05$ level for both classifications. Differences in the contrasts involving diel activity (second ordination axis and length of the antennae, which are highly correlated, Ribera *et al*. 1999) were due to the inclusion of an additional contrast, involving *Badister bullatus*, when the classification of Erwin and Sims (1984) was used (*see* above).

5. Conclusions

In this paper we have demonstrated some significant relationships between the morphology and the life traits of a extensive set of ground beetle species. In particular, diel activity and type of prey seem to be the two variables most influencing the morphology of the studied species. Length of the antenna, diameter of the eyes, and size and shape of the hind legs are the main individual characters that define these associations, which are, however, much better defined using the ordination axes of the multivariate morphospace constructed with a larger set of quantitative variables. An interesting pattern is that of eurytopic widespread and common species that, although retaining the ancestral morphology of the genus, have experienced a shift in habits (diurnal species with morphological characters of related nocturnal ones, or superficial species retaining morphological specialisations to dig). Contrary to what could be expected, these shifts in habit without the accompanying morphological changes seem to be associated with ecological success, and suggest a possible mechanism for the occupation of new adaptive zones.

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