

Morphological diversity of ground beetles (Coleoptera: Carabidae) in Scottish agricultural land

I. Ribera^{1*}, D. I. McCracken¹, G. N. Foster¹, I. S. Downie¹ and V. J. Abernethy²

¹Environmental Division, Scottish Agricultural College, Auchincruive, Ayr KA6 5HW, Scotland, U.K.

²Institute of Biomedical and Life Sciences, Division of Environmental and Evolutionary Biology, University of Glasgow, Glasgow G12 8QQ, Scotland, U.K.

(Accepted 25 June 1998)

Abstract

The morphospace defined by 87 species of ground beetle (Coleoptera: Carabidae) of Scottish non-forested habitats is described with multivariate methods, using 13 linear quantitative measurements of the body, hind legs, eyes and antennae, plus five qualitative characters concerned with body shape, colour, wing development, and pubescence. Relationships between pairs of variables are studied with phylogenetic independent contrasts, using two different taxonomic classifications as an approximation to the phylogeny of the group. The first ordination axis of the morphospace was found mainly to reflect the positive correlation between length of the antennae and length of the hind legs, the second to reflect the width of the head, diameter of the eye and pronotum height, and the third the width of the pronotum and elytra, length of the metatrochanter and width of the metafemur. The principal relationships involving qualitative characters were between colour of the body and legs and shape of the pronotum with ordination axes, wing development with width of the elytra, and pubescence with colour of the legs. Most correlations between quantitative variables, in particular those most influencing the ordination axes of the morphospace, remained significant when measured with phylogenetic independent contrasts using both classifications. Independent contrasts comparing qualitative with quantitative variables or ordination axes were only significant for the colour of the body with the second axis for both classifications used, and length of the antennae with colour of the body and shape of the pronotum for only one of the classifications. The main morphological trends within the morphospace defined are related with published information on their performance, in particular running speed and pushing abilities, following previous work on the functional morphology of the group. The morphospace defined by the species studied is a fundamental tool that will allow further investigations on the relationships between their morphology and life traits, as well as on the relationships of the functional diversity thus characterized with environmental correlates.

Key words: Scotland, agriculture, Carabidae, functional morphology, independent contrasts

INTRODUCTION

The Carabidae, with more than 25 000 species on all major biogeographical regions of the world, is one of the most diverse families of Coleoptera (Thiele, 1977). Carabid taxonomy and biogeography have been thoroughly investigated since the beginning of modern entomology, and there is now a wealth of information on the basic biology and ecology of ground beetles (see e.g. Thiele, 1977; Desender *et al.*, 1994; Lövei & Sunderland, 1996; Niemelä, 1996).

Despite the taxonomic diversity of the family, ground beetles have little variation in basic body structure, being

fairly uniform in morphology (Thiele, 1977). Although early studies on the morphological adaptations of carabids tried to associate morphological characters with habitats (e.g. Sharova, 1974), only a few adaptations to special environments have been found, among them digging, tree-dwelling, or cave-dwelling species. Most morphological variability within the group is associated with differences in habits, especially locomotion and modes of nutrition (Manton, 1977; Evans, 1990).

Early attempts to describe the functional morphology of the group did not quantify characters (e.g. Thiele, 1977). Subsequently, more detailed descriptions of the morphological variability associated with specialized modes of feeding, in particular of species preying on Collembola, were made by Forsythe (1983*a*, 1991), Evans & Forsythe (1985), Bauer (1985*a,b*) and

*Present address: Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, U.K.

Morwinsky & Bauer (1997). Morphological correlates of different modes of locomotion were studied by Evans (1977, 1986), Evans & Forsythe (1984) and Forsythe (1981, 1983*b*, 1987) in an important series of papers. According to these authors, the ancestral design of carabids would be an adaptation to running and wedge-pushing. Possible adaptations to run fast and push forward horizontally superimposed on this basic pattern were identified, in a trade-off of characters mostly affecting the morphology of the hind legs, in particular the size of the metatrochanters. Trochanters contain the femoral rotator muscle, which is hinged longitudinally to the head of the femur to allow its rotation about the trochanter (Evans, 1977). Three main types of locomotion were recognized. 'Group I' species were considered to be adapted to fast running, and had weak horizontal pushing abilities. They had short metatrochanters, long and narrow leg segments, and a lightly built body structure (e.g. the genera *Cicindela*, *Nebria*, *Leistus*, *Notiophilus*, *Loricera*, and *Elaphrus*). 'Group II' species were considered to be adapted to strong wedge-pushing, with medium speed. They had long metatrochanters, with broad femora, and a variable body shape (e.g. *Harpalus* and *Amara*). 'Group III' species were considered to be adapted to strong horizontal-pushing, and were the slowest species. They had short and narrow hind legs, long and pedunculate bodies, and usually front legs with special adaptations for digging (e.g. *Clivina*, *Scarites*, and *Dyschirius*). Carabini (mainly the genus *Carabus*) had intermediate characteristics, more similar to Group II (see Evans, 1986 for a summary of carabid locomotion types and characteristics). Some of these interpretations were supported by direct measurements of the performance of several species in the laboratory for their running velocity, horizontal pushing, and wedge pushing (Evans, 1977; Forsythe, 1981).

Despite the abundant information concerning individual sets of characters, no general multivariate analysis of the shape of ground beetles has been conducted in which the morphological diversity of a representative group of species (the morphospace in the sense of Gould, 1991) is described and the main morphological trends identified. In addition, previous work did not take into account the possible biases introduced in the analysis due to the non-independence of the characters produced by the phylogenetic proximity of the species (Harvey & Pagel, 1991), and in consequence all adaptive interpretations of character correlations must be made with caution.

The aim of this paper is to describe the morphological space defined by species of ground beetles occurring in Scottish agricultural land, and to identify character associations. If such character correlations occur independently in different phyletic lines the hypothesis that they may have evolved as functional adaptations would be supported (Harvey & Pagel, 1991; see Discussion). The pure description of the morphospace is a basic tool for the understanding of the evolutionary history of the group (Gould, 1991), as well as a basis for functional or

ecological studies (Foote, 1992, 1997; Reilly & Wainwright, 1994; Ricklefs & Mails, 1994; Roy & Foote, 1997). In a subsequent paper the relationships between the described morphospace and selected life traits will be explored (Ribera *et al.*, submitted). Future work will study the relationship between functional diversity, as defined here, and environmental characteristics within Scottish agricultural land.

MATERIAL AND METHODS

Material

Specimens were collected during 1995 and 1996 using pitfall traps in different agricultural habitats, ranging from intensive cereal fields to upland moorland with low grazing pressure, in 63 localities around Scotland (see Abernethy *et al.*, 1996, for more details on the sampling method and information on the localities, with the exclusion of 3 coniferous forests the species of which were not included in the present study). 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. All major taxonomic groups represented in the western Palaearctic fauna are included in the study, which 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 (Lövei & Sunderland, 1996), they form a well-defined evolutionary unit with a similar body plan, and are well suited for the quantification of the morphospace they define (e.g. Gould, 1991).

Morphological measurements

Thirteen linear quantitative measurements and 5 qualitative characters were collected from 87 species occurring in Scottish agricultural land (Tables 1 & 2; Appendix 1). All species found were included in the analysis with the exception of 8 (making a total catch of 95 species), of which very similar species of the same genus or subgenus were already measured. Measurements were chosen to best characterize shape, not systematic characters. They included major linear dimensions of the body and the hind legs, following the approach of previous work (e.g. Forsythe, 1987; Ribera & Nilsson, 1995), together with measurements of the size of the eyes and the antennae. Measurements were taken with a micrometer in a stereoscopic microscope

Table 1. List of the species included in the analysis. Nomenclature follows Kryzhanovskij *et al.* (1995) and Lindroth (1985, 1986) (names of common use in U.K. are given in parentheses). Codes of the species are those used in subsequent tables and figures

No.	Species code	Species
1	CICI CAMP	<i>Cicindela campestris</i> Linnaeus, 1758
2	CYCH CARA	<i>Cychrus caraboides</i> (Linnaeus, 1758)
3	CARA GRAN	<i>Carabus granulatus</i> Linnaeus, 1758
4	CARA NITE	<i>Carabus nitens</i> Linnaeus, 1758
5	CARA NEMO	<i>Carabus nemoralis</i> O. Müller, 1764
6	CARA PROB	<i>Carabus problematicus</i> Herbst, 1786
7	CARA ARVE	<i>Carabus arvensis</i> Herbst, 1784
8	CARA VIOL	<i>Carabus violaceus</i> Linnaeus, 1758
9	CARA GLAB	<i>Carabus glabratus</i> Paykull, 1790
10	LEIS FULV	<i>Leistus fulvibarbis</i> Dejean, 1826
11	LEIS TERM	<i>Leistus terminatus</i> (Hellwig in Panzer, 1793) (= <i>L. rufescens</i>)
12	NEBR BREV	<i>Nebria brevicollis</i> (Fabricius, 1792)
13	NEBR SALI	<i>Nebria salina</i> Fairmaire & Laboulbène, 1854
14	NOTI PALU	<i>Notiophilus palustris</i> (Duftschmid, 1812)
15	NOTI SUBS	<i>Notiophilus substriatus</i> Waterhouse, 1833
16	NOTI BIGU	<i>Notiophilus biguttatus</i> (Fabricius, 1779)
17	NOTI AQUA	<i>Notiophilus aquaticus</i> (Linnaeus, 1758)
18	NOTI GERM	<i>Notiophilus germyi</i> Fauvel, 1863
19	ELAP LAPP	<i>Elaphrus lapponicus</i> Gyllenhal, 1810
20	ELAP ULIG	<i>Elaphrus uliginosus</i> Fabricius, 1775
21	ELAP CUPR	<i>Elaphrus cupreus</i> Duftschmid, 1812
22	LORI PILI	<i>Loricera pilicornis</i> (Fabricius, 1775)
23	DYSC GLOB	<i>Dyschiroides globosus</i> (Herbst, 1783) (= <i>Dyschirius globosus</i>)
24	CLIV FOSS	<i>Clivina fossor</i> (Linnaeus, 1758)
25	MISC ARCT	<i>Miscodera arctica</i> (Paykull, 1798)
26	PATR ATRO	<i>Patrobus atrorufus</i> (Ström, 1768)
27	PATR ASSI	<i>Patrobus assimilis</i> Chaudoir, 1844
28	TREC MICR	<i>Trechoblemus micros</i> (Herbst, 1784) (= <i>Trechus micros</i>)
29	TREC RUBE	<i>Trechus rubens</i> (Fabricius, 1792)
30	TREC QUAD	<i>Trechus quadristriatus</i> (Schränk, 1781)
31	TREC OBTU	<i>Trechus obtusus</i> (Erichson, 1837)
32	ASAP FLAV	<i>Asaphidion flavipes</i> (Linnaeus, 1761)
33	BEMB LAMP	<i>Bembidion lampros</i> (Herbst, 1784)
34	BEMB OBTU	<i>Bembidion obtusum</i> Serville, 1821
35	BEMB AENE	<i>Bembidion aeneum</i> Germar, 1824
36	BEMB GUTT	<i>Bembidion guttula</i> (Fabricius, 1792)
37	BEMB MANN	<i>Bembidion mannerheimi</i> C.R. Sahlberg, 1834
38	BEMB TETR	<i>Bembidion tetracolum</i> Say, 1823
39	BEMB BRUX	<i>Bembidion bruxellense</i> Wesmael, 1835
40	STOM PUMI	<i>Stomis punicatus</i> (Panzer, 1796)
41	POEC VERS	<i>Poecilus versicolor</i> (Sturm, 1824) (= <i>Pterostichus versicolor</i>)
42	PTER AETH	<i>Pterostichus aethiops</i> (Panzer, 1797)
43	PTER MADI	<i>Pterostichus madidus</i> (Fabricius, 1775)
44	PTER CRIS	<i>Pterostichus cristatus</i> (Dufour)
45	PTER VERN	<i>Pterostichus vernalis</i> (Panzer, 1796)
46	PTER MELA	<i>Pterostichus melanarius</i> (Illiger, 1798)
47	PTER NIGE	<i>Pterostichus niger</i> (Schaller, 1783)
48	PTER NIGR	<i>Pterostichus nigrita</i> (Paykull, 1790)
49	PTER RHAE	<i>Pterostichus rhaeticus</i> Heer, 1838
50	PTER ADST	<i>Pterostichus adstrictus</i> Eschscholtz, 1823
51	PTER STRE	<i>Pterostichus strenuus</i> (Panzer, 1797)
52	PTER DILI	<i>Pterostichus diligens</i> (Sturm, 1824)
53	CALA ROTU	<i>Calathus rotundicollis</i> Dejean, 1828 (= <i>C. piceus</i>)
54	CALA FUSC	<i>Calathus fuscipes</i> (Goeze, 1777)
55	CALA MELA	<i>Calathus melanocephalus</i> (Linnaeus, 1758)
56	CALA MICR	<i>Calathus micropterus</i> (Duftschmid, 1812)
57	LAEM TERR	<i>Laemostenus terricola</i> (Herbst, 1783)
58	SYNU VIVA	<i>Symuchus vivalis</i> (Illiger, 1798) (= <i>S. nivalis</i>)
59	OLIS ROTU	<i>Olisthopus rotundatus</i> (Paykull, 1790)
60	ANCH DORS	<i>Anchomenus dorsalis</i> (Pontoppidan, 1763) (= <i>Agonum dorsale</i>)
61	PLAT ASSI	<i>Platynus assimile</i> (Paykull, 1790) (= <i>Agonum assimile</i>)
62	AGON MARG	<i>Agonum marginatum</i> (Linnaeus, 1758)
63	AGON MUEL	<i>Agonum muelleri</i> (Herbst, 1784)
64	AGON VIDU	<i>Agonum viduum</i> (Panzer, 1797)
65	AGON DOLE	<i>Agonum dolens</i> (C.R. Sahlberg, 1827) (= <i>A. moestum</i>)
66	AGON FULI	<i>Agonum fuliginosum</i> (Panzer, 1809)
67	AGON GCIL	<i>Agonum gracile</i> (Sturm, 1824)
68	AMAR PLEB	<i>Amara plebeja</i> (Gyllenhal, 1810)
69	AMAR EURY	<i>Amara eurynota</i> (Panzer, 1797)
70	AMAR OVAT	<i>Amara ovata</i> (Fabricius, 1792)
71	AMAR APRI	<i>Amara apricaria</i> (Paykull, 1790)
72	AMAR BIFR	<i>Amara bifrons</i> (Gyllenhal, 1810)
73	AMAR FAMI	<i>Amara familiaris</i> (Duftschmid, 1812)
74	AMAR AENE	<i>Amara aenea</i> (De Geer, 1794)
75	AMAR COMM	<i>Amara communis</i> (Panzer, 1797)
76	AMAR LUNI	<i>Amara lunicollis</i> Schiödte, 1837
77	CURT AULI	<i>Curtonotus aulicus</i> (Panzer, 1797) (= <i>Amara aulica</i>)
78	HARP RUFU	<i>Harpalus rufipes</i> (De Geer, 1774)
79	HARP AFFI	<i>Harpalus affinis</i> (Schränk, 1781)
80	HARP LATU	<i>Harpalus latus</i> (Linnaeus, 1758)
81	DICH COGN	<i>Dicheirotichus</i> (= <i>Trichocellus cognatus</i>) (Gyllenhal, 1827)
82	DICH PLAC	<i>Dicheirotichus</i> (= <i>Trichocellus placidus</i>) (Gyllenhal, 1827)
83	BRAD RUFU	<i>Bradycellus ruficollis</i> (Stephens, 1828)
84	BRAD VERB	<i>Bradycellus verbasci</i> (Duftschmid, 1812)
85	BRAD HARP	<i>Bradycellus harpalinus</i> (Serville, 1821)
86	BADI BULL	<i>Badister bullatus</i> (Schränk, 1798) (= <i>B. bipustulatus</i>)
87	CYMI VAPO	<i>Cymindis vaporariorum</i> (Linnaeus, 1758)

Table 2. Morphological variables used in the analysis. (a) Quantitative, (b) qualitative

(a)	
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 height 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	PL + EL
(b)	
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)

using a magnification of between $10\times$ and $45\times$, i.e. with a resolution between 0.1 and 0.02 mm, depending on the measurement and the size of the species.

Six specimens were measured per species, 1 male and 1 female from 3 different localities and dates. This was to avoid possible biases due to sexual dimorphism, and geographical or temporal variability. For 11 species for which not enough material was collected, additional specimens from north-east England were measured (a total of 30). In 4 species only 5 specimens could be measured, and in 2 species only 4 (Appendix).

Description of the morphospace defined by the studied species

All quantitative variables were normalized before the analyses by a log-transformation. The residuals of the regression of each individual variable with a measure of total length (TL being length of the pronotum (PL) plus length of the elytra (EL); Table 2) were considered to be a measure of shape. Due to the constant general shape of all the species studied, the total length can be considered a very good estimation of size, with a strong log-linear relationship with body biomass for European carabids of 0.98 (Jarošík, 1989).

The morphological space defined by the species included in the analysis was described by a factor analysis of the correlation matrix of the residuals of the 11 quantitative variables, using principal component analysis (PCA) as the extraction method. The score matrix was rotated using the VARIMAX procedure to maximize the coincidence of the variables with the ordination axes (Reyment, Blackith & Campbell, 1984). The residuals of all 514 specimens were used in the analysis, to avoid possible artefacts when averaging individuals of different size and/or sex. Exploratory

analysis of the data (using other extraction methods, or PCA) demonstrated a great robustness of the results, with correlations of the scores for the 3 first ordination axes always close to unity.

Multiple regression was used to analyse the possible relationship between the shape (as measured with the ordination axes) and size (as measured with log total length, LTL). Although individual variables were independent of the measurement of size by construction, there is still the possibility of patterns in the size distribution of the species with different shapes, i.e. a heterogeneous distribution of size in the morphological space defined by the ordination axes.

The relationship between the quantitative and the qualitative morphological variables was studied with multiple analysis of variance (MANOVA), using either the average values per species of the size measurement (LTL), the residuals of the regression of the quantitative variables with LTL, or the average scores of the ordination axes, as predictors, and the qualitative character as the dependent variable.

The significance of the relationship between the qualitative morphological variables was studied using contingency tables with a chi-square test.

Comparative methodology

The description of the associations in the morphospace defined by the species studied cannot be directly interpreted as adaptive, because of the non-independence of the values of phylogenetically related species (Harvey & Pagel, 1991; Miles & Dunham, 1993; Harvey, 1996). The CAIC package (Purvis & Rambaud, 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 on which to base the comparisons. The CAIC package allows the use of incompletely resolved phylogenies (using a modification of the method described by Pagel, 1992), as well as the analysis between quantitative variables and one categorical variable.

There is no agreed phylogeny for the family Carabidae (Lövei & Sunderland, 1996), although the different taxonomic classifications presently in use were all explicitly constructed under a phylogenetic perspective, and take into account the detailed phylogenetic studies of some taxa. Two main general arrangements of the family have been proposed, which can be exemplified as the more conservative arrangement by Kryzhanovskij *et al.* (1995), and the somewhat deviating one by Erwin & Sims (1984) (also included in Lindroth, 1985). Both classifications are coincident at the lower taxonomic levels, the differences being largely restricted to the arrangement of the categories above genus level. Although taxonomies are not substitutes for phylogenies constructed using cladistic methods (e.g. Miles & Dunham, 1993), the use of 2 contrasting arrangements increases the robustness of the analysis.

The classification by Kryzhanovskij *et al.* (1995) allowed the construction of 44 independent contrasts when quantitative variables were compared, and that of Erwin & Sims (1984) gave 43. The number of contrasts when 1 categorical variable was compared with a quantitative variable depended on the distribution of the values in the classification.

The length of the branches of the phylogeny was considered to be equal in all cases (the default procedure in CAIC) 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 & Rambaud, 1995; Díaz-Uriarte & Garland, 1996). The characters used in the analysis were of little systematic use because of their strong plasticity. They were therefore not used in the construction of phylogenies, nor in the arrangement of the taxa in the classifications, avoiding in this way the possible circularity when these characters are compared with independent contrasts (Queiroz, 1996). Four of the qualitative variables had 3 states (CLB, CLB, WIN and PRS, Table 2). The program CAIC was originally designed for use with dichotomous variables, but when there is a clear linear gradient of values the variable can take, which preliminary tests proved to be the case, it can also deal with multi-state variables (Purvis & Rambaud, 1995).

Correlations between independent contrasts comparing quantitative variables were studied using linear regression through the origin. In the contrasts including 1 qualitative variable the 95% confident interval of the mean was computed, and when the whole interval was positive or negative, the quantitative dependent variable was considered to significantly increase or decrease

Table 3. Rotated factor loadings and associated variance of the first three ordination axes of the residuals of the quantitative variables with log size (see text). See Table 2 for the codes of the variables

	Factor 1	Factor 2	Factor 3
Variance	3.50	2.41	2.37
% Variance	32	22	22
Variable			
LFL	0.96	-0.09	0.03
LBL	0.95	-0.09	-0.09
LRL	0.91	0.14	0.01
LAL	0.71	-0.59	-0.15
LHW	-0.04	0.84	-0.19
LYW	0.37	0.71	0.38
LPH	-0.16	0.70	-0.10
LEW	0.23	0.20	-0.42
LPW	-0.36	0.47	-0.68
LTR	0.04	-0.25	-0.85
LFW	0.03	0.06	-0.89

respectively with an increase of the qualitative predictor variable (Purvis & Rambaud, 1995).

The most significant contrasts of the comparisons between quantitative variables were ranked in 4 groups according to the taxonomic level of the taxa compared: contrasts between species of the same subgenus or species group, contrasts between subgenera of the same genus, contrasts between genera of the same subtribe, and contrasts between taxonomic categories higher than genus (subtribes, tribes, supertribes, and subfamilies). Differences in the contrasts between these 4 taxonomic levels were studied with analysis of variance (ANOVA), with *t*-Student multiple individual comparisons corrected by the Bonferroni method (Sokal & Rohlf, 1995). In the analysis of qualitative variables the number of contrasts was insufficient to permit a separate analysis of the different taxonomic levels.

RESULTS

Factor analysis of the residuals of the quantitative variables with log total size (LTL)

The first ordination axis accounted for 32% of the total variance, and the second and third 22% each (Table 3). Subsequent axes did not contribute significantly to the interpretation of the results, explaining less variance than individual variables, and were not considered further.

The first axis was positively correlated mainly with the length of the hind legs (LFL, LBL and LRL) and the length of the antennae (LAL). The second axis was mostly correlated with the width of the head (LHW), the diameter of the eyes (LYW) and the height of the pronotum (LPH). The third axis was mainly negatively correlated with the width of the pronotum and elytra (LPW, LEW), the length of the trochanter (LTR) and the width of the femur (LFW) (Table 3). In general, correlations were low for all axes except one, although

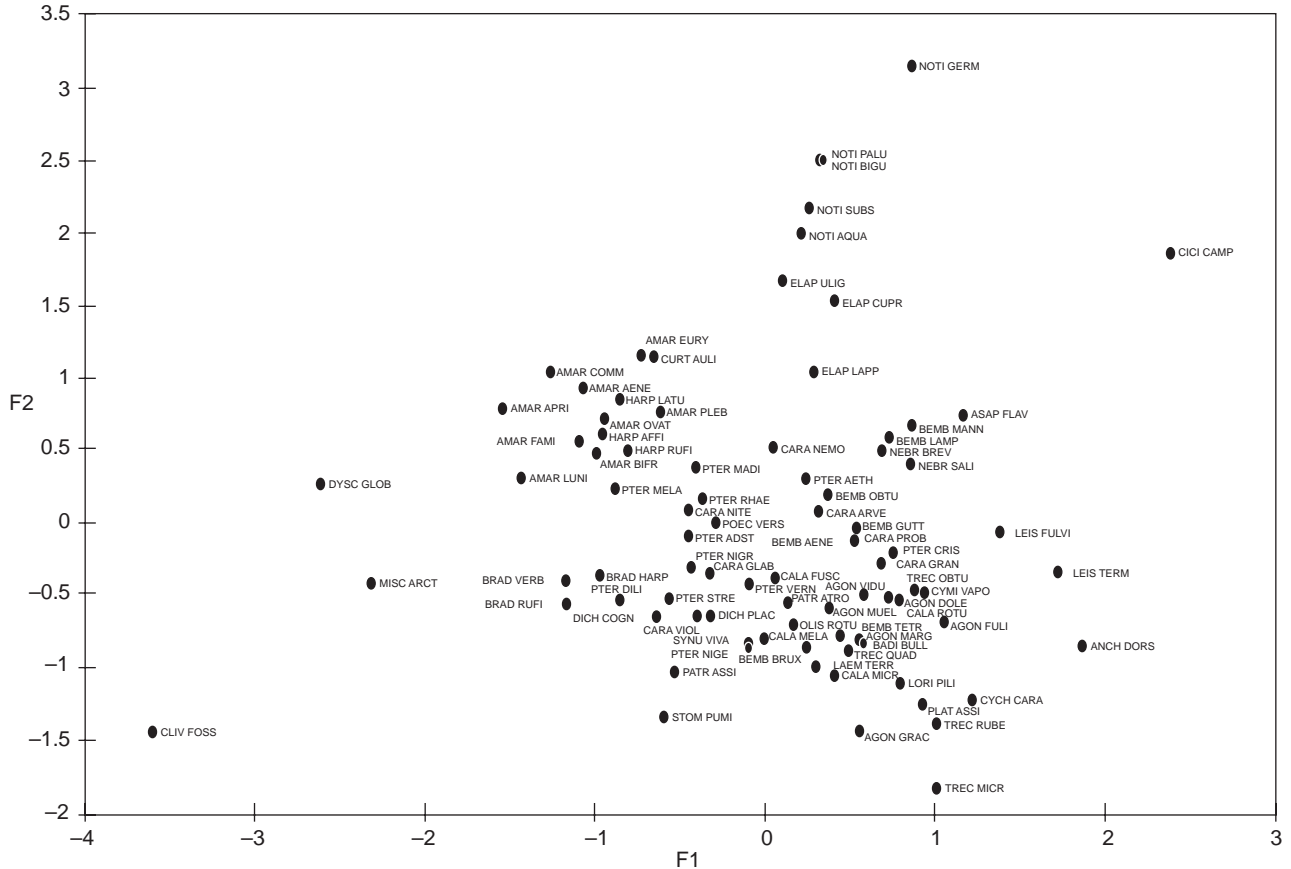


Fig. 1. Plot of the scores of the species in the first and second axes from Factorial Analysis of the residuals of the regression of the log measurements with log total length (LTL). See Table 1 for the codes of the species.

sometimes, despite the use of a VARIMAX rotation, the variable was highly correlated with more than one axis.

In the ordination scatter plots 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 metatrochanters and wide metafemora had lower scores for the third axis (Figs 1 & 2). Variables of lesser importance were the diameter of the eyes and the width of the pronotum, which were negatively correlated with the first axis (i.e. lower values of the variables corresponded to the highest scores of the axis), the length of the antennae and the width of the pronotum in the second axis (which were negatively and positively correlated respectively), and the diameter of the eyes in the third axis (which was positively correlated) (Table 3).

All species were ordered in an almost continuous morphospace (Fig. 1), with the exception of the group formed by *Clivina fossor*, *Dyschiroides globosus* and *Miscodera arctica* (with extreme negative values for the first axis and positive for the third) and *Cicindela campestris* (with extreme positive scores for the first axis). The first three species were the only members of scaritids and broscitids (supertribes in Kryzhanovskij *et al.*, 1995, and subfamilies in Erwin & Sims, 1984), and *Cicindela* was the only tiger beetle (subfamily

Cicindelinae in Kryzhanovskij *et al.*, 1995, and supertribe Cicindelitae in Erwin & Sims, 1984).

Clivina, *Dyschiroides* and *Miscodera* had extremely short and thin hind legs, with trochanters and antennae also short. Their particular morphology was largely due to the coincidence of short hind legs with short trochanters and thin femora, a combination not found in any other species. They also shared a pedunculate body, a character not reflected in the measurements but with possible adaptive functions (see Discussion). *Cicindela campestris* was distinguished by its extremely long and thin hind legs, with small trochanters, and its relatively long antennae.

It is interesting to note the different scores on the second and third ordination axes of species pairs considered to be morphologically very similar, as with *Pterostichus nigrata* and *P. rhaeticus* (only recently recognized as separate species: Koch, 1984; Luff, 1990), *Bembidion guttula* and *B. mannerheimi*, *Notiophilus germinyi* and *N. palustris*, and *Bembidion bruxellense* and *B. tetracolum* (Lindroth, 1974) (Figs 1 & 2). Other similar species had, on the contrary, very close scores on the ordination axes (e.g. *Nebria brevicollis* and *N. salina*: Figs 1 & 2). Differences in the scores on the second axis between *P. nigrata* and *P. rhaeticus* were mostly due to the different relative width and height of the pronotum (narrower and shallower in *P. nigrata*), and on the third axis due to the shape of the metafemora (shorter and

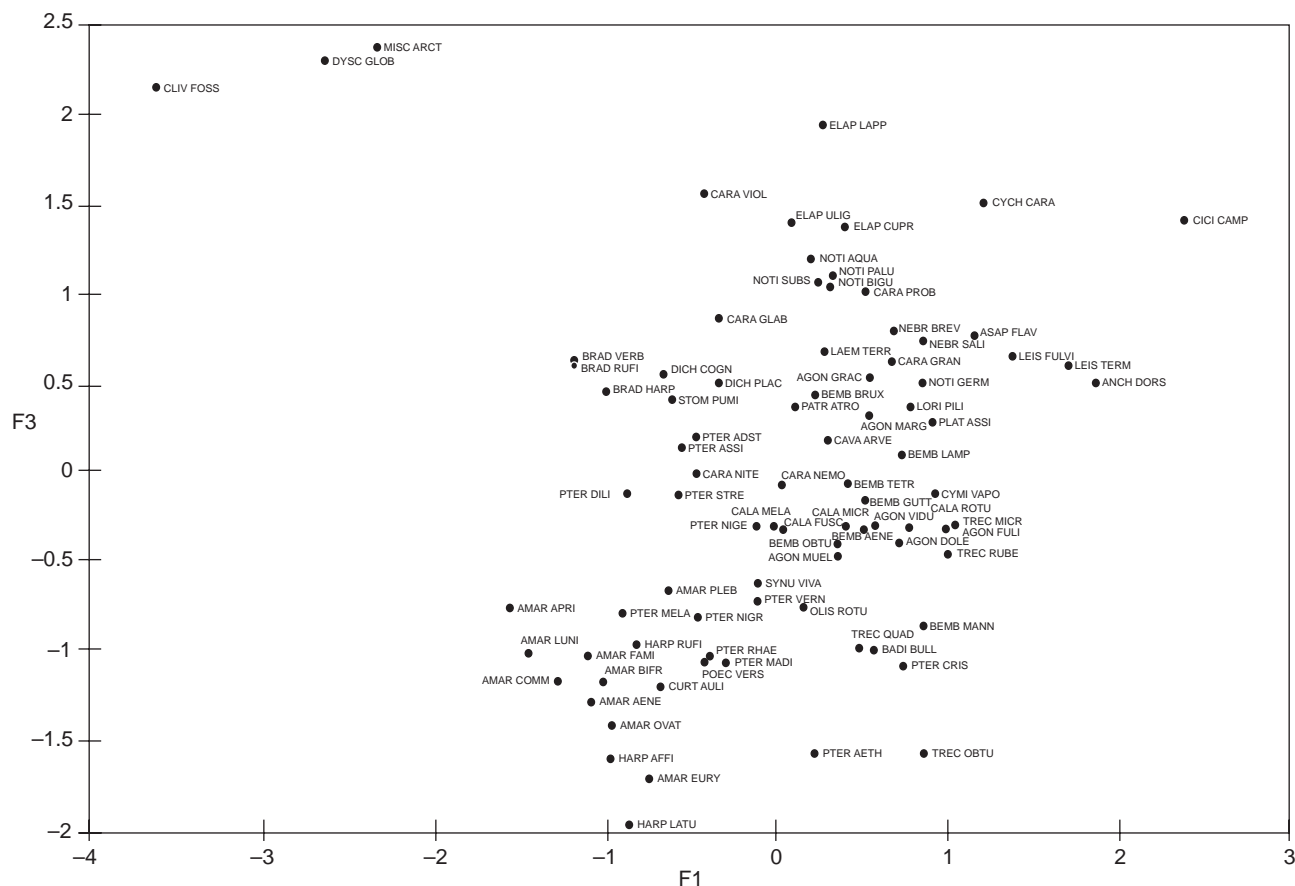


Fig. 2. Plot of the scores of the species in the first and third axes from Factorial Analysis of the residuals of the regression of the log measurements with log total length (LTL). See Table 1 for the codes of the species.

narrower in *P. nigrata*). Differences between *B. guttula* and *B. mannerheimi* were due to the width of the head and the diameter of the eyes for the second axis (narrower and smaller respectively, in *B. guttula*), and the width of the metafemur for the third (much narrower in *B. guttula*, with a negative residual, than in *B. mannerheimi*, with a positive residual). Differences in the species of *Notiophilus* were mainly due to the wider head and pronotum, larger eyes, and wider femora of *N. germinyi*. *Bembidion bruxellense* had relatively smaller antennae, larger eyes, and smaller trochanter when compared with *B. tetracolum*.

Relationship between the ordination axes and size

The correlations of the total length (LTL) with the first three ordination axes were very low ($r < 0.05$ in all cases), either individually considered or when included in a multiple regression. There were no significant size differences between species with different scores in the ordination axes.

Multiple analysis of variance of the qualitative variables

There were significant differences between the shape of species with different body and/or leg coloration both

when comparing the 11 residual variables or the three first ordination axes (Table 4). The largest differences for the colour of the body were between species with metallic colour (CLB: 3) and species with pale (CLB: 1) or black colour (CLB: 2). In metallic species the average value of the residuals of all variables that were individually significant were of an opposite sign to those residuals of the black or pale species. Species with positive residuals had higher values of the variable than the average for all pooled species, and vice versa.

Species with a metallic body had larger eyes (LYW), shorter antennae (LAL), deeper pronotum (LPH), and smaller metatrochanters (LTR) than species with black or pale bodies (Table 4a). Differences for the scores of the ordination axes were also globally significant ($P < 0.001$), although differences were only due to the second factor: metallic species had higher, positive values than black or pale species, which had negative values. Black species had intermediate values between metallic and pale species (Table 4b).

Shape differences associated with the colour of the legs (CLG) paralleled those for the colour of the body. In addition to the differences noted for the colour of the body, which were all maintained, species with metallic legs (CLG: 3) also had longer tarsi (LRL) and thinner femora (LFL), and wider heads, than species with black (CLG: 2) or pale (CLG: 1) legs (Table 4a). Species with metallic legs also had higher values for all three

Table 4. Multiple Analysis of Variance of the quantitative vs. qualitative morphological variables. (a) Differences in the quantitative variables; (b) differences in the scores of the first three ordination axes. The sign and relative value of the residuals are given for individual morphological variables with significant differences. See Tables 2 & 3 for the codes and values of the variables

Variable	Significance of MANOVA	Sig. univariate <i>F</i> -tests ($P < 0.05$)	Positive residuals	Negative residuals
(a)				
CLB	<0.001	LYW	3	2>1
		LAL	1>2	3
		LPH	3	2>1
		LTR	2>1	3
CLG	<0.001	LHW	3	1>2
		LYW	3	2>1
		LAL	1>2	3
		LPH	3>2	1
		LTR	1>2	3
		LRL	3	1>2
		LFW	1	2>3
WIN	<0.001	LEW	3	1>2
PUB	n.s.	n.s.		
PRS	<0.001	LHW	3>2	1
		LYW	2	3>1
		LAL	1>2	3
		LPW	3	1>2
		LFL	2>1	3
		LTR	3>1	2
		LBL	2>1	3
		LRL	2	1>2
		LFW	3	1>2
(b)				
CLB	<0.001	F2	3	2>1
CLG	<0.001	F1	3	1>2
		F2	3	1>2
		F3	3	2>1
WIN	n.s.	n.s.		
PUB	n.s.	n.s.		
PRS	<0.001	F1	2	1>3
		F2	3>2	1

ordination axes. Differences were again most pronounced between species with metallic and species with black or pale legs (Table 4b).

Joint differences in shape between species with different wing development (WIN) were highly significant ($P < 0.001$), although the only individual significant variable was the width of the elytra (LEW) (*F* test, $P < 0.001$, Table 4a). Macropterous species (WIN: 3) had the widest elytra, in accordance with the observations by Kavanaugh (1985). Differences for the scores of the ordination axes were not significant.

Joint differences in the shape of the pronotum (PRS) were also highly significant, both for the residual variables and the scores of the ordination axes ($P < 0.001$). Species with cordiform pronotum (PRS: 2) had larger eyes and longer tarsi than average, while species with trapezoidal (PRS: 3) or oval (PRS: 1) pronotum had smaller eyes and shorter tarsi than average. Species with trapezoidal pronotum also had shorter antennae, wider

pronotum, shorter and wider femora, longer trochanters, and shorter tibiae (LBL) than average, while species with oval pronotum had narrower heads (LHW) (Table 4a). In the ordination space, species with cordiform pronotum had on average positive scores for all three axes, species with oval pronotum had positive scores for axis 3 and negative scores for axes 1 and 2, and species with trapezoidal pronotum had positive scores for axis 2 and negative scores for axes 1 and 3 (Table 4b).

There were no significant differences in shape between pubescent (PUB: 2) and glabrous (PUB: 1) species, either for the individual variables or in ordination space.

Relationships between qualitative variables

There was a significant relationship between the colour of the legs and the pubescence of the body ($P < 0.05$), all pubescent species having pale legs (Appendix). Similarly, all species with metallic legs had a cordiform pronotum (chi-square of the joint differences $P < 0.001$).

Species with pale body also had pale legs, with the exception of *Anchomenus dorsalis* (which had variegated elytra, thus being considered to be of a general pale colour). Black species had either pale or black legs, and metallic species could have legs of either pale, black or metallic colour (chi-square of the joint differences $P < 0.001$) (Appendix).

Phylogenetic independent contrasts of the morphological variables

Quantitative variables

All of the most significant correlations between the residuals of the regression of the log quantitative morphological variables with log size were also significant when compared with phylogenetic independent contrasts using both classifications, the only exceptions being the correlation between the width of the head (LHW) and the diameter of the eye (LYW), the width of the head and the width of the pronotum (LPW), and the length of the antennae (LAL) and the height of the pronotum (LPH) (Tables 5 & 6).

For most of the regressions the correlation coefficient was significant irrespective of the variable that was used as predictor (i.e. the significances of the correlation matrix were symmetrical), and were significant for the two classifications used (Table 6).

The high correlation between the length of the leg segments (LFL, LBL and LTR) and the length of the antennae, which was the basis of the first ordination axis, was still highly significant after the phylogenetic correction with independent contrasts. Of the correlations that define the second axis, that between the height of the pronotum and the diameter of the eyes was maintained, while for those of the third axis, the correla-

Table 5. Correlation matrix of the residuals of the regression of the quantitative variables with log size ($n = 87$, a $P < 0.05$ significance level is attained with $r = 0.2$). n.s., not significant

	LHW	LYW	LAL	LPW	LPH	LEW	LFL	LTR	LBL	LRL
LYW	0.54									
LAL	-0.51	-0.26								
LPW	0.50	n.s.	-0.45							
LPH	0.42	0.31	-0.55		0.44					
LEW	n.s.	n.s.	n.s.	0.31	n.s.					
LFL	n.s.	0.27	0.72	-0.43	-0.33	0.20				
LTR	n.s.	-0.38	0.27	0.36	n.s.	n.s.	n.s.			
LBL	n.s.	0.21	0.74	-0.34	-0.27	0.27	0.94	n.s.		
LRL	n.s.	0.43	0.52	-0.25	n.s.	n.s.	0.84	n.s.	0.84	
LFW	0.26	-0.22	n.s.	0.55	n.s.	0.21	n.s.	0.78	n.s.	n.s.

Table 6. Correlation coefficients of the regression through the origin between the phylogenetic independent contrasts of the residuals of the quantitative morphological variables. Rows: independent variable of the regression. For each variable, first row (K): value obtained with Kryzhanovskij *et al.* (1995) classification ($n = 44$); second row (E): value obtained with Erwin & Sims (1984) classification ($n = 43$). Note the non-symmetrical values of the CAIC regressions, which depend on the variable considered to be independent (due to the different arrangement of the independent phylogenetic contrasts in each case). Only regressions with at least three out of four significant values are given (see text)

		LHW	LYW	LAL	LPW	LPH	LEW	LFL	LTR	LBL	LRL	LFW
LHW	K	1		-0.32								
	E	1		-0.35								
LYW	K		1			n.s.					0.40	
	E		1			0.28					0.36	
LAL	K	n.s.		1	-0.32			0.67		0.61	0.53	
	E	-0.37		1	-0.33			0.64		0.64	0.54	
LPW	K			-0.36	1	0.32			0.50			0.56
	E			n.s.	1	n.s.			0.47			0.56
LPH	K		0.31		0.33	1	0.31					
	E		0.29		0.43	1	0.37					
LEW	K					0.43	1	0.34		0.40	0.35	
	E					n.s.	1	0.42		0.45	0.34	
LFL	K			0.72			0.41	1		0.82	0.74	
	E			0.71			0.47	1		0.88	0.82	
LTR	K				n.s.				1			0.75
	E				0.34				1			0.69
LBL	K			0.72			0.40	0.82		1	0.76	
	E			0.74			0.45	0.86		1	0.76	
LRL	K		0.38	0.60			0.40	0.70		0.76	1	
	E		n.s.	0.63			0.36	0.73		0.76	1	
LFW	K				0.42				0.74			1
	E				0.47				0.69			1

tion between the length of the trochanter and the width of the femur, and between the length of the trochanter and the width of the pronotum (LPW), were also highly significant.

Differences between the taxonomic level of the contrasts were investigated for two of the most significant correlations, trochanter length with femur width (using the length of the trochanter as the predictor variable), and antennae length with femur length (using length of the antennae as the predictor variable). All were significant for all variables in all the comparisons (as measured with ANOVA, $P < 0.05$), with the exception of the femur width when compared with the trochanter length using the Erwin & Sims (1984) classification (Table 7). Contrasts comparing high-level taxonomic groups were larger than those comparing species, the

differences were most pronounced between contrasts comparing taxa above the genus level (subtribes, tribes, supertribes and subfamilies) and contrasts comparing genera or lower categories (subgenera, species groups or species) (Table 7).

In all comparisons the contrast with highest values was that of the 13 supertribes of Carabinae when the classification by Kryzhanovskij *et al.* (1995) was used, and between the five subfamilies of Carabidae when the classification was that of Erwin & Sims (1984) (Figs 3 & 4). In the comparison between the length of the trochanter and the width of the femur, the second highest value was that of the contrast between subtribes of Harpalini (the genera *Bradycellus* plus *Dicheirotrichus* vs the genera *Harpalus* plus *Ophonus*) when the classification by Kryzhanovskij *et al.* (1995) was used, and

Table 7. Significance of the differences between the phylogenetic independent contrasts grouped by taxonomic level for the comparison of the length of the trochanter (LTR) with the width of the femur (LFW), and the length of the antenna (LAL) with the length of the femur (LFL). Taxonomic levels: 1 above genus, 2 genus, 3 subgenus or species group, 4 species

	Kryzhanovskij <i>et al.</i> (1995)				Erwin & Sims (1984)			
	LTR	LFW	LAL	LFL	LTR	LFW	LAL	LFL
ANOVA	+	+	+	+	+	-	+	+
$P < 0.05$								
Individual comparisons between taxonomic levels (Bonferroni's corrected <i>t</i> -tests, $P < 0.0042$)								
1 with 2	-	-	-	+	-	-	+	+
1 with 3	+	+	-	+	-	-	+	+
1 with 4	+	+	+	+	-	-	+	+
2 with 3	-	-	-	-	-	-	-	-
2 with 4	-	-	-	-	-	-	-	-
3 with 4	-	-	-	-	-	-	-	-

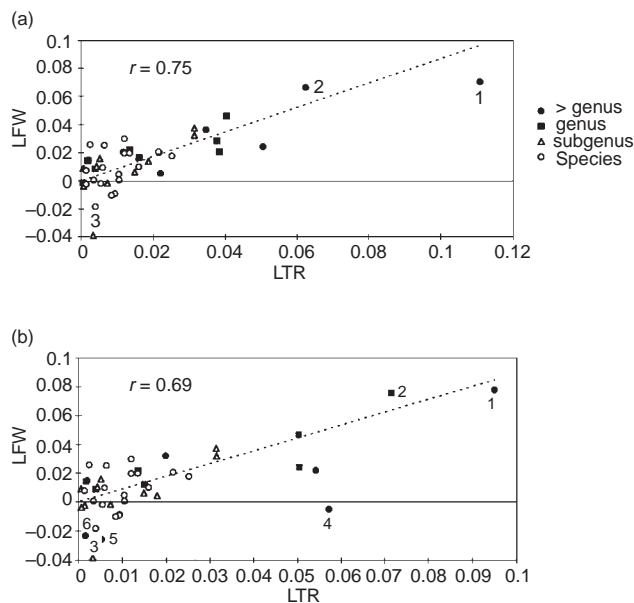


Fig. 3. Plot of independent contrasts on log length of the trochanter (LTR) vs independent contrasts on log width of the femur (LFW) using the classifications by (a) Kryzhanovskij *et al.* (1995) and (b) Erwin & Sims (1984).

- 1, (a) Supertribes of Carabinae or (b) subfamilies of Carabidae
- 2, (a) *Bradycellus* + *Dicheirotichus* vs *Harpalus* + *Ophonus* or (b) *Bradycellus* vs *Dicheirotichus* vs *Harpalus* vs *Ophonus*
- 3, *Trechus rubens* vs *T. quadristriatus* + *T. obtusus*
- 4, Loricerini (*Loricera pilicornis*) vs Carabini (*Carabus*)
- 5, Pterostichini (*Stomis* + *Poecilus* + *Pterostichus* + *Calathus* + *Laemostenus* + *Synuchus* + *Olisthopus* + *Anchomenus* + *Platynus* + *Agonum*) vs Zabrinini (*Amara* + *Curtonotus*)
- 6, *Leistus* + *Nebria* vs *Notiophilus*

between these four genera (in a polytomy not arranged in subtribes) when that of Erwin & Sims (1984) was used (Fig. 3). The contrasts with the most negative values for the femur width was in both cases that comparing *Trechus rubens* with the species of the *T. quadristriatus* group (*T. quadristriatus* plus *T. obtusus*). Other contrasts with negative values were comparisons between close species, except those contrasting *Nebria*

plus *Leistus* vs *Notiophilus*, *Loricera* vs *Carabus*, and Pterostichini vs Zabrinini when Erwin & Sims (1984) classification was used (Fig. 3). In all these cases, an increase in trochanter length was correlated with a decrease the femur width, in opposition to the general trend in the family.

In the comparison between the length of the antennae and the length of the femur, for both classifications the contrasts between the species of *Nebria* (*N. salina* vs *N. brevicollis*), the subgenera of *Elaphrus* (*E. lapponicus* vs *E. uliginosus* plus *E. cupreus* vs. *E. riparius*), and the genera *Asaphidion* vs *Bembidion*, were negative, i.e. an increase of the length of the antennae was negatively correlated with an increase of the length of the femur (Fig. 4). The contrast between the genera *Laemostenus* and *Calathus* was also negative when the Kryzhanovskij *et al.* (1995) classification was used, but, because of the different arrangement of genera within the tribe Pterostichini, this contrast was not studied when the classification used was that of Erwin & Sims (1984).

When the Erwin & Sims (1984) classification was used in the comparison of the length of the femur and the length of the antennae, the contrasts between Nebriini (*Leistus* plus *Nebria*) vs Notiophilini (*Notiophilus*), and between the supertribes of Carabinae (Nebriitae, Loriceritae, Carabitae, Cicindelitae and Elaphritae) had relatively low values (Fig. 4). These contrasts were not included when the Kryzhanovskij *et al.* (1995) classification was used owing to the different arrangement of the subfamilies and supertribes. In all of them a group that included exclusively diurnal visual hunters (*Notiophilus*, *Elaphrus* and *Cicindela*) was compared with nocturnal or day/night hunters (*Nebria*, *Leistus* and *Loricera*) (Bauer, 1982, 1985a; Luff, 1998). In these cases changes in the length of the antennae were not or only slightly positively correlated with changes in the length of the femur.

Quantitative vs qualitative variables

Few of the significant relationships between quantitative and qualitative morphological variables were reproduced

Table 8. Relationships between qualitative and quantitative morphological variables, as compared with phylogenetic independent contrasts. Only values for significant relationships ($P < 0.05$) are given. n , number of contrasts. See Table 2 for the codes of the variables

Independent variable	Dependent variable	Kryzhanovskij <i>et al.</i> (1995)			Erwin & Sims (1984)		
		Mean	95% conf. interval	n	Mean	95% conf. interval	n
CLB	LAL	-0.012	0.0095	17			
	F2	0.18	0.17	17	0.21	0.18	17
PRS	LAL	-0.032	0.023	4	-0.034	0.025	4

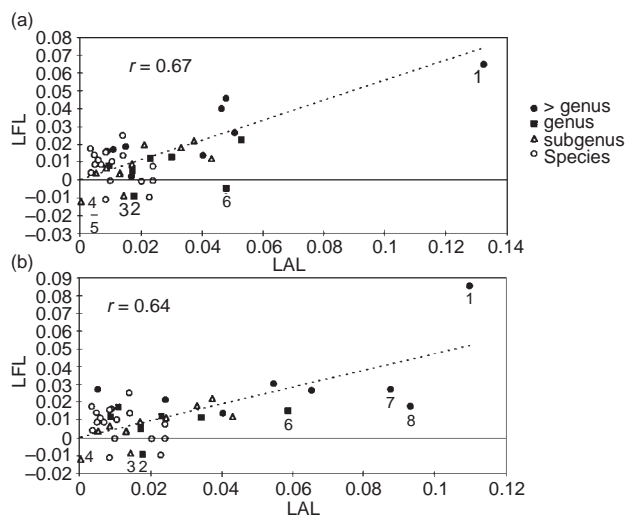


Fig. 4. Plot of independent contrasts on log length of the antennae (LAL) vs independent contrasts on log length of the femur (LFL) using the classifications by (a) Kryzhanovskij *et al.* (1995) and (b) Erwin & Sims (1984). 1. (a) Supertribes of Carabinae (Nebriitae, Notiophilitae, Carabitae, Elaphritae, Loriceritae, Scarititae, Broscitae, Trechitae, Patrobitae, Pterostichitae, Harpalitae, Callistitae, Lebiitae) or (b) subfamilies of Carabidae (Carabinae, Scaritinae, Broscinae, Psydrinae, Harpalinae); 2. *Asaphidion* vs *Bembidion*; 3. Subgenera of *Elaphrus* (*E. lapponicus* vs (*E. uliginosus* + *E. cupreus*) vs *E. riparius*); 4. Species of *Nebria* (*N. salina* vs *N. brevicollis*); 5. *Calathus* vs *Laemostenus*; 6. Genera of Perostichini, (a) *Stomis* vs *Poecilus* vs *Pterostichus*, (b) *Stomis* vs *Poecilus* vs *Pterostichus* vs *Calathus* vs *Laemostenus* vs *Synuchus* vs *Olisthopus* vs *Anchomenus* vs *Platynus* vs *Agonum*; 7. *Leistus* + *Nebria* vs *Notiophilus*; 8. Supertribes of Carabinae (Nebriitae, Loriceritae, Carabitae, Cicindelitae, Elaphritae).

when studied with phylogenetic independent contrasts. The relationship between the colour of the body (CLB) and the second ordination axis was still significant when compared using CAIC, with both classifications (Table 8, Fig. 5). The relationship between colour and length of the antennae (LAL) was also supported, but only for the classification of Kryzhanovskij *et al.* (1995). Similarly, the relationship between the shape of the pronotum (PRS) and the length of the antennae was significant only when the classification of Kryzhanovskij *et al.* (1995) was used (Table 8).

No additional relationships between the qualitative

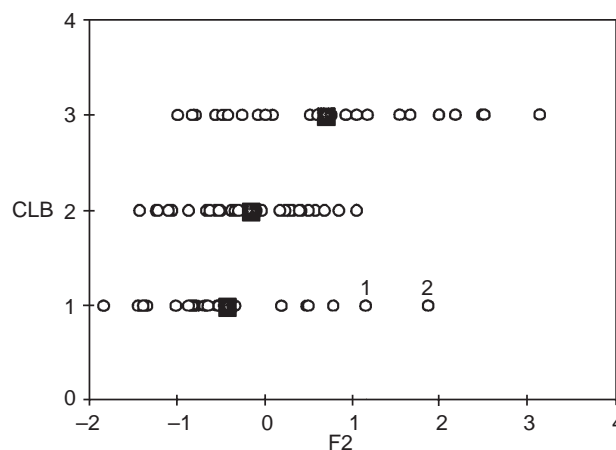


Fig. 5. Plot of the scores of the species in the second ordination axis (F2) on the colour of the body (CLB). 1, *Curtonotus aulicus*, 2, *Cicindela campestris*. Squares: average value per colour.

and quantitative morphological variables for the raw data described above proved significant when compared with phylogenetic independent contrasts.

DISCUSSION

Description of the morphospace

One of the surprising results of the multivariate ordination of the species studied was the placement of species considered to be morphologically similar at a relatively large distance from each other in the morphospace. This could be due partly to sampling errors owing to the low number of specimens measured, with an under-representation of the between and within population variability in size and shape. In extensive comparisons of multiple species, in which the total range of the morphologies included is much broader than the intraspecific variability of any of the individual species included, a small number of specimens is enough to obtain a good description of the wider morphospace (Marcus, 1990), but the detailed position of some species (in particular for intermediate scores) may have some uncertainty.

However, even in the most striking cases (the pairs *Bembidion guttula* and *B. mannerheimi*, *Pterostichus*

nigrita and *P. rhaeticus*, *Notiophilus germinyi* and *N. palustris*, for the second and the third axes), differences were mainly due to quantitative characters not used in general identification. They may reflect differences in mode of life, as with *P. rhaeticus* (closer to species of *Harpalus* and *Amara*, which have a higher proportion of plant material in their diets) or *B. bruxellense* in relation to *B. tetracolum*, which are diurnal and nocturnal respectively (Luff, 1998). Thus, in a comparative study of the morphology of the head, eyes and antennae of several species of the apparently homogeneous genus *Bembidion*, Morwinsky & Bauer (1997) did find significant differences among them, which were associated with differences in their hunting behaviour.

The species with larger eyes, wider heads and a higher pronotum (high scores for the first and second axes), basically *Notiophilus*, *Elaphrus* and *Cicindela*, are all typical visual hunters. *Elaphrus lapponicus* and *Asaphidion* had the lowest values among this group: the eye adaptations to visual hunting of the latter are less specialized than in *Notiophilus*, with less binocular overlap (Bauer, 1985b).

Species with smaller eyes, relatively flatter pronotum, and in general smaller antennae (lower values on the second axis) included interstitial species (e.g. *Trechoblemus micros* and *Trechus rubens*), or diggers (*Clivina fossor*) (Lindroth, 1945), together with *Platynus assimile* and *Agonum gracile*. *Platynus assimile* is found mainly under moss and bark of rotting stumps, or under foliage and twigs (Lindroth, 1945), and *A. gracile* is found associated with *Sphagnum* moss (Lindroth, 1945; Luff, 1998): the morphology of both species may be equally well suited to interstitial habits, bark or coarse debris the former, and dense *Sphagnum* the latter.

The third ordination axis reflected the strong correlation between length of the trochanter and width of the femur, which was in accordance with the observations by Evans (1977) and Forsythe (1981). Species with long trochanters and wide femora also had wide pronota and elytra (more robust shape), and small eyes. Most of them are included among 'Group II' of species by Forsythe (1981, 1983b), i.e. poor runners but strong wedge-pushers. *Asaphidion* spp. were also included in this group, mainly due to their relatively large trochanter (a characteristic also noted by Bauer & Kredler, 1993), despite being active hunters. Their relative long trochanter was interpreted as a phylogenetic remnant, due to the younger condition of the 'visual hunting' character (Bauer & Kredler, 1993). However, in the morphospace defined by the species included in this study *Asaphidion flavipes* was placed close to fast running species of 'Group I', such as *Leistus* spp., *Nebria* spp., or *Loricera pilicornis*, more in accordance with its general way of life (Figs 1 & 2). The same happened with *L. pilicornis*: a special case is made by Forsythe (1981, 1983b) with this species, including it among those of 'Group I' owing to its measured high fast running, despite its relatively large trochanters. When a multivariate approach is used there is no need of such a special allowance to accommodate *L. pilicornis*

among other fast runners (Figs 1 & 2). The particular character of its large trochanters (related to its special mode of feeding according to Forsythe, 1981 and Bauer, 1982) is not enough to conceal other morphological modifications common to fast runners.

According to Evans (1986), species of Carabinae (in this study *Cyrrhus* and *Carabus*) had intermediate characters between fast runners and strong pushers, having long and slender legs, but a more deep and robust body shape. The species investigated by Forsythe (1981) (*Cyrrhus caraboides*, *Carabus arvensis*, *C. violaceus*, *C. problematicus* and *C. nemoralis*) had moderate running velocity, but were strong horizontal and wedge pushers. The results of the multivariate ordination in this study show that these species do not form a homogeneous group. *Cyrrhus* has the most deviating morphology, positive for the first axis and negative for the second. It is closest to *Agonum gracile*, *Platynus assimile*, *Trechus rubens*, or *Loricera pilicornis*. It has also high values for the third axis, with extremely long and thin femora, and small trochanters. Species of *Carabus* had less deviating morphologies, although with some differences among them. *Carabus nitens*, *C. nemoralis* and *C. arvensis* were closer to species of the genera *Amara* and *Harpalus* in their position on the second and third axes: they were more robust, with larger trochanters, wider femora, and shorter antennae. *Carabus violaceus* shows the opposite trend, being closer to *Cyrrhus*, *Elaphrus* and *Notiophilus* on the third axis (i.e. with long thin legs and short trochanter). *Carabus glabratus*, *C. problematicus* and *C. granulatus* had intermediate scores for all axes, being closer to *C. violaceus*. It would be most interesting to know if these different morphologies are associated with differences in locomotion or feeding strategies.

A particular case is the group formed by *Miscodera arctica*, *Clivina fossor* and *Dyschiroides globosus*. All three species had extreme low scores for the first axis and extreme high scores for the third, largely due to their short and thin hind legs, short trochanters and antennae, and small eyes. This combination of characters, in addition to their pedunculate body, is not found in any other species, as seen above. *Clivina* is a digger species, except in the reproductive period (Desender, 1983). Known morphological characters interpreted to be adaptations to life in the soil are a flat (e.g. *Trechus* or *Trechoblemus*) or cylindrical (e.g. *Clivina*, *Dyschiroides*) body (Coiffait, 1960). Other characters recognized by the same author include a narrower base of the pronotum and elongation of the mesothorax, with the prothorax often pedunculate. These may allow a better mobility inside the soil cracks and galleries, and the possibility to easily change the orientation of the movement between soil particles. They also have shorter legs, and smaller trochanters (Coiffait, 1960). *Dyschirius* and *Dyschiroides* are closely related genera living mostly in sand or mud, digging galleries to predate rove beetles of the genus *Bledius* (Staphylinidae), on which many species depend (Lindroth, 1945; Luff, 1998). *Dyschiroides globosus* is the most eurytopic and abundant of the

British species of this group, being found in many kinds of habitats preying on a wider range of species (Lindroth, 1945; Luff, 1998). This has been accomplished without changing its morphology, which has still all the characters of specialized digger species.

There are few data on the biology of *Miscodera arctica*. It is essentially a montane species, with a boreo-alpine distribution, living in moors and heaths, especially on well draining stony moraine soils with a high content of fine sand, where it is supposed to be a specialized predator on beetles of the family Byrrhidae (Lindroth, 1945). There are several beetle species known to live in alpine moraine habitats which show the typical morphology of interstitial or subterranean life (e.g. Sømme, 1989; Molenda, 1996). *Miscodera* is the only Broscitid included in the study (with a classification of supertribe in Kryzhanovskij *et al.*, 1995, and subfamily in Erwin & Sims, 1984), and its morphological similarity with *Dyschiroides globosus* and *Clivina fossor* is a remarkable case of homoplasy.

The absence of significant relationships between the ordination axes and size demonstrates that the basic structure and range of the morphospace is reproduced at different body sizes, parallel groups of species having similar morphologies but different body size. This is the case of the group formed by *Trechoblemus micros*, *Trechus* spp., *Loricera pilicornis*, *Agonum gracile*, *Platynus assimile*, and *Cychrus caraboides*; that formed by *Bembidion mannerheimi*, *B. lampros*, *Asaphidion flavipes*, *Notiophilus* spp., *Elaphrus* spp., and *Cicindela*; or the one formed by *Dyschiroides globosus*, *Clivina fossor* and *Miscodera arctica*. All three groups had similar scores for the first and second axes, despite their wide differences in body size (from 3.3 mm in *T. micros* to 13.8 mm in *C. caraboides*, from 2.6 mm in *B. mannerheimi* to 10.8 mm in *C. campestris*, and from 2.3 mm in *D. globosus* to 6.4 mm in *M. arctica*: Appendix). Despite their similar morphology (as measured with the defined morphospace) the species of these groups vary widely in taxonomy, with a high degree of homoplasy in the morphological characters involved. This can be taken as an indication of parallel morphological trends, probably associated with ecological or biological strategies, occurring independently in different phyletic lines.

It is interesting to note the nested occurrence of body and leg colours: pale species have only pale legs, black species can have black or pale legs, and metallic species can have any type of leg colours. This is compatible with a plesiomorphic condition of the pale colour, although phylogenetic information is not enough to allow conclusions on the polarization of the colour character (as is the case of most of the characters involved in this study). Black species have in general an intermediate shape between pale and metallic ones. A particular problem arose with species with variegated colours, such as *Anchomenus dorsalis*, *Bembidion bruxellense*, *B. tetracolum*, or *Badister bullatus*. All of them have generally pale elytra, but with some dark metallic patches. All of them belong to genera or groups of genera with general

pale or black colour, with the exception of *Badister*, which has a more varied colour pattern.

Phylogenetic independent contrasts

Most correlations between quantitative characters were supported when compared with phylogenetic independent contrasts, i.e. character associations arose independently several times in the phylogeny of the group. In particular, all major relationships defining the three ordination axes were still significant when measured with phylogenetic independent contrasts, with the only exception of the correlations with width of the head (influencing scores of the second axis), which were not significant when studied with CAIC. The comparison of independent contrasts according to the taxonomic level at which they were constructed showed that the largest shape differences corresponded to the highest taxonomic and phylogenetic distances. Main morphological types were defined at the supertribe level in the classification of Kryzhanovskij *et al.* (1995), or the subfamily level in that of Erwin & Sims (1984). Conversely, contrasts comparing species of the same subgenus or genus were not significant, and often of opposite sign to the major trend of the whole group. Part of this result may be due to noise in the data, with the contrast between close taxa being more sensitive to errors in the measurement due to their lower absolute differences (Purvis & Rambaud, 1995).

Contrasts including qualitative variables were mostly not significant, due in some cases to the low number of contrasts that could be constructed. This was because of the high number of polytomies in the classifications used. Only the most apparent relationships were validated, such as colour of the body with the second axis.

In evaluating the differences between the results obtained with the direct comparison of the data, and those obtained with independent contrasts, some cautionary notes had to be made. When a data set is phylogenetically well balanced, and does include members of different phyletic lines, results obtained with the direct comparison of morphological trends are likely to be not very different from those obtained with phylogenetically independent contrasts (Ricklefs & Starck, 1996), as seen with the comparison of the quantitative variables. The uncertainty underlying some of the assumptions of the phyletic methods, as well as the reduced degrees of freedom due to the limited number of independent contrasts that can be constructed (which was the case with the comparisons that include one categorical variable), has led some authors to doubt the convenience of systematically discarding the patterns found with a non-phylogenetic approach (e.g. Ricklefs & Starck, 1996).

The existence of significant associations of characters is a strong suggestion that such associations have been selected independently in different lines, and thus may represent adaptive characters. However, alternative explanations do exist and must be considered (Leroi,

Rose & Lauder, 1994; Doughty, 1996). According to Frumhoff & Reeve (1994), phylogenetic analysis cannot be used to determine whether a character arose in ancestral populations through natural selection for its current function (a true adaptation in the sense of Gould & Vrba, 1982), or whether its presence in an extant taxon results from a phylogenetic constraint on adaptive evolution, but does not contribute to the increase in fitness of the present species (irrespective of its origin). Thus, characters that are genetically correlated can have similar topologies in a phylogeny, even if one of them does not contribute to the increase of fitness and in consequence is not an adaptation (Lauder, Leroi & Rose, 1993; Koehl, 1996). Even if a character is known to be correlated with an increase in performance, there is still the possibility that this increase has no effect on the fitness of populations in natural conditions (Lauder *et al.*, 1993). In the conceptual process that leads to the acceptance of the functional condition of a character (morphology – function – theoretical performance – actual resource use – fitness: Reilly & Wainwright, 1994; Koehl, 1996), the demonstration of its independent occurrence in the evolutionary history of a group is only indirect evidence compatible with its appearance through natural selection.

Likewise, the lack of significance of the independent contrasts does not always mean a lack of adaptation of the characters involved. Unique apomorphies may have been caused by natural selection, but statistical comparative methods can only evaluate general trends occurring independently in several phyletic lines, treating independent evolutionary events as replicates. Evidence has to be gathered from other sources (use of a wider data set, direct measurements of performance and fitness: Doughty, 1996). Experimental manipulations are often the only definitive way to discriminate among these alternative hypotheses, and to demonstrate the true functional condition of the characters involved.

The recognition of the main trends in the morphospace defined by the species under study, and the demonstration that some of the association of characters had evolved independently in different phyletic lines (even when an approximate phylogeny is used), is an important step towards the understanding of their functional morphology. The evolutionary trends leading to the diversification and extension of many clades had their origin in key adaptations, which can be considered as a relaxation of previous trade-offs through increasing the number of independent parameters controlling form (Vermeij, 1973; Rosenzweig & McCord, 1991). It is still not possible with the descriptive approach of this paper to ascribe adaptive value to the morphological trends found, but the interpretation of the adaptive radiation of carabids may undoubtedly benefit from the basic identification of homoplastic character associations within the morphospace, which are likely to include among them those trade-offs governing their functional morphology. Once these morphological associations of characters have been detected and defined, it is possible

to investigate their relationships with the life traits or ecological strategies of the species, with the aim to characterize their functional diversity in a broader sense.

Acknowledgements

We thank Shona Blake, Martin Luff and Alfried Vogler for their comments on earlier versions of the manuscript. Martin Luff provided us with additional specimens of selected species to be measured. We also thank M. E. G. Evans and an anonymous referee for their comments on the manuscript. The Scottish Agricultural College receives financial support from the Scottish Office Agriculture, Environmental and Fisheries Department.

REFERENCES

- Abernethy, V. J., McCracken, D. I., Adam, A., Downie, I., Foster, G. N., Furness, R. W., Murphy, K. J., Ribera, I., Waterhouse, A. & Wilson, W. L. (1996). Functional analysis of plant–invertebrate–bird biodiversity on Scottish agricultural land. In *The spatial dynamics of biodiversity: towards an understanding of spatial patterns & processes in the landscape*: 51–59. Simpson, A. & Dennis, P. (Eds). Stirling: International Association for Landscape Ecology.
- Bauer, T. (1982). Predation by a carabid beetles specialized for catching Collembola. *Pedobiologia* **24**: 169–179.
- Bauer, T. (1985a). Beetles which use a setal trap to hunt springtails: the hunting strategy and apparatus of *Leistus* (Coleoptera, Carabidae). *Pedobiologia* **28**: 275–287.
- Bauer, T. (1985b). Different adaptation to visual hunting in three ground beetle species of the same genus. *J. Insect Physiol.* **31**: 593–601.
- Bauer, T. & Kredler, M. (1993). Morphology of the compound eyes as an indicator of life-style in carabid beetles. *Can. J. Zool.* **71**: 799–810.
- Coiffait, H. (1960). Les adaptations des coléoptères édaphobies. *Ver. XI Int. Congr. Ent.* **1**: 378–382.
- Desender, K. (1983). Ecological data on *Clivina fossor* (Coleoptera, Carabidae) from a pasture ecosystem. *Pedobiologia* **25**: 157–167.
- Desender, K., Dufrière, M., Loreau, M., Luff, M. L. & Maelfait, J. P. (Eds) (1994). *Carabid beetles: ecology and evolution*. Dordrecht: Kluwer Academic Publishers.
- Díaz-Uriarte, R. & Garland, T. Jr (1996). Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from brownian motion. *Syst. Biol.* **45**: 27–47.
- Doughty, P. (1996). Statistical analysis of natural experiments in evolutionary biology: comments on recent criticisms of the use of comparative methods to study adaptation. *Am. Nat.* **148**: 943–956.
- Downie, I. S., Abernethy, V. J., Foster, G. N., McCracken, D. I., Ribera, I. & Waterhouse, A. (1998). Spider biodiversity on Scottish agricultural land. In *Proceedings of the 17th European Colloquium on Arachnology*, 1997: 311–317. Selden, P. A. (Ed.). Edinburgh: British Arachnological Society.
- Erwin, T. L. & Sims, L. L. (1984). Carabid beetles of the West Indies (Insects: Coleoptera): a synopsis of the genera and checklists of tribes of Caraboidea, and of the West Indian species. *Quaest. Entomol.* **20**: 351–466.

- Evans, M. E. G. (1977). Locomotion in the Coleoptera Adephaga, especially Carabidae. *J. Zool. (Lond.)* **181**: 189–226.
- Evans, M. E. G. (1986). Carabid locomotor habits and adaptations. In *Carabid beetles: their adaptations and dynamics*: 59–77. Den Boer, P. J., Mossakowski, D., Luff, M. L. & Weber, F. (Eds). Stuttgart: Gustav Fisher.
- Evans, M. E. G. (1990). Habits or habitats: do carabid locomotor adaptations reflect habitats or lifestyles? In *The role of ground beetles in ecological and environmental studies*: 295–305. Stork, N. E. (Ed.). Newcastle: Intercept.
- Evans, M. E. G. & Forsythe, T. G. (1984). A comparison of adaptations to running, pushing and burrowing in some adult Coleoptera, specially Carabidae. *J. Zool. (Lond.)* **202**: 513–534.
- Evans, M. E. G. & Forsythe, T. G. (1985). Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *J. Zool. (Lond.)* **206**: 113–143.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Foote, M. (1992). Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology* **18**: 1–16.
- Foote, M. (1997). The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* **28**: 129–152.
- Forsythe, T. G. (1981). Running and pushing in relationship to hind leg structure in some carabidae (Coleoptera). *Coleopt. Bull.* **35**: 353–378.
- Forsythe, T. G. (1983a). Mouthparts and feeding of certain ground beetles (Coleoptera: Carabidae). *Zool. J. Linn. Soc.* **79**: 319–376.
- Forsythe, T. G. (1983b). Locomotion in ground beetles (Coleoptera: Carabidae): an interpretation of leg structure in functional terms. *J. Zool. (Lond.)* **200**: 493–507.
- Forsythe, T. G. (1987). The relationship between body form and habit in some Carabidae (Coleoptera). *J. Zool. (Lond.)* **211**: 643–666.
- Forsythe, T. G. (1991). Feeding and locomotory functions in relation to body form in five species of ground beetle (Coleoptera: Carabidae). *J. Zool. (Lond.)* **223**: 233–263.
- Frumhoff, P. C. & Reeve, H. K. (1994). Using phylogenies to test hypotheses of adaptation: a critique of some current proposals. *Evolution* **48**: 172–180.
- Gould, S. J. (1991). The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology* **17**: 411–423.
- Gould, S. J. & Vrba, E. (1982). Exaptation: a missing term in the science of form. *Paleobiology* **8**: 4–15.
- Harvey, P. H. (1996). Phylogenies for ecologists. *J. Anim. Ecol.* **65**: 255–263.
- Harvey, P. H. & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Jarošík, V. (1989). Mass vs length relationship for carabid beetles (Col., Carabidae). *Pedobiologia* **33**: 87–90.
- Kavanaugh, D. H. (1985). On wing atrophy in carabid beetles (Coleoptera: Carabidae), with special reference to Nearctic *Nebria*. In *Taxonomy, phylogeny and zoogeography of beetles and ants*: 408–432. Ball, G. E. (Ed.). Dordrecht: Dr. W. Junk Publishers.
- Koch, D. (1984). *Pterostichus nigrita*, ein Komplex von Zwillingarten. *Ent. Bl. Biol. Syst. Käfer* **79**: 141–152.
- Koehl, M. A. R. (1996). When does morphology matter? *Annu. Rev. Ecol. Syst.* **27**: 501–542.
- Kryzhanovskij, O. L., Belousov, I. A., Kabak, I. I., Kataev, B. M., Makarov, K. V. & Shilenkov, V. G. (1995). *A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae)*. Sofia: Pensoft Publishers.
- Lauder, G. V., Leroi, A. M. & Rose, M. R. (1993). Adaptations and history. *Trends Ecol. Evol.* **8**: 294–297.
- Leroi, A. M., Rose, M. R. & Lauder, G. V. (1994). What does the comparative method reveal about adaptation? *Am. Nat.* **143**: 381–402.
- Lindroth, C. H. (1945). *Ground beetles (Carabidae) of Fennoscandia* **1**. Washington, D.C.: Smithsonian Institution Libraries. (Translated from the German, edited in 1992.)
- Lindroth, C. H. (1974). *Coleoptera: Carabidae. Handbooks for the identification of British insects* **4(2)**. London: Royal Entomological Society.
- Lindroth, C. H. (1985). *Fauna Entomologica Scandinavica* **15. The Carabidae (Coleoptera) of Fennoscandia and Denmark, I**. Leiden: E. J. Brill.
- Lindroth, C. H. (1986). *Fauna Entomologica Scandinavica* **15. The Carabidae (Coleoptera) of Fennoscandia and Denmark, II. With an appendix on the family Rhysodidae**. Leiden: E. J. Brill.
- Lövei, G. L. & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu. Rev. Entomol.* **41**: 231–256.
- Luff, M. L. (1990). *Pterostichus rhaeticus* Heer (Col., Carabidae). A British species previously confused with *P. nigrita* (Paykull). *Entomol. Month. Mag.* **126**: 245–249.
- Luff, M. L. (1998). *Provisional atlas of the Coleoptera: Carabidae (ground beetles) of Britain and Ireland*. Huntingdon: Institute of Terrestrial Ecology.
- Manton, S. M. (1977). *The Arthropoda, habits, functional morphology and evolution*. Oxford: Clarendon Press.
- Marcus, L. F. (1990). Traditional morphometrics. *Proceedings of the Michigan Morphometrics Workshop, 16–18 May 1988, Ann Arbor*: 77–122. Rohlf, F. J. & Bookstein, F. L. (Eds). Ann Arbor: Special Publication No. 2, University of Michigan Museum of Zoology.
- Miles, D. B. & Dunham, A. E. (1993). Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annu. Rev. Ecol. Syst.* **24**: 587–619.
- Molenda, R. (1996). Zoogeographische Bedeutung Kaltluft erzeugender Blockhalden im außeralpinen Mitteleuropa: Untersuchungen an Arthropoda, insbesondere Coleoptera. *Verh. naturwiss. Ver. Hamburg (NF)* **35**: 5–93.
- Morwinsky, T. & Bauer, T. (1997). Prediction of life style by eye morphology in *Bembidion* species (Coleoptera, Carabidae). *Pedobiologia* **41**: 472–480.
- Niemelä, J. (Ed.) (1996). Population biology and conservation of carabid beetles. 3rd International Symposium of Carabidology. *Ann. Zool. Fenn.* **33**: 1–241.
- Pagel, M. D. (1992). A method for the analysis of comparative data. *J. theor. Biol.* **156**: 431–442.
- Purvis, A. & Rambaud, A. (1995). Comparative analysis by independent contrasts (CAIC): and Apple Macintosh application for analysing comparative data. *Computer Appl. Biosciences* **11**: 247–251.
- Queiroz, K. de (1996). Including the characters of interest during tree reconstruction and the problems of circularity and bias in studies of character evolution. *Am. Nat.* **148**: 700–708.
- Reilly, S. M. & Wainwright, P. C. (1994). Conclusion: ecological morphology and the power of integration. In *Ecological morphology: integrative organismal biology*: 339–354. Wainwright, P. C. & Reilly, S. M. (Eds). Chicago: University of Chicago Press.
- Reyment, R. A., Blackith, R. E. & Campbell, N. A. (1984). *Multivariate morphometrics* (2nd edn). London: Academic Press.
- Ribera, I. & Nilsson, A. N. (1995). Morphometric patterns among diving beetles (Coleoptera: Noteridae, Hygrobiidae, Dytiscidae). *Can. J. Zool.* **73**: 2343–2360.
- Ricklefs, R. E. & Mails, D. B. (1994). Ecological and evolutionary inferences from morphology: an ecological perspective. In *Ecological morphology: integrative organismal biology*: 13–41. Wainwright, P. C. & Reilly, S. M. (Eds). Chicago: University of Chicago Press.
- Ricklefs, R. E. & Starck, J. M. (1996). Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**: 167–172.

- Rosenzweig, M. L. & McCord, R. D. (1991). Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* **17**: 202–213.
- Roy, K. & Foote, M. (1997). Morphological approaches to measuring biodiversity. *Trends Ecol. Evol.* **12**: 277–281.
- Sharova, J. K. (1974). [Life forms of imago in Carabidae.] *Zool. Zh.* **53**: 692–709. [In Russian.]
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. (3rd edn). New York: Freeman & Co.
- Sømme, L. (1989). Adaptations of terrestrial arthropods to the alpine environment. *Biol. Rev.* **64**: 367–407.
- Thiele, H. U. (1977). *Carabid beetles in their environments*. Berlin: Springer-Verlag.
- Vermeij, G. J. (1973). Biological versatility and earth history. *Proc. Nat. Acad. Sci., U.S.A.* **70**: 1936–1938.

Appendix. Average values of the measurements per species. Quantitative measurements in mm/10. For codes of the species, variables names, and values of the qualitative variables, see Tables 1 & 2. *n*, number of specimens measured (males / females)

Code	<i>n</i>	HW	YW	AL	PW	PH	EW	FL	TR	BL	RL	FW	PL	EL	TL	F1	F2	F3	CLG	CLB	PUB	WIN	PRS
AGON DOLE	3/3	11.9	2.8	45.2	22.9	18.9	34.0	25.3	24.3	23.8	20.8	5.2	17.3	50.3	67.6	0.73	-0.51	-0.37	2	2	1	3	1
AGON FULI	3/3	9.0	2.3	35.0	16.4	14.0	24.5	19.3	8.2	18.0	15.2	4.0	13.9	37.0	50.9	1.05	-0.68	-0.28	2	2	1	2	1
AGON GRAC	2/3	8.3	2.1	32.2	14.2	12.1	22.8	17.2	5.0	16.0	13.6	3.4	12.1	36.7	48.8	0.56	-1.43	0.55	2	2	1	3	1
AGON MARG	3/3	14.9	3.9	50.3	25.7	20.9	40.3	31.3	9.8	28.7	25.4	6.0	18.7	63.8	82.5	0.55	-0.80	0.34	1	3	1	3	1
AGON MUEL	3/3	11.9	2.8	41.8	21.8	17.7	31.8	23.6	20.6	21.1	18.7	5.5	16.5	48.5	65.0	0.38	-0.58	-0.46	2	3	1	3	1
AGON VIDU	3/3	11.8	2.9	44.5	22.6	19.0	33.5	25.1	12.8	22.7	20.1	5.1	17.1	50.1	67.2	0.58	-0.50	-0.28	2	2	1	3	1
AMAR AENE	3/3	13.8	2.5	25.0	27.4	18.4	31.9	19.2	17.8	17.5	15.6	5.4	16.6	45.9	62.5	-1.07	0.93	-1.27	1	3	1	3	3
AMAR APRI	3/3	16.7	2.9	29.5	27.6	19.6	33.7	19.5	7.4	18.0	15.3	6.0	17.8	50.6	68.5	-1.55	0.79	-0.76	1	1	1	3	3
AMAR BIFR	3/3	12.3	2.1	25.7	22.3	15.7	26.4	16.4	5.0	15.1	12.7	4.9	15.1	39.3	54.4	-1.00	0.47	-1.16	1	1	1	3	3
AMAR COMM	3/3	15.5	2.4	28.2	29.2	18.7	31.7	18.9	19.5	17.3	14.9	5.2	17.5	45.7	63.2	-1.27	1.04	-1.16	2	2	1	3	3
AMAR EURY	3/3	19.8	3.3	37.7	42.6	27.3	48.0	30.1	11.6	27.8	26.5	8.3	23.7	66.8	90.5	-0.73	1.16	-1.70	1	3	1	3	3
AMAR FAMI	3/3	12.7	2.4	26.2	25.4	16.8	29.4	17.8	5.0	16.4	13.6	4.9	16.3	42.3	58.6	-1.10	0.57	-1.02	1	2	1	3	3
AMAR LUNI	3/3	15.4	1.9	30.3	30.9	19.9	34.4	20.8	19.3	19.4	17.3	5.7	19.1	50.7	69.7	-1.43	0.30	-1.00	2	2	1	3	3
AMAR OVAT	3/3	16.8	3.1	35.3	36.3	23.2	40.7	25.3	14.5	23.6	20.9	6.9	21.3	58.2	79.5	-0.95	0.72	-1.40	2	3	1	3	3
AMAR PLEB	3/3	13.4	2.8	28.7	26.3	18.4	30.7	20.4	6.3	18.4	16.7	5.1	17.5	45.3	62.8	-0.62	0.77	-0.65	1	3	1	3	3
ANCH DORS	3/3	10.1	3.0	43.2	15.3	14.6	26.6	23.0	7.9	20.6	20.2	4.0	13.6	41.9	55.5	1.87	-0.85	0.53	3	1	1	3	2
ASAP FLAV	3/3	7.7	3.9	20.2	10.8	10.5	17.0	13.5	4.4	11.6	10.9	2.7	9.2	27.6	36.9	1.16	0.75	0.78	1	3	2	3	2
BADI BULL	3/3	9.7	1.7	33.6	17.0	12.9	23.3	17.2	9.4	15.5	15.7	4.5	12.7	36.5	49.2	0.58	-0.83	-0.98	1	3	1	3	1
BEMB AENE	3/3	7.6	2.1	21.7	12.1	9.3	17.8	12.1	6.5	10.5	9.1	2.7	8.4	27.1	35.6	0.52	-0.11	-0.30	2	2	1	2	1
BEMB BRUX	3/3	7.8	2.0	24.9	12.3	10.2	19.2	14.0	5.4	11.6	10.1	2.8	9.4	30.9	40.3	0.24	-0.86	0.45	1	1	1	3	2
BEMB GUTT	3/3	6.2	1.7	17.0	9.6	7.5	13.5	9.7	16.3	8.1	7.0	2.0	7.0	21.2	28.2	0.53	-0.03	-0.14	1	2	1	2	1
BEMB LAMP	3/3	6.9	2.6	17.6	10.2	8.4	14.5	10.5	19.5	9.0	8.0	2.3	7.7	22.9	30.6	0.74	0.59	0.12	1	2	1	2	2
BEMB MANN	3/3	6.3	1.7	15.9	9.6	7.2	12.9	9.2	15.1	7.7	6.2	2.1	7.1	18.8	25.9	0.86	0.69	-0.85	1	2	1	1	1
BEMB OBTU	3/3	6.0	1.4	14.4	9.0	6.6	12.0	8.3	12.9	6.7	6.1	1.9	6.5	18.5	24.9	0.37	0.19	-0.38	1	1	1	2	1
BRAD HARP	3/3	7.8	1.8	17.7	12.5	9.8	18.6	11.2	9.9	10.1	7.0	2.5	9.2	28.6	37.8	-0.98	-0.38	0.48	1	1	1	2	1
BRAD RUF1	3/3	5.9	1.2	13.1	9.6	7.4	14.3	8.1	19.7	7.3	5.1	1.8	7.1	21.8	28.8	-1.18	-0.57	0.61	1	2	1	3	1
BRAD VERB	3/1	8.9	1.8	19.7	13.9	11.2	20.7	12.5	7.3	11.3	7.8	2.7	10.2	32.1	42.3	-1.17	-0.41	0.65	1	1	1	3	1
CALA FUSC	3/3	17.9	3.8	53.9	33.9	27.6	42.9	34.5	7.3	34.0	33.1	8.1	27.3	70.2	97.4	0.05	-0.38	-0.31	1	2	1	1	3
CALA MELA	3/3	11.8	2.4	38.7	23.4	17.5	29.1	21.7	5.3	21.0	20.9	4.9	18.4	46.9	65.2	0.00	-0.80	-0.29	1	1	1	2	3
CALA MICR	3/3	11.3	2.1	38.4	21.9	16.8	29.3	23.0	9.3	21.8	20.9	4.8	17.8	46.1	63.9	0.41	-1.05	-0.28	1	2	1	1	3
CALA ROTU	3/3	14.4	3.1	50.4	26.8	21.3	36.6	30.0	9.4	27.7	27.1	6.1	22.1	55.7	77.8	0.78	-0.52	-0.29	1	2	1	2	1
CARA ARVE	3/3	25.7	5.7	92.2	53.2	46.3	71.4	58.4	8.8	57.2	55.0	11.8	34.5	115.9	150.4	0.31	0.08	0.20	2	3	1	1	1
CARA GLAB	3/3	33.4	6.4	116.0	70.6	60.3	90.3	81.3	8.2	74.8	66.5	14.7	46.0	155.8	201.8	-0.33	-0.35	0.89	2	2	1	1	2
CARA GRAN	3/3	26.4	6.5	105.9	49.7	45.6	70.5	62.9	12.8	60.1	59.2	11.9	33.4	121.1	154.5	0.68	-0.27	0.64	2	3	1	1	2
CARA NEMO	3/3	33.8	7.5	111.0	67.8	58.5	90.5	71.6	5.1	68.3	64.6	15.0	42.8	141.7	184.5	0.05	0.52	-0.05	2	3	1	1	2
CARA NITE	3/3	23.3	3.6	63.4	48.0	42.1	64.2	48.9	7.5	47.5	42.9	10.3	31.6	101.9	133.6	-0.45	0.09	0.00	2	3	1	1	1
CARA PROB	3/3	34.9	8.0	123.4	62.3	57.4	90.6	81.4	4.6	77.4	73.3	13.2	41.7	152.2	193.9	0.53	-0.04	1.03	2	2	1	1	2
CARA VIOL	3/3	34.6	7.0	121.0	65.5	60.6	88.9	80.8	7.2	77.6	68.4	13.8	47.0	161.0	208.1	-0.41	-0.64	1.57	2	2	1	1	2
CICI CAMP	3/3	26.5	8.7	73.1	32.1	34.4	53.8	48.0	4.4	47.3	52.4	6.5	22.9	85.1	108.0	2.39	1.86	1.44	3	1	1	3	2
CLIV FOSS	3/3	8.6	1.6	18.0	15.7	13.2	18.9	11.9	8.9	9.7	8.1	3.1	14.9	35.4	50.3	-3.61	-1.44	2.16	1	1	1	2	1
CURT AULI	3/3	26.3	4.2	49.1	41.1	30.9	49.4	34.0	8.7	31.6	29.5	9.7	26.1	76.2	102.3	-0.66	1.15	-1.18	1	1	1	3	3
CYCH CARA	3/3	20.3	4.9	101.1	37.2	39.1	64.9	64.6	7.9	58.7	47.9	9.2	36.2	101.9	138.1	1.22	-1.22	1.53	2	2	1	1	1
CYMI VAPO	3/3	12.4	3.0	43.9	19.1	16.5	31.0	23.7	10.9	20.8	19.1	5.0	15.9	46.3	62.2	0.94	-0.49	-0.10	1	3	2	2	2
DICH COGN	3/3	8.0	1.5	20.0	12.2	9.5	18.1	11.5	4.6	10.3	7.6	2.4	8.9	28.4	37.3	-0.64	-0.65	0.57	1	1	2	3	1

Code	<i>n</i>	HW	YW	AL	PW	PH	EW	FL	TR	BL	RL	FW	PL	EL	TL	F1	F2	F3	CLG	CLB	PUB	WIN	PRS
DICH PLAC	3/1	8.2	1.7	21.9	12.5	9.8	19.0	12.6	4.5	10.6	8.7	2.6	9.2	29.6	38.8	-0.32	-0.64	0.52	1	1	2	3	1
DYSC GLOB	3/3	4.2	1.1	8.3	7.6	6.9	9.7	5.4	10.2	4.5	3.4	1.2	7.1	15.6	22.7	-2.63	0.26	2.30	2	2	1	1	1
ELAP CUPR	3/3	16.4	5.8	33.1	22.0	22.5	36.3	26.4	8.5	24.3	21.2	4.8	19.8	53.1	72.9	0.41	1.54	1.39	3	3	1	3	2
ELAP LAPP	3/3	16.4	5.9	32.0	23.6	23.0	37.2	29.9	7.2	26.3	25.3	5.0	20.5	59.2	79.7	0.28	1.05	1.95	3	3	1	3	2
ELAP ULIG	3/3	16.5	6.8	31.5	24.7	23.7	37.4	27.1	14.4	25.5	22.0	5.3	20.9	56.3	77.2	0.10	1.67	1.42	3	3	1	3	2
HARP AFFI	3/3	18.5	3.0	36.6	31.3	23.6	37.7	25.1	9.0	23.9	18.7	7.8	21.2	57.4	78.7	-0.96	0.60	-1.59	1	3	2	3	3
HARP LATU	3/3	20.0	2.7	36.5	32.1	22.9	37.0	24.9	9.3	23.8	17.0	7.5	20.8	54.9	75.8	-0.85	0.86	-1.95	1	2	1	3	3
HARP RUF1	3/3	26.8	4.8	54.5	43.0	33.6	52.5	38.5	8.3	37.1	30.9	10.4	29.6	85.1	114.7	-0.81	0.50	-0.95	1	1	2	3	3
LAEM TERR	2/3	22.7	3.7	72.1	38.3	32.5	54.5	51.6	8.9	44.4	40.3	8.5	33.7	88.4	122.2	0.30	-0.99	0.70	1	3	1	1	2
LEIS FULVI	3/3	12.0	3.4	43.6	22.7	16.9	30.0	26.2	14.2	24.2	20.6	4.1	14.9	48.1	63.0	1.39	-0.07	0.67	1	3	1	3	2
LEIS TERM	3/3	9.9	2.9	40.6	18.2	13.9	24.3	21.6	4.0	21.1	17.6	3.7	12.3	40.5	52.8	1.71	-0.34	0.63	1	1	1	2	2
LORI PILI	3/3	10.2	3.2	39.7	20.6	15.9	28.6	24.7	4.3	21.5	19.8	4.4	15.1	47.7	62.8	0.79	-1.09	0.39	2	2	1	3	1
MISC ARCT	3/3	11.2	2.2	24.9	19.0	18.7	27.7	16.8	15.4	15.2	13.5	3.6	19.1	44.8	63.9	-2.32	-0.42	2.38	2	3	1	3	1
NEBR BREV	3/3	22.3	4.8	65.0	35.5	27.7	47.6	39.2	9.3	34.6	34.2	6.2	23.1	75.8	98.9	0.69	0.50	0.81	1	2	1	3	2
NEBR SALI	3/3	21.6	4.3	61.5	33.9	25.9	44.8	39.1	10.7	33.5	32.7	6.0	21.8	72.1	93.9	0.87	0.41	0.76	1	2	1	3	2
NOTI AQUA	3/3	13.5	5.1	17.2	15.4	12.2	19.5	15.7	7.0	12.8	13.9	3.5	10.9	34.7	45.6	0.21	2.00	1.21	3	3	1	3	2
NOTI BIGU	3/3	13.7	5.0	16.4	15.8	11.8	18.8	14.9	1.8	12.3	12.4	3.1	10.3	32.4	42.7	0.33	2.49	1.06	3	3	1	2	2
OTI PALU	2/3	14.3	5.2	17.2	16.3	12.7	19.8	15.5	4.4	13.6	13.2	3.1	11.3	33.7	45.1	0.34	2.50	1.11	3	3	1	2	2
NOTI SUBS	3/3	13.1	4.7	15.6	14.8	11.3	18.6	14.2	7.1	12.2	12.4	3.0	9.6	32.5	42.1	0.25	2.18	1.09	3	3	1	1	2
NOTI GERM	3/3	14.5	5.4	17.3	16.3	13.0	19.4	15.6	8.1	13.5	13.7	3.4	10.8	32.3	43.1	0.87	3.15	0.52	3	3	1	2	2
OLIS ROTU	3/3	10.7	2.3	31.3	19.5	14.9	26.3	20.5	3.8	18.4	15.0	5.0	14.9	41.6	56.5	0.17	-0.70	-0.74	1	1	1	2	1
PATR ASSI	3/3	11.8	2.7	38.9	19.4	16.6	27.2	20.4	14.0	18.5	14.7	5.4	15.9	46.9	62.7	-0.53	-1.03	0.15	1	1	1	1	2
PATR ATRO	3/3	12.8	3.4	42.3	20.5	17.5	29.4	23.0	7.1	20.5	17.5	5.1	16.6	48.7	65.3	0.13	-0.54	0.39	1	1	1	1	2
PLAT ASSI	3/3	15.2	3.9	61.1	27.4	22.1	43.7	35.9	12.9	33.3	28.7	6.5	21.4	67.8	89.2	0.92	-1.25	0.30	2	2	1	3	2
POEC VERS	3/3	17.8	3.9	50.0	37.2	27.3	43.0	32.3	8.0	30.0	31.7	8.6	25.7	68.8	94.5	-0.29	0.01	-1.05	2	3	1	3	1
PTER ADST	3/3	20.1	3.9	50.6	34.0	26.9	44.2	33.2	11.4	31.2	27.1	6.3	25.0	71.1	96.1	-0.46	-0.10	0.21	2	2	1	3	3
PTER AETH	3/3	22.3	3.7	56.7	36.9	29.8	46.5	38.1	14.4	35.2	30.8	9.7	27.8	71.5	99.3	0.23	0.30	-1.55	2	2	1	1	1
PTER CRIS	3/2	26.6	4.8	80.5	43.2	32.6	54.7	47.9	4.6	46.1	42.2	10.4	33.4	85.7	119.1	0.75	-0.19	-1.07	2	2	1	1	2
PTER DILI	3/3	9.7	2.0	26.0	17.2	13.7	21.5	15.7	5.3	13.5	11.0	3.7	14.1	35.0	49.1	-0.86	-0.52	-0.11	2	2	1	2	2
PTER MADI	3/3	27.5	4.7	63.4	44.0	35.0	52.0	40.9	18.8	40.7	34.1	11.0	32.4	85.1	117.5	-0.41	0.39	-1.05	1	2	1	1	1
PTER MELA	3/3	28.9	4.8	63.6	46.7	36.0	56.4	42.3	12.9	40.1	34.0	11.2	33.4	91.7	125.1	-0.88	0.24	-0.78	2	2	1	2	3
PTER NIGE	3/3	29.0	6.2	89.6	49.9	39.7	68.2	58.7	3.4	55.2	45.8	12.8	39.7	112.3	151.9	-0.10	-0.87	-0.29	2	2	1	3	3
PTER NIGR	3/3	18.0	3.7	49.7	31.9	24.3	40.0	28.9	6.3	28.6	24.0	7.7	23.4	64.4	87.8	-0.45	-0.30	-0.80	2	2	1	2	3
PTER RHAE	3/3	16.6	3.3	41.6	29.2	22.6	34.2	26.3	8.8	24.5	20.8	7.0	22.1	55.0	77.0	-0.38	0.16	-1.02	2	2	1	2	3
PTER STRE	3/3	10.5	2.3	29.2	18.0	14.0	24.0	16.7	3.4	14.9	12.3	4.0	14.9	37.4	52.3	-0.56	-0.52	-0.11	1	1	1	2	2
PTER VERN	3/3	10.4	2.4	31.9	20.6	15.7	24.6	18.5	6.4	17.6	15.5	4.5	16.1	39.5	55.6	-0.10	-0.41	-0.71	1	1	1	2	3
STOM PUMI	3/3	10.9	2.3	37.5	17.4	14.8	23.5	18.4	4.6	16.0	13.9	4.5	16.3	40.9	57.2	-0.60	-1.34	0.43	1	1	1	1	2
SYNU VIVA	3/3	10.9	2.2	33.5	19.0	14.9	25.2	19.2	4.4	17.3	14.9	5.0	15.1	41.0	56.1	-0.10	-0.84	-0.61	1	1	1	2	1
TREC MICR	3/3	6.9	0.7	24.3	10.5	8.0	14.2	12.8	19.2	11.2	9.4	2.5	8.3	24.6	32.9	1.00	-1.83	-0.30	1	1	2	3	2
TREC OBTV	3/3	6.8	1.2	19.9	10.8	8.0	15.7	11.5	20.3	9.7	7.4	3.1	7.5	23.2	30.7	0.88	-0.46	-1.55	1	1	1	1	1
TREC QUAD	3/3	6.7	1.3	20.5	10.9	8.1	16.2	11.7	16.3	9.7	7.7	3.0	7.7	24.8	32.5	0.49	-0.88	-0.97	1	1	1	3	1
TREC RUBE	3/3	8.1	1.3	31.2	13.4	11.6	20.9	17.5	4.3	15.0	12.5	3.5	10.0	34.0	44.0	1.01	-1.39	-0.44	1	1	1	3	1