



## A revision of the *Dibrachys cavus* species complex (Hymenoptera: Chalcidoidea: Pteromalidae)

RALPH S. PETERS<sup>1,3</sup> & HANNES BAUR<sup>2</sup>

<sup>1</sup>Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany. E-mail: r.peters@zfmk.de

<sup>2</sup>Department of Invertebrates, Natural History Museum, Bernastrasse 15, 3005 Bern, Switzerland. E-mail: hannes.baur@nmbe.ch

<sup>3</sup>Corresponding author

### Abstract

The taxonomy and host ranges of the *cavus* species complex within *Dibrachys* Förster (Chalcidoidea: Pteromalidae) are revised. Examination of about 810 specimens, including multivariate morphometric analysis of 21 quantitative characters clearly separated three species, *Dibrachys microgastri* (Bouché, 1834), *Dibrachys lignicola* Graham, 1969, and *Dibrachys verovesparum* Peters & Baur **sp. n.**, but allowed no further subdivision of taxa according to origin, host association or previous taxonomic concepts. A neotype is designated for *D. microgastri* and under this name are placed in synonymy the names *Dibrachys cavus* (Walker, 1835) **syn. n.** (including eight current junior synonyms), *Dibrachys clisiocampae* (Fitch, 1856) **syn. n.** (including five current junior synonyms), *Dibrachys boarmiae* (Walker, 1863) **syn. n.**, and *Dibrachys elegans* (Szelényi, 1981) **syn. n.** *Dibrachys goettingenus* Doganlar, 1987 **syn. n.** is synonymized under *D. lignicola*. The morphological analyses revealed several new qualitative and quantitative characters for separating taxa in this species complex and an identification key and diagnoses are provided for females and males. *Dibrachys microgastri* is a polyphagous generalist pupal ectoparasitoid of several different orders of holometabolous insects, whereas *D. lignicola* is a polyphagous ectoparasitoid of hosts in Diptera, Lepidoptera and Hymenoptera, and *D. verovesparum* is a primary or secondary parasitoid in nests of Vespidae.

**Key words:** *Dibrachys microgastri*, *Dibrachys lignicola*, *Dibrachys verovesparum*, taxonomy, principal component analysis (PCA), linear discriminant analysis (LDA), host range, ratio analysis

### Introduction

*Dibrachys* Förster, 1856 (Hymenoptera: Chalcidoidea: Pteromalidae) is a genus of small parasitoid wasps that is mainly Holarctic. Individuals can be identified using the keys of Graham (1969), Bouček & Rasplus (1991) and Bouček & Heydon (1997). A total of 21 species (Noyes 2003) are recognized in two subgenera, *Dibrachys* sensu stricto and *Allodibrachys* Bouček (Bouček 1965). Graham (1969) and Doganlar (1987) revised the Western European and Holarctic fauna, respectively, and keyed most species. Among them, *D. cavus* (Walker) is the best-known species because it is the most polyphagous pteromalid known, with hundreds of host records from several insect orders including Holo- and Hemimetabola and parasitism of different stages (Peck 1963, Noyes 2003). Even though ectoparasitoids are known to be quite polyphagous (Askew & Shaw 1986), such a broad host range is most unusual.

Within the subgenus *Dibrachys*, what has been identified previously as *D. cavus*, *D. boarmiae* (Walker), *D. clisiocampae* (Fitch), *D. goettingenus* Doganlar and *D. lignicola* Graham forms a complex called the *cavus* species complex. The species of this complex are distinguished from other species of the subgenus by moderate body size of less than 3 mm, slightly reticulate lower face lacking transverse wrinkles, only slightly emarginate anterior margin of clypeus, and hyaline wings (Graham 1969, Kusevska 1977, Doganlar 1987). The recognition and separation of certain species of this complex has always proved difficult. For instance, Bouček (1965) suspected that *D. cavus* might consist of a number of cryptic species. Graham (1969: 812) admitted that the differences between *D. cavus* and *D. boarmiae* “are very small” and although he gave numerous distinguishing characters (p. 811–813) they are

difficult to use because the limits of variation mostly merge and sometimes even overlap. Doganlar (1987) acknowledged the difficulties and presented an entirely new set of quantitative characters of the hypopygium that he used to distinguish most of these critical species.

During a study on parasitoids reared from bird nests (Peters 2007, Peters & Abraham 2010), reliable identification of species of the *cavus*-complex was found to be very difficult. For instance, the range of variation in a single species reared under laboratory conditions from a single host specimen usually was much larger than expected and often encompassed the range of variation for two or more species considered distinct in the above studies. Conversely, cryptic species within *D. cavus* were suspected (e.g., Bouček 1965) which, if true, would have proved that the ecological inferences of Peters (2007) and Peters & Abraham (2010) were flawed. This raised serious doubts concerning the validity of the taxonomic status of the putative species listed above. We thus conducted a thorough morphological study to determine the true limits of species in the *cavus*-complex. In particular, we examined all relevant nominal taxa and numerous specimens from various museums as well as from our own collectings and rearings. We re-considered all qualitative characters mentioned in the literature, most notably those of Graham (1969) and Doganlar (1987), and also checked many traits that had been neglected by these authors. A comprehensive quantitative character matrix was compiled, including most measurements used for calculation of standard ratios (Graham 1969), and we applied multivariate statistical methods for investigating patterns of variation. Multivariate morphometrics (Reyment *et al.* 1984, Claude 2008) has provided powerful tools for discovering cryptic species and subtle morphological differences, not only in Pteromalidae (Baur 2002) and other chalcidoid wasps (Polaszek *et al.* 2004), but also in taxa like ants (Wang & Lester 2004) and mites (Klimov *et al.* 2004). The results of our morphological analyses are summarized in a key, diagnoses, and descriptions.

After completion of the taxonomic study, we critically re-examined the host relationships of each species. This was particularly illuminating for what had been interpreted as *D. cavus* because of its innumerable hosts. Once the taxonomic status of each species had been clarified we could address questions concerning their host ranges, including: is there really such a polyphagous parasitoid species?

## Material and methods

**Specimens examined.** About 810 specimens were examined from the museums listed below as well as from our own field collectings and laboratory rearings. The museum acronyms are used in the “Material examined” section of each species to indicate deposition of specimens.

BMNH	The Natural History Museum, London, UK
HDOU	Hope Department, Oxford University, Oxford, UK
HNHM	Hungarian Natural History Museum, Budapest, Hungary
IFUG	Institut für Forstzoologie der Universität Göttingen, Göttingen, Germany
INHS	Illinois Natural History Survey, Urbana, Illinois, USA
MDC	Miklat Doganlar collection, Mustafa Kemal University, Antakya-Hatay, Turkey
MZUF	Zoological Museum “La Specola”, University of Florence, Florence, Italy
NMBE	Naturhistorisches Museum Bern, Bern, Switzerland
NMW	Naturhistorisches Museum Wien, Vienna, Austria
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
USNM	United States Museum of Natural History, Washington D.C., USA
ZMH	Zoologisches Museum Hamburg, Hamburg, Germany
ZSM	Zoologische Staatssammlung München, Munich, Germany

Special attention was paid to all nominal taxa that are included in the *cavus*-complex (*D. cavus*, *D. boarmiae*, *D. clisiocampae*, *D. goettingenus* and *D. lignicola*) and their synonyms (see Noyes 2003). Furthermore, the name-bearing types and accessible information for the following names were considered: *Pteromalus microgastri* Bouché, which was synonymized under *D. cavus* by Graham (1969: 810) with question mark, but considered as a valid taxon by Vidal (2001) and Noyes (2003); *Pteromalus perversus* Walker, which was also doubtfully synonymized with *D. cavus* by Graham (1969: 810); *Pteromalus vesparum* Ratzeburg, which was synonymized with *D.*

*boucheanus* (Ratzeburg) (= *D. cavus*) by Kurdjumov (1913: 11), but considered as a valid taxon by Graham (1969: 810); and *Tritneptis elegans* Széleányi, which was transferred to *Dibrachys* by Bouček & Rasplus (1991: 134) and judging from the original description of the single type specimen might belong to the *cavus*-complex.

Some species of *Dibrachys* that were not treated by Graham (1969) and Doganlar (1987) are also not considered here because they obviously are not part of the *cavus*-complex. This includes *D. kojimae* (Ishii) and *D. yunnanensis* Yang, both of which have a short, straight occipital carina situated close to the occipital foramen and therefore belong to the subgenus *Allodibrachys*. *Dibrachys crassiscapus* Sharkov and *D. koraiensis* Yang both have a deeply emarginate and impressed anterior margin of the clypeus, which places them near *D. fuscicornis* (Walker) (see Graham 1969: 809).

A subset of only 198 female specimens was suitable for the morphometric analysis. All female paratypes of *Dibrachys verovesparum* except one (no head) were used for the analysis. For the other species, those females used in the analysis are indicated by an “A” within the “Material examined” section, with only one female measured from any series with the same data except where stated otherwise. Specimens included in the morphometric analysis included the following type material: lectotype and paralectotype of *Pteromalus cavus*; lectotype and paralectotype of *P. boarmiae*; holotype of *Tritneptis elegans*; syntype of *Cleonymus clisiocampae*; lectotype of *Eupelmus cereanus* Rondani; paralectotype of *P. gelechia* Webster; neotype of *Dibrachys microgastri*; holotype and paratypes of *D. verovesparum*; holotype and paratypes of *D. lignicola*; holotype and paratypes of *D. goettingenus*. Specimens from two laboratory stocks were also included. The HBM stock (27 specimens) was established from specimens reared from puparia of *Triarthria setipennis* (Fallén) (Diptera: Tachinidae) originally collected in Hamburg-Bramfeld, Germany, in 2004. This stock belongs to the group *cavus* (see below). The HRL stock (20 specimens) was established from specimens reared from puparia of *T. setipennis* originally collected in Hamburg-Rotherbaum, Germany, in 2006. This stock belongs to the group *lignicola* (see below). Laboratory rearings were done on freeze-killed puparia of *Calliphora vomitoria* (Linnaeus) (Diptera: Calliphoridae) in Petri dishes at room temperature. A single specimen of the HBM stock used for the morphometric analyses was reared on a pupa of *Galleria mellonella* (Linnaeus) (Lepidoptera: Pyralidae).

For complete data of the morphometric analyses please see Supplementary files 1 and 2. In these files, some specimens are given codes or unambiguous names that can also be found on the specimen labels; specimens named only by consecutive numbers cannot be re-associated with certain examined specimens.

**Character selection.** The terminology used in this study follows Gibson (1997). All specimens were examined for external features used in Pteromalidae taxonomy (e.g., Graham 1969, Bouček & Rasplus 1991). Additional body parts that were neglected by these authors (e.g., posterior of head, lower and lateral sides of mesosoma) were also carefully examined. These characters are mentioned in the descriptions only if they proved to be of taxonomic value.

For the main morphometric analysis, 21 characters were measured (Table 1). Only females were used because most of the available types were females. Females were also more readily available than males. With regard to the choice of characters for morphometrics we mainly followed Graham (1969), which is still the standard work in this respect. We initially included 12 additional characters, but these were later excluded because they proved to be strongly correlated with the remaining characters and contained no new information.

Doganlar (1987) suggested three ratios of the hypopygium to differentiate between group *cavus* species: (1) greatest median width of posterior lobe:greatest sublateral width of posterior lobe; (2) hypopygium breadth:hypopygium length; (3) distance between the branches of hind edge of sublateral sclerotized area:shortest distance between anterolateral incision and interior lobe (see Doganlar 1987: 198, Fig. 11). To test the separation of *D. cavus*, *D. clisiocampae* and *D. boarmiae* we measured 15 genetically similar specimens of our HBM laboratory stock (slides deposited at ZMH) for the morphometric characters used by Doganlar (1987).

**Measurements and equipment.** Measurements for morphometrics were made with a Leitz stereomicroscope using an eyepiece micrometer (1 mm divided in 20 units). The magnification used for all characters was 160x (16x eyepiece, 10x objective lenses) with one exception, gaster length was measured at 64x (16x, 4x). Additional measurements were made with a Keyence VHX-500F digital microscope. Qualitative and additional examinations were made with a Leica M165 C stereomicroscope. For study and measurement of the hypopygia, the gaster of specimens was dissected and the hypopygium mounted in Faure’s medium on a slide. For all measurements we ensured that the points of reference were equidistant from the objective of the microscope. Because the quality of museum specimens varied, no strict side preference was followed and characters were measured from the side with better condition or easier access. Distorted structures (e.g., bent flagellum or gaster) were not measured.

Photos were taken with a Keyence VHX-500F digital microscope and modified with Adobe Photoshop CS4. Specimens for photos were taken from stock HBM, stock HRL II and the type series of *D. verovesparum*. HRL II is the same as HRL, except that it was collected a few years later.

**TABLE 1.** Characters used in the morphometric analyses.

no.	character	abbreviation	definition
1	head breadth	hea.b	maximum breadth of head in dorsal view
2	OOL	ool.l	minimal distance between posterior ocellus and eye (s. Graham 1969)
3	POL	pol.l	distance between posterior ocelli (s. Graham 1969)
4	mouth breadth	mou.b	breadth of mouth opening (s. Graham 1969)
5	malar space	msp.l	distance between outer mouth margin and lower eye margin (s. Graham 1969)
6	eye distance	eye.d	distance between eyes at level of anterior ocellus
7	eye height	eye.h	maximum height of eye in lateral view
8	eye breadth	eye.b	maximum breadth of eye in lateral view
9	eye–toruli	et.d	distance between outer toruli margin and inner eye margin at the level of toruli
10	lower face	lof.l	distance between lower toruli margin and lower clypeus margin (s. Gibson 1997)
11	scape	scp.l	length of scape (s. Graham 1969)
12	pedicel	pdl.l	length of pedicel
13	flagellum	flg.l	length of entire flagellum (s. Gibson 1997)
14	mesoscutum breadth	msc.b	maximum breadth of mesoscutum
15	mesoscutum length	msc.l	length of mesoscutum (in dorsal view)
16	scutellum length	sct.l	length of scutellum (including frenum)
17	scutellum breadth	sct.b	breadth of scutellum at anterior margin
18	marginal vein	mv.l	length of marginal vein (s. Graham 1969)
19	stigmal vein	stv.l	length of stigmal vein (s. Graham 1969)
20	submarginal vein	smv.l	length of submarginal vein (s. Graham 1969)
21	gaster length	gst.l	length of gaster excluding ovipositor sheaths

**Statistical analysis.** For the analysis of morphometric data, principal component (PCA) and Fisher's linear discriminant analysis (LDA) were applied. Both are ordination methods that endeavor to transform the original variables into a new system of coordinate axes whereby most of the variance is contained in the first two or three axes. Traditionally, the results are then presented as scatter plots (see Pimentel (1979) and Reymont *et al.* (1984) for readable accounts for biologists and Sorensen & Footitt (1992) for a collection of illustrative applications). Though the output of PCA and LDA looks very similar, their application and interpretation differ in many ways. For a PCA, the entire data matrix is considered as a single group. The analysis then reveals the unconstrained structure of variation in the data. The method can be used for contrasting morphometric data with other sets of characters (e.g., qualitative features, molecular markers) or criteria (e.g., host association, geographic origin), which, in turn, may illuminate taxonomic relationships. For instance, if delimitation of groups based on particular hosts is congruent with non-overlapping morphometric variation as revealed by a PCA, this could support the existence of separate taxa. Concerning computation, PCA is sensitive to the magnitude of the measurements. Hence, the raw data were transformed into natural logarithms. This transformation further enables interpreting the results of a PCA in terms of size and shape. According to Jolicoeur (1963; see also Klingenberg 1996 and Claude 2008) the first component can usually be interpreted as an allometric size axis, whereas all subsequent components define the allometry free shape space. The coefficients of the first component also allow estimation of the extent of allometry present in the data whereby too much allometry might affect the use of ratios (Janzon 1986). We used the test developed by Anderson (2003, section 11.6.2) to check whether the coefficients significantly deviated from the null hypothesis of isometry.

In contrast to PCA, a LDA necessitates that each specimen is assigned to a group before the analysis. The LDA then finds the optimal separation of those groups. Hence, contrasting groups based on different criteria, as exemplified above for PCA, would always be strongly biased and the method is thus inappropriate for such purposes. However, with the help of the coefficients of the discriminant function(s) the original variables with the highest discrimination power can be determined and used for identification keys or descriptions (usually by calculating ratios). The performance of the LDA is assessed by means of cross validation (Rencher 2002: 310), where one specimen is omitted from the analysis and classified according to the discriminant function(s) found for the remaining specimens in the data set. The number of correctly classified cases is a measure of how well the result will generalize for an independent data set.

All calculations and graphics were made with the R statistical software, version 2.12.1 (R Development Core Team 2010). For the PCA, the function “prcomp()” was used, with the options “center=TRUE” and “scale=FALSE”. Eigenvalues and eigenvectors were thus calculated on the covariance matrix. In order to decide how many components to retain we plotted the scree graph (Rencher 2002: 398–399). For LDA and cross validation we applied the function “lda()” from the package “MASS”, also for the log-transformed data. Priors were set to equal values for all groups. Further details for computation of all these methods can be found in Venables & Ripley (2002) and Claude (2008). The entire morphometric data set potentially included 4158 measurements based on 21 characters for 198 specimens, but numerous characters were missing or otherwise not measurable on certain specimens (Supplementary file 1). Table 2 gives an overview of the number of missing values for each variable (totaling 159 values). In order to be able to include all specimens for the multivariate analyses, missing values were imputed with the help of the package “mice”, using the default settings of the function “mice()” (Supplementary file 2).

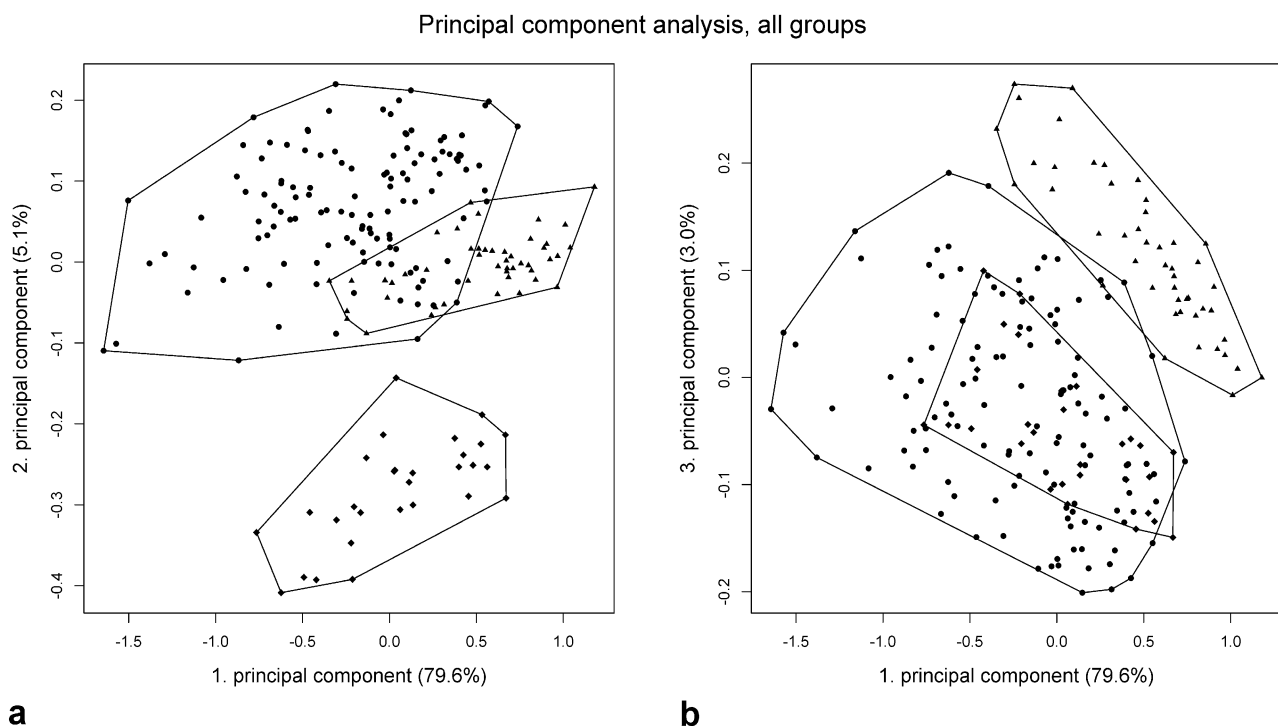
**TABLE 2.** Numbers of missing values in the data set used for morphometric analyses.

character	missing values
head breadth	1
OOL	0
POL	1
mouth breadth	20
malar space	10
eye distance	0
eye height	0
eye breadth	0
eye–toruli	1
lower face	4
scape	1
pedicel	2
flagellum	39
mesoscutum breadth	11
mesoscutum length	10
scutellum length	17
scutellum breadth	15
marginal vein	1
stigmatal vein	0
submarginal vein	13
gaster length	13
total missing values	159
total measurements	3999

## Morphological results

**Qualitative morphology.** Visual inspection of qualitative morphological traits resulted in three groups being defined within the complex. A “group *lignicola*” included males with a distinct lobe on the outer side of the apex of the scape (used by Graham (1969) and Doganlar (1987) to separate *D. lignicola* males from other *Dibrachys* males). Females were included as long as these could be attributed unambiguously, for instance, if they had been reared from the same host specimen as males. A “group *verovesparum*” was defined for those specimens lacking any metallic lustre, and a “group *cavus*” included all other specimens belonging to the *cavus*-complex that lacked any a priori recognized qualitative traits. At this stage prior to the morphometric analysis we deliberately avoided the concept of species and rather interpreted the groups in the sense of operational taxonomic units.

**Principal component analysis (PCA) of body measurements, all groups.** The entire data set of 21 body measurements for 198 specimens (Supplementary file 2) was subjected to a PCA to determine whether there was support for the groups *cavus*, *lignicola* and *verovesparum* that were delineated based on qualitative characters. Inspection of the scree graph (not shown) suggested that the first three components explained 87.7 % of the total variance in the data. The first component, which explains 79.6 % of the variance, clearly dominated the analysis, which is usually the case in morphometric analyses of body measurements (Jolicoeur 1963, Baur 2002). Scatter-plots of first against second and first against third principal components are shown in Figure 1. Generally, the groupings are unambiguously recovered by the PCA. The second component (Fig. 1a) clearly separated group *verovesparum* from the other groups, while only a combination of first and third component (Fig. 1b) distinguished group *lignicola* from the other two groups. This reflects the fact that it was much more difficult to differentiate females of group *lignicola* from females of group *cavus*.



**FIGURE 1.** Result of the principal component analysis (PCA) of all groups: circles = group *cavus*, triangles = group *lignicola*, diamonds = group *verovesparum*. For coefficients of principal components see Table 3.

For interpretation of the principal components, the coefficients (sometimes called loadings) of the variables have to be examined (Table 3). For the first component, the coefficients were all positive but differed to a certain extent in magnitude. Because the p-value for Anderson's test was virtually zero ( $\chi^2 = 406.147$  and  $p < 0.0001$ ) and clearly rejected the null hypothesis of isometry, this component could be interpreted as an allometric size axis (Jolicoeur 1963, Klingenberg 1996). Hence, it comprised not only isometric size differences but also shape changes associated with size. According to this interpretation, the other components define the size-uncorrelated shape space in the analysis. Obviously, the separation of group *verovesparum* along the second component can be entirely

attributed to allometry-free shape variation. Based on the coefficients of the second component, the relevant characters were mouth breadth, marginal vein and gaster length (Table 3). For the third component, only malar space and stigmal vein showed significant coefficients. However, combining these two characters into a ratio did itself not contribute much to the differentiation of group *lignicola* from group *cavus*, which reflects the fact that the third component explained only a marginal portion of 3.0 % of the total variance in the data set.

**TABLE 3.** Coefficients of first three principal components (PC1–PC3) of the PCA of all groups. PC1 has positive values of roughly the same magnitude. Significant coefficients for PC2 and PC3 are indicated in bold.

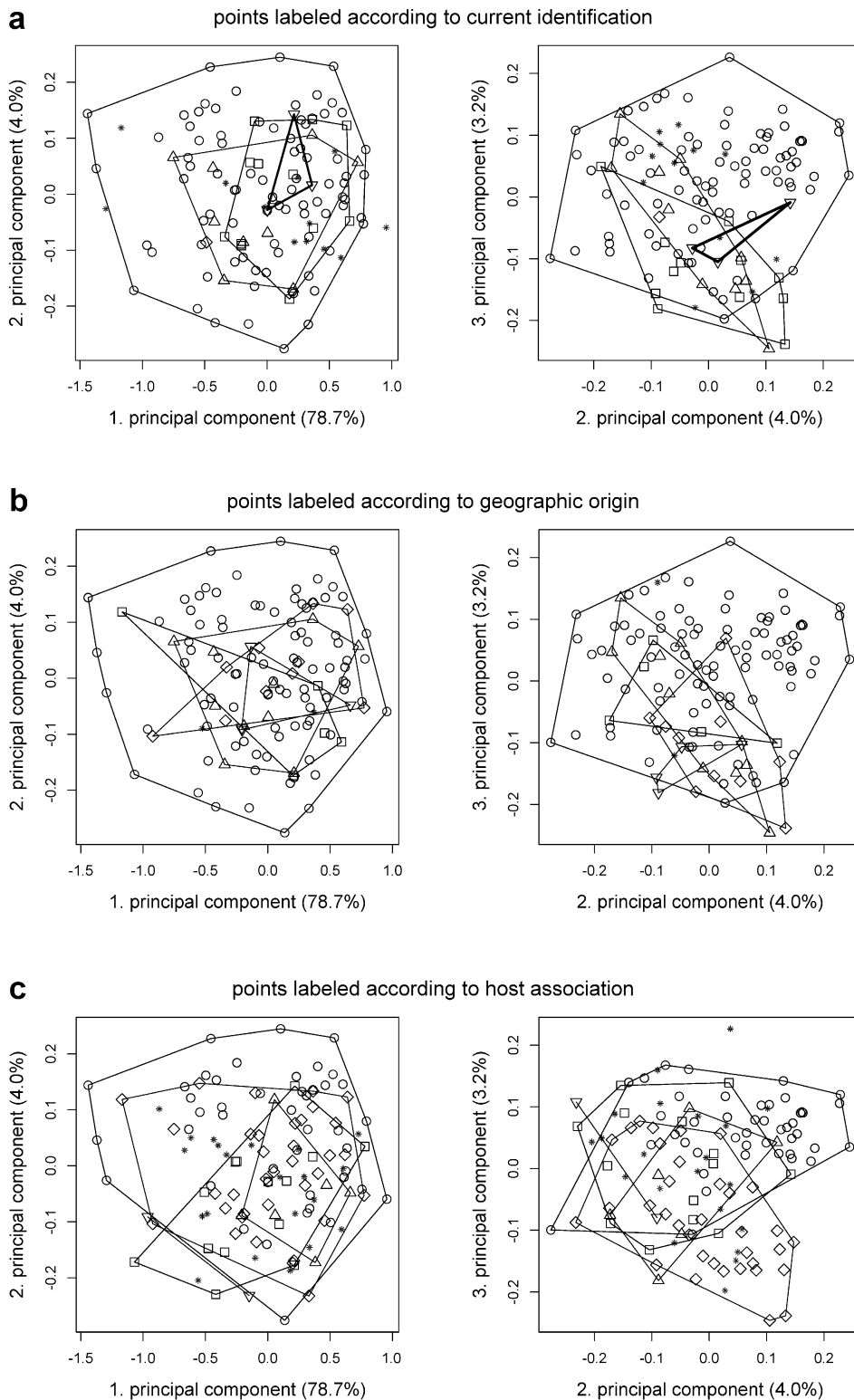
character	PC 1	PC 2	PC3
head breadth	0.215	-0.007	-0.047
OOL	0.210	-0.022	-0.125
POL	0.187	-0.166	-0.271
mouth breadth	0.247	<b>-0.445</b>	-0.076
malar space	0.165	-0.003	<b>-0.469</b>
eye distance	0.207	0.001	-0.162
eye height	0.220	0.309	0.020
eye breadth	0.247	-0.022	0.236
eye–toruli	0.246	-0.298	-0.070
lower face	0.231	0.122	0.203
scape	0.183	0.067	0.021
pedicel	0.187	-0.263	0.143
flagellum	0.198	0.023	0.137
mesoscutum breadth	0.250	-0.012	-0.086
mesoscutum length	0.248	0.040	-0.147
scutellum length	0.252	0.027	-0.069
scutellum breadth	0.256	0.026	0.050
marginal vein	0.152	<b>0.561</b>	0.077
stigmal vein	0.262	-0.057	<b>0.645</b>
submarginal vein	0.209	0.037	-0.080
gaster length	0.153	<b>0.421</b>	-0.226

**Principal component analysis (PCA) of body measurements, separate groups.** Combining several distinct groups into a single PCA can sometimes mask a more subtle but nevertheless significant structure of within-group variation. We thus performed separate analyses for each of the three groups that were delineated based on qualitative characters.

For the group *cavus* several important criteria were available. As mentioned previously, group *cavus* was split into several taxa by Graham (1969) and Doganlar (1987). Under the header “current identification”, we labeled the specimens according to the characters given in their keys (identification by us or as shown on specimen label). In the case of type material the names of the respective nominal taxa were used. The material also allowed labeling of specimens with respect to geographic origin and host association. Scatterplots of the first three principal components are shown in Figure 2 (only the first two components are significant according to the scree plot, but we wanted to stay on the “safe side” by presenting the first three). The plots do not support delineation of subgroups as these were almost completely overlapping. In most instances, the variation of one particular category covers also the remaining points.

Qualitative morphology provided no clue for subdividing the group *lignicola*. A meaningful subgroup labeling according to host relationships and geographic origin was not possible. Taxonomically, this group comprised two nominal taxa, *D. goettingenus* Doganlar and *D. lignicola* Graham. We labeled the type specimens accordingly and added the third category “no type” for all remaining specimens. Figure 3 shows scatterplots of the first three principal components, though the scree graph suggested only the first two. The specimens labeled “no type” appear to

Principal component analysis, group *cavus*

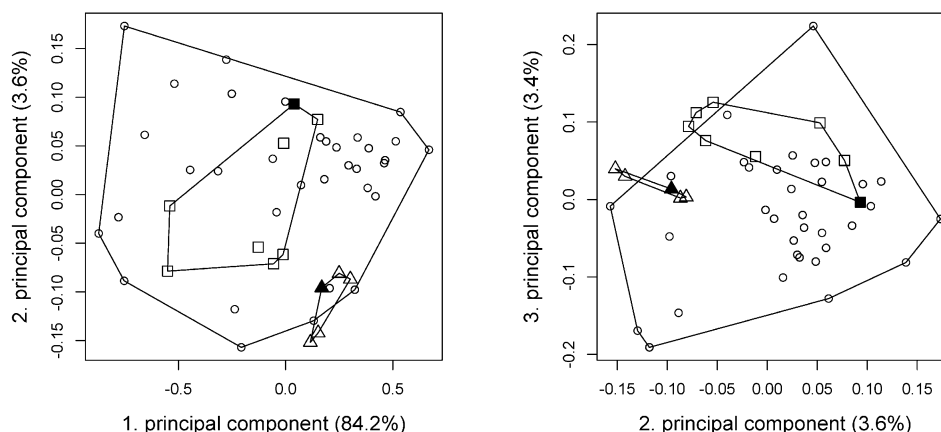


**FIGURE 2.** Results of the principal component analysis (PCA) of group *cavus*. a) specimens marked according to their current identification: circles = *Dibrachys cavus* (Walker); squares = *D. boarmiae* (Walker); triangles = *D. clisiocampae* (Fitch); diamonds = *D. elegans* (Szelényi) (holotype); inverse triangles = *D. microgastri* (Bouché) (neotype and two specimens with same data); asterisks = no identification. b) specimens marked according to their place of origin: circles = Europe; squares = Africa; triangles = America; diamonds = Asia; inverse triangles = Australasia; asterisks = origin unknown. c) specimens marked according to their host association: circles = Diptera; squares = Hymenoptera parasitoids; triangles = Hymenoptera non-parasitoids; diamonds = Lepidoptera; inverse triangles = Coleoptera or Neuroptera; asterisks = host unknown.



Principal component analysis, group *lignicola*

points labeled according to type series or no types



**FIGURE 3.** Results of the principal component analysis (PCA) of group *lignicola*. Specimens marked according to types series: circles = not belonging to a type series; squares = *Dibrachys lignicola* Graham; triangles = *D. goettingenus* Doganlar (filled symbols = holotypes).

cover the range of variation of the type series of *D. lignicola* and *D. goettingenus*, though the ranges of the last two do not overlap. This is not surprising because the type series of both *D. lignicola* and *D. goettingenus* consist of very similar individuals. *D. goettingenus* was described from specimens reared from a single host pupa, which is why they show almost no variation. The PCA thus did not support any further subdivision of the group *lignicola*.

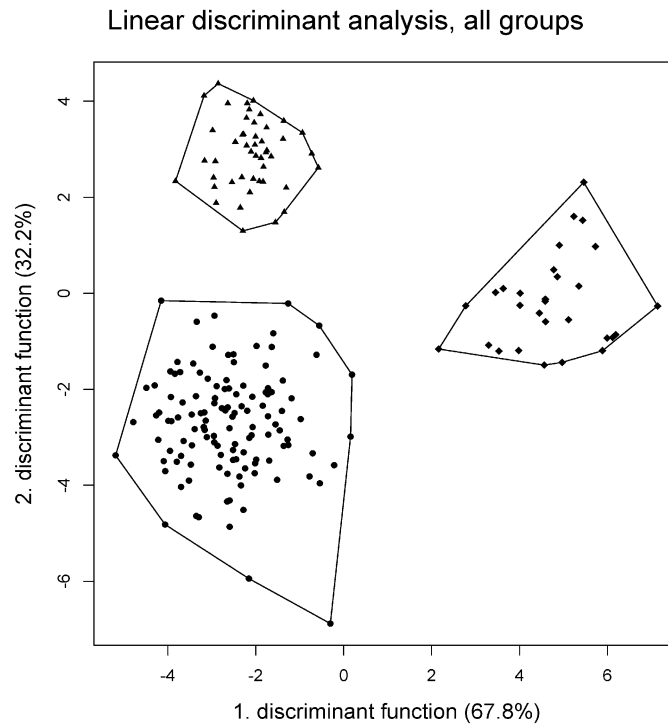
Qualitative morphology provided no clue for subdividing the group *verovesparum*, and no meaningful information on hosts and geographic origin was available. The PCA (not shown) revealed a fairly homogenous cluster of points.

**Linear discriminant analysis (LDA) of body measurements.** The entire data matrix was subjected to a LDA in order to find the best separation of the groups *cavus*, *lignicola* and *verovesparum*. The scatterplot in Figure 4 shows that the discriminant functions completely separated the three groups. The first function distinguished group *verovesparum* from the other two groups and the second function separated group *lignicola* from group *cavus*. Cross validation strongly supported this result because only two specimens of group *cavus* were misclassified as belonging to group *lignicola* (Table 4).

**TABLE 4.** Results of cross validation for all groups. All specimens of groups *lignicola* and *verovesparum* were correctly classified whereas only 2 of 122 specimens (1.6 %) of group *cavus* were misclassified as belonging to group *lignicola*.

group	classification		
	<i>lignicola</i>	<i>cavus</i>	<i>verovesparum</i>
<i>lignicola</i>	47	0	0
<i>cavus</i>	2	120	0
<i>verovesparum</i>	0	0	29

**Morphometric analysis of the hypopygium.** We used the key of Doganlar (1987) to test the separation between three taxa of group *cavus*. First, we tried to distinguish between *D. cavus* plus *D. clisiocampae* and *D. boarmiae* based on the posterior lobe ratio (Doganlar 1987, couplet 11). This resulted in the assignment of all 15 measured specimens to the first two species (Table 8). Second, employing the hypopygial ratios 2 and 3 of Doganlar (1987, couplet 12), which he used to separate *D. cavus* from *D. clisiocampae*, 8 of 15 specimens could be assigned to *D. clisiocampae* and the others were found to lie beyond or between the given ranges (Table 8). In addition to the ambiguity resulting from measurement of putatively genetically similar specimens reared from a single puparium, there is the problem of accessibility of the hypopygium for easy and practical identification. The gaster has to be destroyed and slide preparation is necessary. In our view, these characters are thus not suitable for separating the species in question.

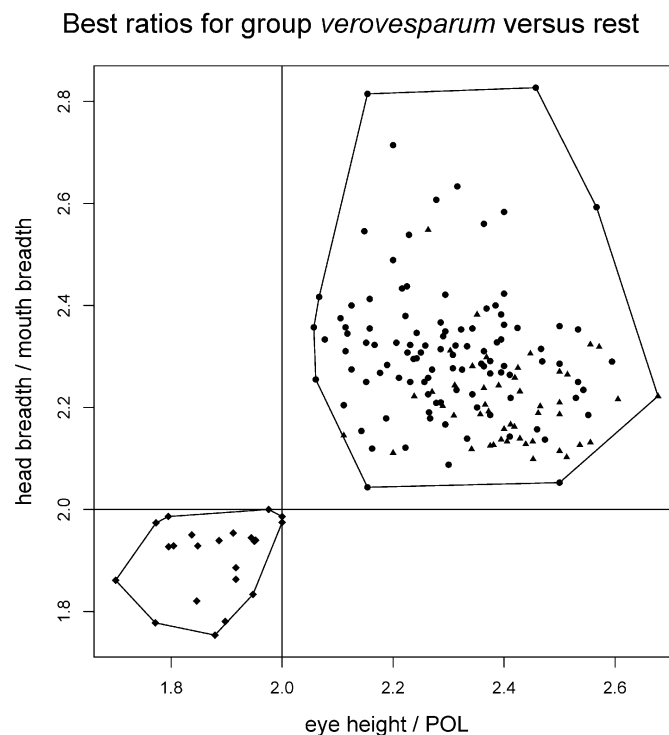


**FIGURE 4.** Results of the linear discriminant analysis (LDA) of all groups: circles = group *cavus*, triangles = group *lignicola*, diamonds = group *verovesparum*. For coefficients of discriminant functions see Table 5; see also results of cross validation, Table 4.

**Finding the best character ratios for use in key and descriptions.** As demonstrated above, multivariate statistical methods like PCA and LDA are useful for analyzing similar taxa. They often reveal differences in variation that are not evident using simple uni- or bivariate character analysis. Unfortunately, the output of these methods cannot be used efficiently within keys and descriptions of a taxonomic revision. For example, it would be very awkward to include in a key the numerical results of our first discriminant function where, according to Table 5, one would have to calculate to calculate  $-7.31x$  head breadth  $+ 1.49x$  OOL  $+ \dots + -3.96x$  gaster length for separating group *verovesparum* from the remaining groups. Of course, one could reduce the number of characters in the model by a variable selection procedure (Rencher 2002: 293–296), but even such a reduced model would still be unpractical. What is usually done in such instances is to calculate ratios, as for example Graham (1969), which also reflect geometric differences in a very intuitive manner. To our knowledge, no mathematical consistent framework exists for the interpretation of numerical results of PCA and LDA in terms of ratios. We therefore developed a graphical approach for finding the optimal ratios. First, discriminant functions (DF) were checked for significant variable coefficients. For instance, DF1 separated group *verovesparum* from the other two groups (Fig. 4). The most significant coefficients of DF1 involved head breadth, POL, mouth breadth, eye distance and eye height (Table 5). Second, from these five characters all informative ratios were calculated (for  $p$  variables there are  $p(p - 1)/2$  ratios). Of the resulting 10 ratios those with the highest discriminating power were finally sorted out by visual inspection of scatter- and boxplots. The best ratios were in this case eye height:POL and head breadth:mouth breadth (Fig. 5, Table 6). The same procedure was applied for the separation of group *lignicola* from group *cavus*. DF2 was relevant here and revealed gaster length:eye breadth and head breadth:stigmatal vein as the best discriminating characters (Fig. 6, Table 7). The specimen of group *cavus* that lies within the range of group *lignicola* is one of those misclassified with cross validation above. It is noteworthy that with just two ratios almost the same discrimination power is achieved as with DF2.

**TABLE 5.** Coefficients of the two linear discriminant functions (DF1 and DF2) of the LDA of all groups. Significant coefficients are indicated in bold.

character	DF 1	DF 2
head breadth	<b>-7.31</b>	<b>-9.74</b>
OOL	1.49	0.33
POL	<b>7.88</b>	-1.33
mouth breadth	<b>10.92</b>	0.56
malar space	0.90	-3.84
eye distance	<b>7.97</b>	2.55
eye height	<b>-17.39</b>	1.15
eye breadth	-1.84	<b>15.93</b>
eye-toruli	5.79	2.48
lower face	-4.08	2.90
scape	1.87	1.39
pedicel	2.38	-1.13
flagellum	2.98	0.89
mesoscutum breadth	4.04	-6.48
mesoscutum length	-2.57	-6.93
scutellum length	-2.26	<b>10.41</b>
scutellum breadth	-1.36	1.58
marginal vein	-3.73	-2.75
stigma vein	0.01	<b>7.57</b>
submarginal vein	-0.97	-1.61
gaster length	-3.96	<b>-10.39</b>



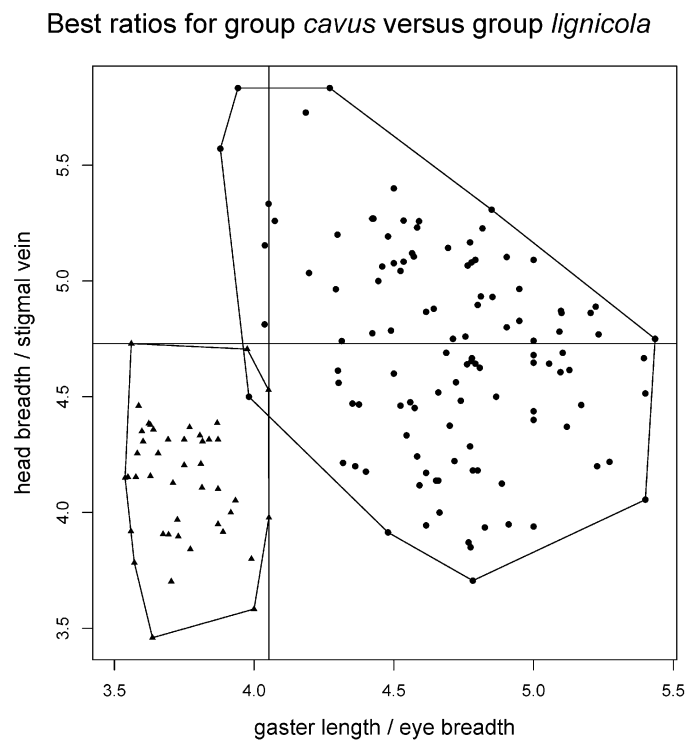
**FIGURE 5.** Scatterplot of the two best ratios for separating group *verovesparum* (diamonds) from groups *cavus* (circles) and *lignicola* (triangles) (see also Table 6). Specimens with missing values not included.

**TABLE 6.** Range, interquartile range and median of best ratios separating group *verovesparum* from the two other groups, *cavus* and *lignicola*.

eye height / POL						
group	min.	1st quartile	median	3rd quartile	max.	N
<i>verovesparum</i>	1.70	1.81	1.89	1.95	2.00	22
rest	2.06	2.24	2.34	2.42	2.68	154

head breadth / mouth breadth						
group	min.	1st quartile	median	3rd quartile	max.	N
<i>verovesparum</i>	1.75	1.86	1.93	1.95	2.00	22
rest	2.04	2.19	2.27	2.34	2.83	154



**FIGURE 6.** Scatterplot of the two best ratios for separating group *cavus* (circles) from group *lignicola* (triangles) (see also Table 7). Specimens with missing values not included.

**Summary of morphological analyses.** The material examined through morphometric analyses comprised only three groupings that are consistent with group *verovesparum*, group *lignicola*, and group *cavus* delineated through preliminary morphological analysis. We interpret group *verovesparum* as a new species. Group *lignicola* included two nominal taxa, *D. lignicola* and *D. goettingenus*, which lack qualitative or quantitative morphological differences. Group *cavus* included four valid nominal taxa, *D. cavus*, *D. boarmiae*, *D. clisiocampae*, and *D. elegans*, but specimens attributable to these names also showed no detectable differences relative to morphology, geographic origin or host association, i.e. we found no evidence that these names represent separate species or of cryptic species within *D. cavus* itself. Our analyses imply the presence of only three valid species. Because of this we propose the synonymy of *D. cavus*, *D. boarmiae*, *D. clisiocampae* and *D. elegans* under *D. microgastri*, but for the sake of continuity retain the informal group name “*cavus*-complex” for the group of three recognized species.

## Taxonomy

### Key to species of the *cavus* species complex

- 1 Eyes smaller, eye height equal to or less than 2.0x POL. Head and mesosoma black, without metallic gloss or with only slight tinges of bronze, brown or green . . . . . *D. verovesparum* Peters & Baur **sp. n.**  
- Eyes larger, eye height more than 2.0x POL. Head and body usually with distinct metallic green, blue or bronze gloss, especially in males . . . . . 2
- 2 Females . . . . . 3  
- Males . . . . . 4
- 3 Usually, gaster length equal to or less than 4.05x eye breadth **and** head breadth equal to or less than 4.73x stigmal vein; mesoscutum without blue color. . . . . *D. lignicola* Graham  
- Usually, gaster length more than 4.05x eye breadth **or** head breadth more than 4.73x stigmal vein; mesoscutum sometimes with tinge of or distinct blue color . . . . . *D. microgastri* Bouché
- 4 Outer side of apex of scape and pedicel with distinct lobe (Fig. 9e); gaster with distinct ventral testaceous spot (Fig. 9b) . . . . . *D. lignicola* Graham  
- Outer side of scape and pedicel without a lobe (Fig. 9d); gaster with ventral testaceous spot absent to distinct. . . . . *D. microgastri* Bouché

### *Dibrachys microgastri* (Bouché, 1834)

(Figs 7a, 7d, 8a, 8d, 9a, 9d)

*Diplolepis microgastri* Bouché, 1834: 168, neotype female in ZMH, present designation. Syntypes presumed lost (see Graham, 1969: 811).

*Pteromalus cavus* Walker, 1835: 477–478, lectotype female in BMNH (B.M. TYPE no. 5.2987), designated by Graham (1969: 811) (examined by Peters); **syn. n.**

*Pteromalus decedens* Walker, 1835: 478, lectotype female in BMNH (B.M. TYPE no. 5.2988), designated by Graham (1969: 811) (examined by Peters); synonymized with *D. cavus* by Graham (1956: 261, but see also Graham, 1969: 811); **syn. n.**

*Pteromalus albinervis* Ratzeburg, 1844: 199, name-bearing types presumed destroyed (see comment of Graham (1969: 811) for *P. tenuis* Ratzeburg, 1844 and *P. boucheanus* Ratzeburg, 1844); synonymized with *D. boucheanus* by Kurdjumov (1913: 11); **syn. n.**

*Pteromalus boucheanus* Ratzeburg, 1844: 196, name-bearing types presumed destroyed (Graham, 1969: 811); *Dibrachys boucheanus*, combination by Thomson (1878); synonymized with *D. cavus* by Gahan (1938: 211); **syn. n.**

*Pteromalus boarmiae* Walker in Newman, 1863: 8609–8610 (English description accidentally transposed, see comment of Graham (1969: 812)), lectotype female in BMNH (B.M. TYPE no. 5.2989), designated by Graham (1969: 812) (examined by Peters); **syn. n.**

*Pteromalus tenuis* Ratzeburg, 1844: 195, name-bearing types presumed destroyed (Graham, 1969: 811); synonymized with *P. boucheanus* by Ratzeburg (1848: 189); **syn. n.**

*Pteromalus zelleri* Ratzeburg, 1848: 190, name-bearing types presumed destroyed (see comment of Graham (1969: 811) for *P. tenuis* Ratzeburg, 1844 and *P. boucheanus* Ratzeburg, 1844); synonymized with *D. boucheanus* by Kurdjumov (1913: 11); **syn. n.**

*Pteromalus vesparum* Ratzeburg, 1852: 233, name-bearing types presumed destroyed (see Graham, 1969: 809); synonymized with *D. boucheanus* by Kurdjumov (1913: 11); **syn. n.**

*Cleonymus clisiocampae* Fitch, 1856: 431–432, syntype female and male in USNM (USNM type no. 1831) (examined by Peters); synonymized with *D. cavus* by Gahan (1938: 211), but considered valid by Doganlar (1987: 204); **syn. n.**

*Cheipachus nigrocyaneus* Norton, 1869: 327, syntype females in USNM (USNM type no. 61079) (examined by Peters); *Pachyneuron nigrocyaneum*, combination by Ashmead (1888); synonymized with *D. clisiocampae* by Girault (1916b: 408), with *D. cavus* by Gahan (1938: 211), and subsequently with *D. clisiocampae* by Doganlar (1987: 204); **syn. n.**

*Eupelmus cereanus* Rondani, 1876: 38, 40, lectotype female in MZUF (no. 32), designated by Bouček (1974: 247) (examined by Peters); synonymized with *D. cavus* by Delucchi (1955: 174); **syn. n.**

*Pteromalus gelechia* Webster, 1883: 151, lectotype male in INHS (INHS Insect Collection 213,068), designated by Frison (1927: 220) (examined by Peters); nine paralectotypes in INHS (one female labeled “lectoallotype”, INHS Insect Collection 213,069; four males and four females labeled “paratypes”, INHS Insect Collection 257,879–257,886) (examined by Peters); synonymized with *D. clisiocampae* by Girault (1916b: 408), with *D. cavus* by Gahan (1938: 211), and subsequently with *D. clisiocampae* by Doganlar (1987: 204); **syn. n.**

*Pteromalus chionobae* Howard, 1889: 1889, syntypes in USNM (USNM type no. 2673) (examined by Peters); synonymized with *D. clisiocampae* by Girault (1916b: 408), with *D. cavus* by Gahan (1938: 211), and subsequently with *D. clisiocampae* by Doganlar (1987: 204); **syn. n.**

*Arthrolytus apatela* Ashmead, 1893: 162, syntypes in USNM (USNM type no. 26215 examined by Peters); *Dibrachys apate-*

*lae*, combination by Girault (1916b); synonymized with *D. cavus* by Gahan (1938: 211), and with *D. clisiocampae* by Doganlar (1987: 204); **syn. n.**

*Arthrolytus pimplae* Ashmead, 1894: 339, syntypes in USNM (USNM type no. 2182) (examined by Peters); synonymized with *Arthrolytus apatelae* by Girault (1916a: 297; 1916b: 408), with *D. cavus* by Gahan (1938: 211), and with *D. clisiocampae* by Doganlar (1987: 204); **syn. n.**

*Trichomalus truyilloi* Blanchard, 1938: 178, name-bearing types unknown; synonymized with *D. cavus* by Gahan (1942: 45); **syn. n.**

*Tritneptis elegans* Szelenyi, 1981: 178, holotype female in HNHM (Hym. Typ. nr. 6821) (examined by Peters); assigned to *Dibrachys* by Bouček & Rasplus (1991); **syn. n.**

**Diagnosis.** *Both sexes.* Eyes large, eye height greater than 2.0x POL. Head and mesosoma mostly with distinct metallic coloration, predominantly green or dark green (Figs 7a, 7d, 8a, 9a), but sometimes distinctly blue or with distinct blue tinge on mesoscutum.

*Female.* Gaster long and eyes elongate, gaster length usually greater than 4.05x eye breadth (3.88–5.43, but only 6 of 114  $\leq 4.05$ ) (Figs 6, 7a, Table 7). Outer margin of eyes straight or slightly to distinctly emarginate (Fig. 7a). Stigmal vein short compared to marginal vein, marginal vein usually 2.0x or more stigmal vein (1.62–2.86, but only 11 of 121  $< 2.0$ ) (Fig. 8d). Mouth narrow, head breadth greater than 2.0x mouth breadth (Fig. 7d).

*Male.* Scape and pedicel apically both without lobe on outer side (Fig. 9d). Gastral spot absent to distinct (Fig. 9a).

**TABLE 7.** Range, interquartile range and median of best ratios separating group *cavus* from group *lignicola*.

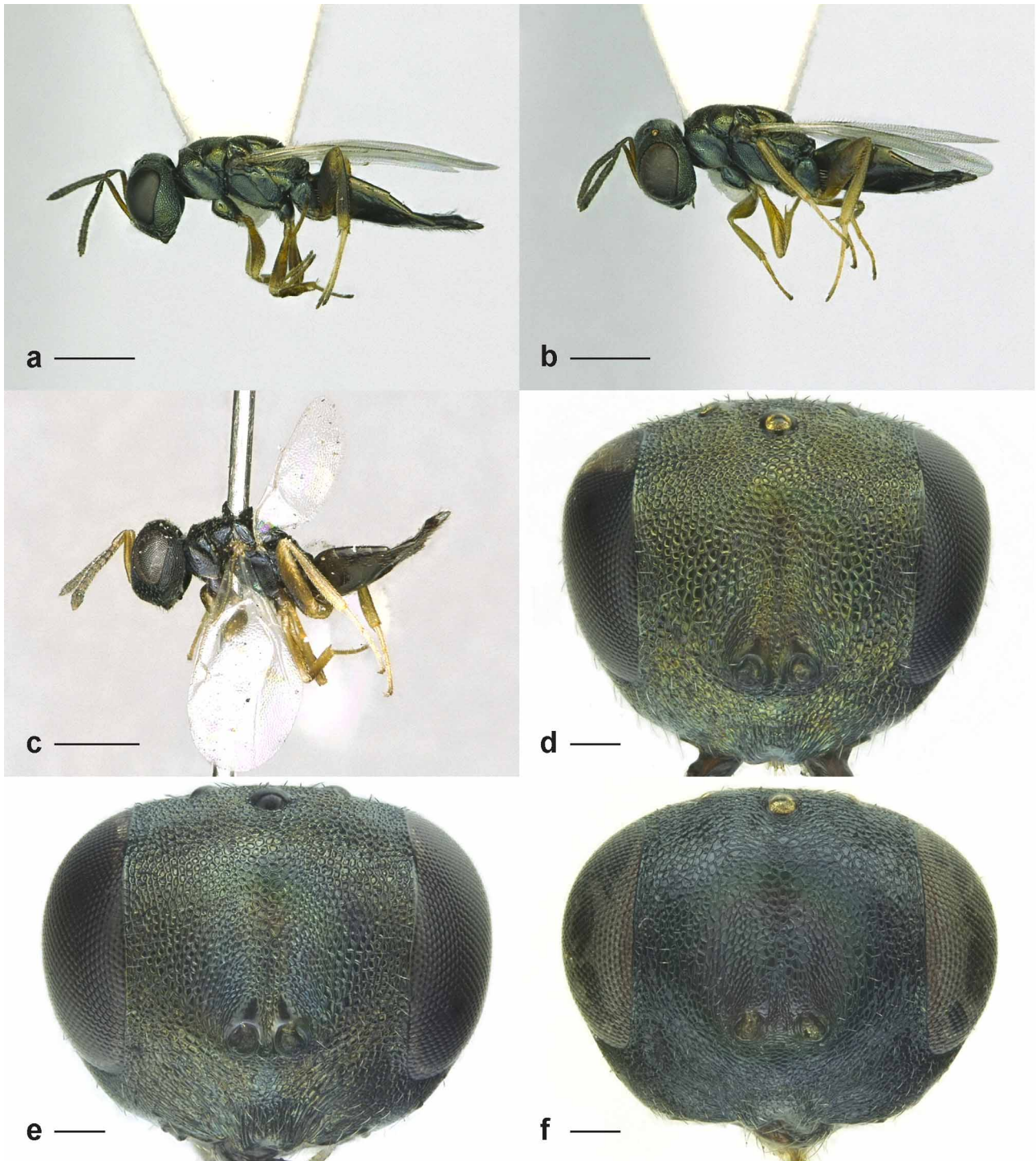
group	gaster length / eye breadth					N
	min.	1st quartile	median	3rd quartile	max.	
<i>lignicola</i>	3.54	3.63	3.73	3.87	4.05	44
<i>cavus</i>	3.88	4.50	4.72	4.90	5.43	113

group	head breadth / stigmal vein					N
	min.	1st quartile	median	3rd quartile	max.	
<i>lignicola</i>	3.46	3.94	4.16	4.32	4.73	44
<i>cavus</i>	3.71	4.40	4.69	5.06	5.83	113

**Description.** FEMALE (Figs 7a, 7d, 8a, 8d). Body length 1700–2950  $\mu\text{m}$ .

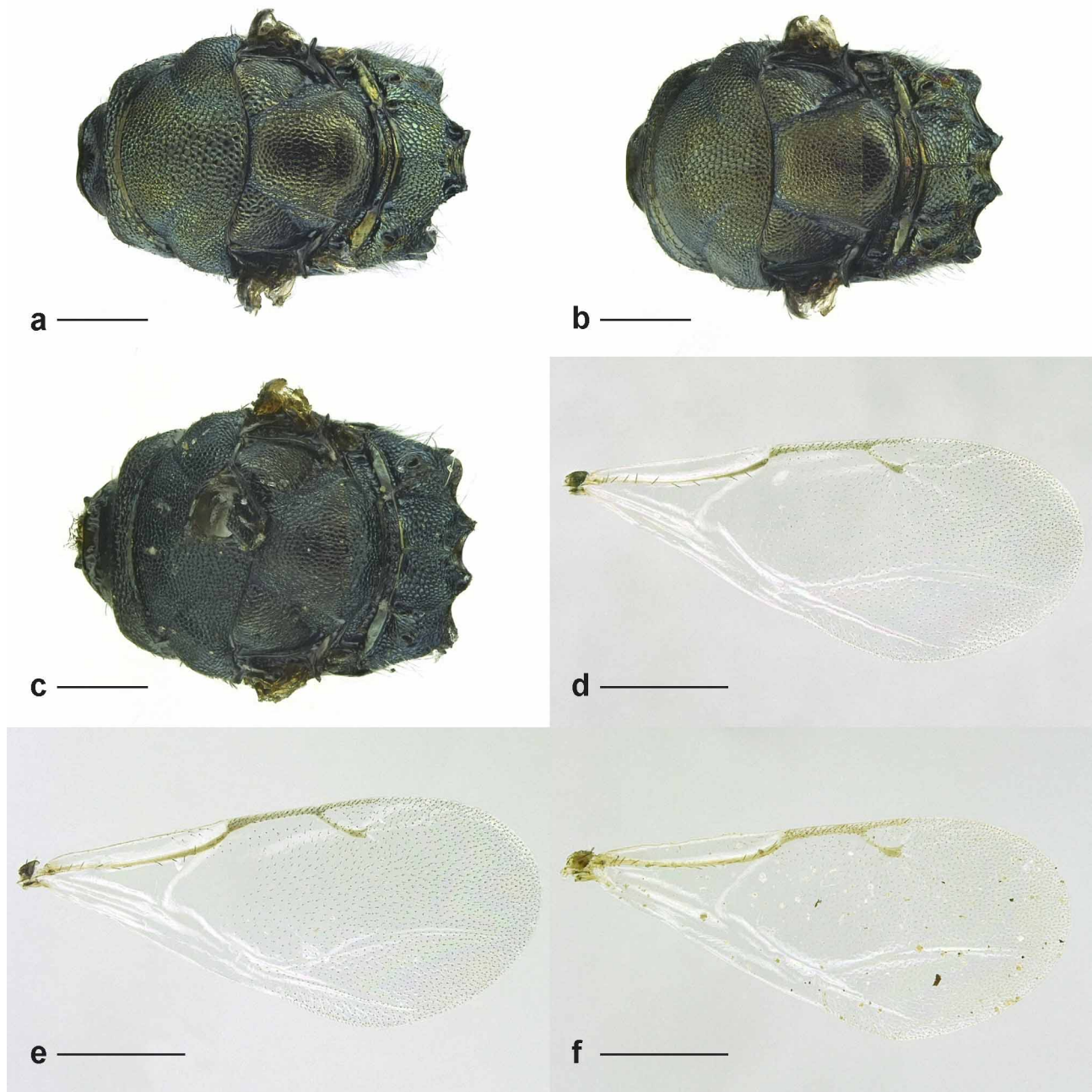
*Head* (Figs 7a, 7d). Eyes large and elongate, sometimes kidney shaped, outer margin straight or slightly to distinctly emarginate; eye 1.39–1.83x as high as broad; eye height 2.05–2.59x POL. Level of lower margin of antennal toruli at level of lower ocular line. Clypeus distinctly striate vertically, though less distinct towards lower margin. Lower face only moderately receding. Mouth narrow, head breadth 2.04–2.83x mouth breadth, mouth breadth 1.73–2.95x malar space. POL 1.55–2.31x OOL. First anellus transverse, second anellus slightly longer than broad; first funicular segment slightly longer than broad, second to fifth quadrate, and sixth slightly transverse; flagellum 0.61–0.80x head breadth.



**FIGURE 7.** a–c, habitus (lateral) of female: (a) *Dibrachys microgastri* (Bouché); (b) *D. lignicola* Graham; (c) *D. verovesparum* Peters & Baur, holotype. d–f, head (frontal) of female: (d) *D. microgastri*; (e) *D. lignicola*; (f) *D. verovesparum*. Scale bars a–c = 500  $\mu\text{m}$ ; d–f = 100  $\mu\text{m}$ .

*Mesosoma* (Fig. 8a). Mesoscutum and scutellum slightly convex in lateral view. Mesoscutum 0.46–0.68x as long as broad. Reticulation coarse, 11.7–14.5 meshes/200  $\mu\text{m}$  in anterior part of mesoscutum, sometimes finer on scutellum than on mesoscutum. Marginal rim of scutellum only moderately turned upwards. Plicae weak and straight; median carina occasionally missing or interrupted.

*Wings* (Fig. 8d). Wings hyaline; stigmal vein short, marginal vein 1.62–2.86x stigmal vein; submarginal vein 1.4–2.2x marginal vein.



**FIGURE 8.** a–c, mesosoma (dorsal) of female: (a) *Dibrachys microgastri* (Bouché); (b) *D. lignicola* Graham; (c) *D. verovesparum* Peters & Baur. d–f, forewing of female: (d) *D. microgastri*; (e) *D. lignicola*; (f) *D. verovesparum*. Scale bars a–c = 250  $\mu$ m; d–f = 500  $\mu$ m.

*Metasoma* (Fig. 7a). Gaster varying from almost as long as to longer than head plus mesosoma; elongate and pointed; length 3.88–5.43x eye breadth. Tergites smooth, weakly alutaceous in apical half of gaster and with strong hairs, especially in apical half; sternites with few hairs.

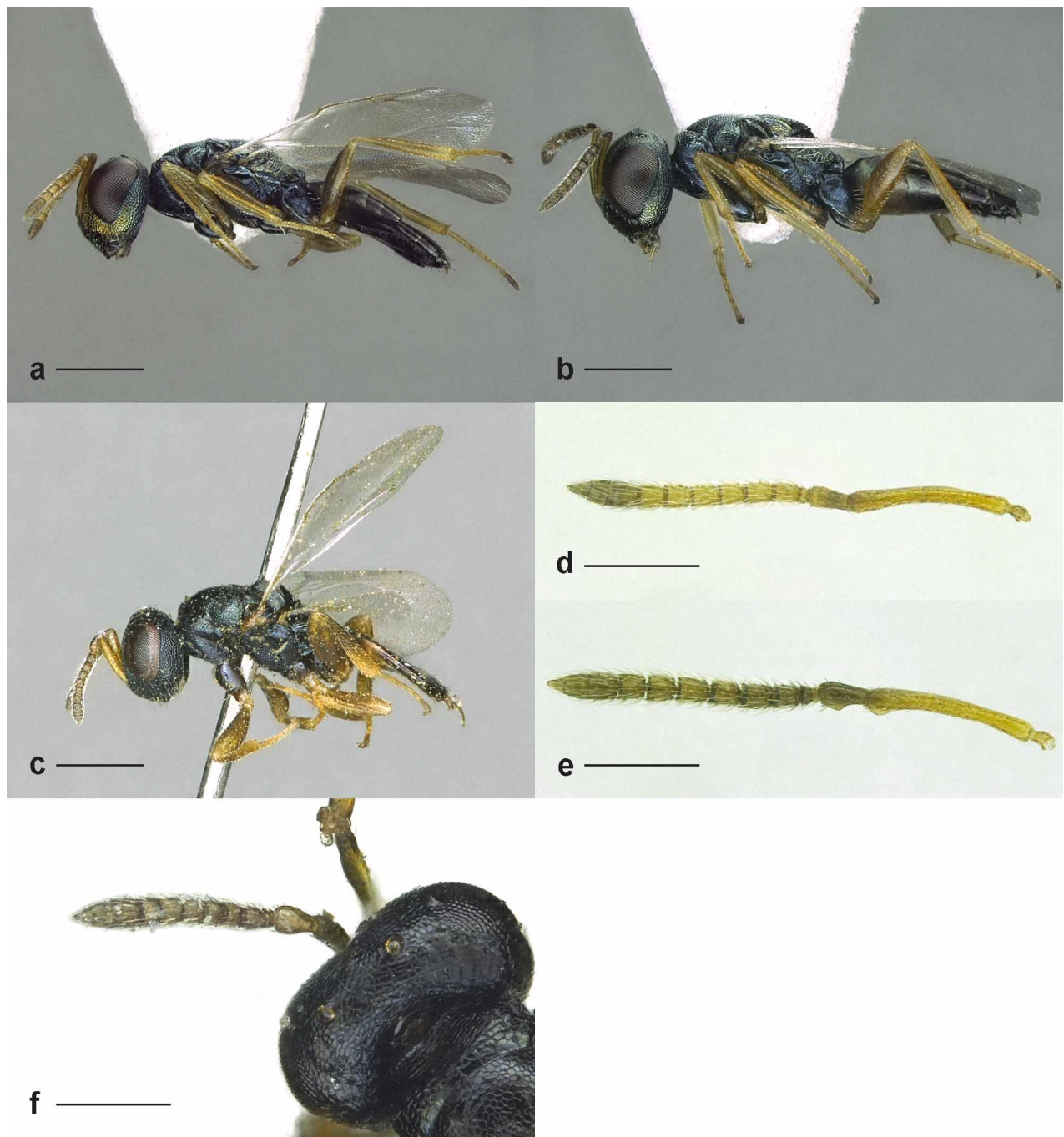
*Hypopygium*. See Table 8 (characters used by Doganlar 1987).

*Color* (Figs 7a, 7d, 8a, 8d). Head and mesosoma very variable, but head and dorsal surface of mesosoma always with distinct metallic coloration or black with distinct metallic tinge. Antenna varying from yellow to dark brown. Ventral surface of mesosoma black or dark brown with slight metallic tinge or with distinct metallic coloration. Venation of wings testaceous to distinctly brown. Procoxa usually concolorous with mesosoma; meso- and metacoxa sometimes concolorous with mesosoma, but mostly brown. Trochanters, femora and tibiae varying from yellow to dark brown. Tarsi varying from pale yellow to brown, segments 4 and 5 of metatarsus usually darker than others. Gaster dark brown and shiny.



**TABLE 8.** Ranges of three characters of the hypopygium used by Doganlar (1987) to separate *D. boarmiae*, *D. cavus*, and *D. clisiocampae*, compared with ranges of specimens from the *D. microgastri* laboratory stock HBM (N = 15); character 1 = greatest median width of posterior lobe:greatest sublateral width of posterior lobe; character 2 = hypopygium breadth:length; character 3 = distance between the branches of hind edge of sublateral sclerotized area:shortest distance between anterolateral incision and interior lobe.

	character 1	character 2	character 3
<i>D. boarmiae</i>	1.00–1.07	-	-
<i>D. cavus</i>	1.21–1.41	1.65–1.70	1.33–1.63
<i>D. clisiocampae</i>	1.21–1.41	1.85–2.00	1.83–2.90
<i>D. microgastri</i> stock HBM	1.22–1.50	1.78–2.08	1.71–2.25



**FIGURE 9.** a–c, habitus (lateral) of male: (a) *Dibrachys microgastri* (Bouché); (b) *D. lignicola* Graham; (c) *D. verovesparum* Peters & Baur. d and e, antenna (dorsal) of male: (d) *D. microgastri*; (e) *D. lignicola*. f, head with antenna (dorsal) of male; *D. verovesparum*. Scale bars a–c = 500 µm; d–f = 250 µm.

MALE (Figs 9a, 9d). Similar to female except as follows. Smaller, body length 1450–2360 µm.

*Head.* Eyes not emarginate and more circular in shape; eye height 2.11–2.60x POL. Level of lower margin of antennal toruli slightly above lower ocular line. Scape and pedicel apically without lobe on outer side.

*Metasoma.* Gaster distinctly shorter than rest of body, 0.63–0.93x length of head plus mesosoma; elongate, not distinctly pointed, broader than in female.

*Color.* Head always with distinct metallic coloration. Antenna varying from yellow to brown, clava sometimes a little darker than rest. Mesoscutum always with distinct green or blue metallic coloration; scutellum often with distinct bronze or gold-bronze. Coxae usually brown, sometimes at least in part concolorous with mesosoma. Gaster brown with light testaceous spot on ventral side of anterior segments (“gastral spot”) absent to distinct, and if distinct then also visible in dorsal view.

**Material examined.** Neotype female (hereby designated): **Germany:** Schleswig-Holstein: Halstenbek, garden of Langkoppelweg 24, N53.6197 E9.8283 (WGS84), reared from cocoon of *Cotesia glomerata* (Hymenoptera: Braconidae), leg. L. Krogmann 26/04/2006, det. R. Peters 2009. Deposited at ZMH (A, 1 female).

Other material: **Afghanistan:** Chakav, labeled “Chakav, C.I.B.C.”, reared from “larva boring in branches of *Juglans regia*” (A, 2 females) (BMNH) (det. *Dibrachys* sp.). **Algeria:** Delassus (?), reared from *Lobesia botrana* (A, 9 females, 3 males) (BMNH) (det. *D. cavus*). **Australia:** Victoria, reared from *Galleria mellonella* (A, 1 female) (BMNH) (det. *D. boarmiae*); Victoria, reared from *Cydia molesta*, originally identified as *D. australia*, Korr. Bouček (A, 2 females, 1 male) (BMNH) (det. *D. boarmiae*). **Bulgaria:** reared from *Cephus* sp. (A, 3 females) (BMNH) (det. *D. cavus*). **Canada:** British Columbia: Burnaby, reared from *Eutromula pariana*, leg. Doganlar 10/09/1977 (all 7 females A (ZSM01–07), 3 males) (ZSM) (det. *D. clisiocampae*); British Columbia: Burnaby, reared from *Apanteles longicauda*, leg. 01/09/1977 (A, 1 female) (MDC) (det. *D. clisiocampae*); British Columbia: Burnaby, reared from *Apanteles* sp., leg. 30/08/1977 (1 male) (MDC) (det. *D. boarmiae*). **Croatia:** Rovinj, reared from Diptera puparium (8 females, 1 male) (ZMH) (det. *D. cavus*). **Cyprus:** reared from stored wheat (A, 9 females) (BMNH) (det. *D. cavus*); Nicosia, reared from *Coleophora* sp. (A, 1 female) (BMNH) (det. *D. cavus*). **Czech Republic:** Bohemia: Stepanov, reared from *Diprion polytomum* (= *Gilpinia hercyniae*) (A, 19 females) (BMNH) (det. *D. cavus*); Bohemia: Dobris, reared from *Diprion polytomum* (A, 3 females) (BMNH) (det. *D. cavus*); Bohemia: Dobris, reared from *Diprion polytomum*, different host specimen than previous, prob. different collection date than previous (18 females) (BMNH) (det. *D. cavus*); Bohemia: Holovousy, reared from tachinid puparium ex *Cydia pomonella* (A, 1 female) (BMNH) (det. *D. cavus*); Bohemia: Plese, reared from *Diprion polytomum* (11 females, 2 males) (BMNH) (det. *D. cavus*); Bohemia: Vlastijovice (? , probably wrong spelling), reared from *Diprion polytomum* (A, 9 females, 10 males) (BMNH) (det. *D. cavus*). **Egypt:** reared from *Platyedra gossypiella* (= *Pectinophora gossypiella*) (A, 1 female) (BMNH) (det. *D. cavus*); Kafr el Sheikh, reared from *Galleria mellonella* (7 females, 1 male) (BMNH) (det. *D. boarmiae*). **England:** no host, identified as *D. fuscicornis* by Walker, corrected by Bouček (A, 1 female) (BMNH) (det. *D. cavus*); Buckinghamshire, no host (A, 1 female) (BMNH) (det. *D. cavus*); Buckinghamshire, same location and different collection date than previous, no host (1 female) (BMNH) (det. *D. cavus*); Wiltshire: Salisbury, reared from *Galleria melonella* ex beehive (A, 1 female, 2 males) (BMNH) (det. *D. cavus*); no host (1 female) (BMNH) (det. *D. cavus*); no host (1 female) (BMNH) (det. *D. cavus*); Bristol, reared from *Ocytata pallipes* 18/09/1979, em. June 1980 (2 of 12 females A, 3 males) (BMNH) (det. *D. cavus*); Bristol, reared from *Triarthria setipennis*, leg. 11/10/1979, em. June 1980 (A, 7 females) (BMNH) (det. *D. cavus*); Bristol, reared from *Triarthria setipennis*, leg. 12/10/1979, em. June 1980 (A, 6 females) (BMNH) (det. *D. cavus*); Worcestershire, reared from *Phygadeuon* pr. *vexator* on *Triarthria setipennis* (A, 6 females, 2 males) (BMNH) (det. *D. cavus*); Hampshire, no host (A, 5 females) (BMNH) (det. *D. boarmiae*); no host, lectotype of *Pteromalus cavus* (A, 1 female) (BMNH); no host, paralectotypes of *Pteromalus cavus* (A, 5 females, 1 male) (BMNH) (det. *D. cavus*); no host, labeled *Pteromalus decedens* Walker (6 females, 3 males) (BMNH) (det. *D. cavus*); no location (but most probably from England), no host, lectotype and paralectotype *Pteromalus decedens* (1 female, 1 male) (BMNH) (det. *D. cavus*); Kensington, reared from *Orgyia antiqua* (A, 7 females, 3 males) (BMNH) (det. *D. cavus*); London, reared from cocoons of *Apanteles solitarius* (A, 7 females, 4 males) (BMNH) (det. *D. cavus*); Cambridge, reared from puparium of *Calliphora* sp. (A, 7 females, 4 males) (BMNH) (det. *D. cavus*); Cambridge, reared from puparium of *Calliphora* sp., different collection date than previous (A, 2 females) (BMNH) (det. *D. cavus*); Cambridge, reared from puparium of *Calliphora* sp., different collection date than previous (2 males) (BMNH) (det. *D. cavus*); London: Osterley Park, reared from *Triarthria setipennis*, labeled Altson Collection (A, 4 females) (BMNH) (det. *D. cavus*); Fryer (?), reared from psychid (4 females, 1 male) (BMNH)

(det. *D. cavus*); Norfolk, reared from larva of *Tyria jacobaeae* (7 females) (BMNH) (det. *D. cavus*); Leeds, reared from tachinid of *Acronicta psi* (A, 5 females, 3 males) (BMNH) (det. *D. cavus*); London, no host (1 female) (BMNH) (det. *D. cavus*); Cheshire: Romiley, reared from *Hemerobius subnebulosus* (= *Wesmaelius subnebulosus*) cocoons (A, 5 females) (BMNH) (det. *D. cavus*); London, reared from pupa of *Orgyia antiqua*, labeled “on defoliating plane” (1 female) (BMNH) (det. *D. cavus*); London, reared from *Orgyia antiqua* larva, labeled “on defoliating planes”, probably same location as previous (A, 14 females, 6 males) (BMNH) (det. *D. cavus*); Essex, reared from pupae of *Apanteles* sp. from *Leucoma salicis* (A, 41 females and males) (BMNH) (det. *D. cavus*); Cambridge, reared from *Galleria mellonella* cocoon (A, 1 female) (BMNH) (det. *D. cavus*); London, reared from *Apanteles* sp. on larva of *Orgyia antiqua* (A, 6 females, 6 males) (BMNH) (det. *D. cavus*); London, reared from *Apanteles* sp. cocoons on *Orgyia antiqua*, different from previous (A, 3 females) (BMNH) (det. *D. cavus*); Cambridge, reared from *Galleria mellonella* (2 males) (BMNH) (det. *D. cavus*); Farnham Royal, reared from prob. *T. setipennis* (host attached, det. R. Peters), bred from nest of blackbird (A, 5 females) (BMNH) (det. *Dibrachys* sp.); Berkshire, reared from small unidentified Diptera puparium attached to specimen, labeled “reared from Decov nest” (?) (A, 1 female) (BMNH) (det. *Dibrachys* sp.); Berkshire, no host, reared from nest of wren (A, 2 females) (BMNH) (det. *Dibrachys* sp.); Hampshire (Hants), reared from *Triarthria* sp. (A, 7 females, 1 male) (BMNH) (det. *Dibrachys* sp.); Buckinghamshire (Bucks), reared from pupae of *Hofmannophila pseudospretella*, Woodroffe material 1961 (A, 15 females, 3 males) (BMNH) (det. *Dibrachys* sp.); Wiltshire: Malmesbury, reared from puparium of *Stenepteryx hirundinis* (A, 1 female, 1 male) (BMNH) (det. *Dibrachys* sp.); Stratford-on-Avon, reared from „? *Gelis* cocoon ex egg sac of *Zygiella x-notata*“ (1 male) (BMNH) (det. *D. cavus*); London, no host, labeled *Pteromalus lucilla* Walker (1 male) (BMNH) (det. *D. cavus*); Cambridge, reared from sawfly cocoon in old bird nest (4 males) (BMNH) (det. *D. cavus*); Cambridge, reared from “brown cocoon” (2 males) (BMNH) (det. *D. cavus*); Enfield, reared from tachinid ex *S. salicis* (probably *Stilpnotia* (= *Leucoma*) *salicis*) (2 males) (BMNH) (previously unidentified specimen); Farnham Royal, no host, reared from nest of greenfinch (3 males) (BMNH) (det. *Dibrachys* sp.); British Islands, reared from unidentified tachinid puparium (3 males) (BMNH) (det. *Dibrachys* sp.); Berkshire: Shillingford, reared from *Digonichaeta spinipennis* (= *Triarthria setipennis*) under bark, labeled by Graham “per-versus? see type” (1 male) (BMNH) (det. *Dibrachys* sp.). **Eritrea:** Asmara, labeled “ex no. 12, epiparasites of *Ocinara ficicola* (?)” (?), host record unclear; either *Ocinara ficicola* or epiparasites of *Ocinara ficicola* are host) (2 of 7 females A) (BMNH) (det. *Dibrachys* sp.). **France:** Auxonne, reared from *Cotesia glomerata* (A, 1 females, 1 male) (BMNH) (det. *D. cavus*); Lyon, reared from *Cotesia glomerata* (A, 4 females, 3 males) (BMNH) (det. *D. cavus*); Lyon, reared from *Cotesia glomerata*, different collection date than previous with same location and same host species (A, 1 female) (BMNH) (det. *D. cavus*); Lyon, reared from *Cotesia glomerata*, different collection date than previous with same location and same host species (1 female) (BMNH) (det. *D. cavus*); Lyon, reared from *Cotesia glomerata*, different collection date than previous with same location and same host species (A, 1 female, 1 male) (BMNH) (det. *D. cavus*); reared from moth in beehive (A, 1 female) (BMNH) (det. *D. cavus*); reared from moth in beehive, different location than previous (1 male) (BMNH) (det. *D. cavus*); Vizille, reared from *Apanteles liparidis* (= *Glyptapanteles liparidis*) on *Lymantria dispar* on *Populus* sp. (A, 3 females, 1 male) (BMNH) (det. *D. cavus*); Châteauneuf Valais, reared from unidentified tachinid in *Archips rosana* (2 females, both A) (BMNH) (det. *D. cavus*); South of France, no host, labeled *Pteromalus cavus* Walker (3 males) (BMNH) (det. *D. cavus*). **Germany:** Schleswig-Holstein: Halstenbek, garden of Langkoppelweg 24, N53.6197 E9.8283 (WGS84), reared from *Cotesia glomerata*, leg. L. Krogmann 26/04/2006, same data as neotype (2 females, both A (ZMH01–02), 2 males; 2 females in 96 % EtOH) (ZMH); Hamburg-Bramfeld, Umweltzentrum Karlshöhe, reared from *Triarthria setipennis*, leg. Peters 22/09/2004 (A, 1 female, 1 male) (ZMH); Hessen: Bad Arolsen, reared from *Triarthria setipennis*, leg. K. Staiber March 2005 (A, 1 female, 2 males in EtOH) (ZMH); Stock HBM laboratory rearing on *Galleria mellonella* (A, 2 females, 1 male) (ZMH); Stock HBM laboratory rearing on *Calliphora vomitoria* (numerous females (26 A) and males, including specimens in Figs 7–9) (ZMH); Berlin, reared from *Protocalliphora* sp. from tit nest (A, 1 female) (BMNH) (det. *D. cavus*); Kitzberg, reared from *Pieris* sp. (2 of 7 females A, 2 males) (BMNH) (det. *D. cavus*); Rheinhessen, reared as hyperparasitoid (?) from *Aporia crataegi* (A, 1 female, 3 males) (BMNH) (det. *D. cavus*); Berlin, reared from *Acronycta aceris* (A, 1 female) (BMNH) (det. *D. boarmiae*); Berlin, reared from *Euproctis chrysorrhoea* (1 male) (BMNH) (det. *D. boarmiae*); Wangerooe (1 female) (ZMH) (det. *D. boarmiae*); F.S. Elbe I, leg. 14/08/65 (1 prob. female) (ZMH) (det. *D. boarmiae*); Bavaria: Oberwaiz, leg. 15/07/1983, reared from calliphorid puparium (12 females and males, some in bad condition) (ZMH) (det. *D. boarmiae*); Schleswig-Holstein: Nützen, leg. 01/12/2002, reared from *Triarthria setipennis* in nest of *Passer montanus*,

Voucher specimen Dissertation Lars Krogmann 2005, morphological voucher CH\_0044 Krogmann & Vilhelmsen 2006 (1 female) (ZMH) (det. *D. cavus*, Krogmann 2003). **Hungary:** Hortobágy, Ujszentmargita védett erdő, holotype of *Tritneptis elegans* (A, 1 female) (HNHM). **India:** Stinagar, reared from *Lymantria obfuscata* pupa (A, 5 females) (BMNH) (det. *D. cavus*). **Iran:** Gilan, reared from *Galleria mellonella* (A, 3 females, 1 male) (BMNH) (det. *D. boarmiae*); Kerman, reared from *Kermania pistaciella* (A, 1 female) (BMNH) (det. *D. ? cavus*). **Italy:** Aosta, no host (A, 1 female) (BMNH) (det. *D. cavus*). **Morocco:** Middle Atlas, reared from larva (?) of *Thaumetopoea pityocampa* on *Cedrus atlantica* (1 female) (BMNH) (det. *D. boarmiae*). **Moldova:** Kishinev, reared from *Orgyia* sp. (3 males) (BMNH) (det. *D. cavus*). **New Zealand:** Lincoln, reared from cultured *Vespula germanica* (A, 2 females, 6 males) (BMNH) (det. *D. boarmiae*); Christchurch, reared from *Vespula germanica* (in part cultured) (A, 14 females) (BMNH) (det. *D. boarmiae*). **Pakistan:** Mongora, reared from codling moth on apple (prob. *Cydia pomonella*) (A, 1 female) (BMNH) (det. *D. ? cavus* by Bouček); Baluchistan (no further location labeled, Baluchistan maybe belonging to Iran), reared from pupa of *Cacoecia* sp. (A, 2 females) (BMNH) (det. *D. boarmiae*); Quetta, reared from codling moth on apple (A, 6 females, 1 male) (BMNH) (det. *D. ? boarmiae* by Bouček); Mingora C.I.B.C., no host, reared from galls on twigs of *P. nigra* (could be *Pinus nigra* or *Populus nigra*) (A, 1 female, 1 male) (BMNH) (det. *Dibrachys* sp.). **Portugal:** Central Coast, reared from *Pempelia genistella* (A, 2 females) (BMNH) (det. *D. boarmiae*). **Serbia:** Beograd, no host (A, 1 female) (BMNH) (det. *D. cavus*); Belgrad, no host (2 females, 1 male) (BMNH) (det. *D. cavus*). **Switzerland:** Saxon, reared from *Grapholita funebrana* (A, 2 females, 2 males) (BMNH) (det. *D. cavus*); no host (1 female) (BMNH) (det. *D. cavus*); Nyon, reared from *Lobesia botrana* (A, 1 female) (BMNH) (det. *D. cavus*); Simplon, reared from *Phytodietus grisianae* (A, 2 females, 1 male) (BMNH) (det. *D. cavus*); Nyon, reared from *Grapholita funebrana* (1 male) (BMNH) (det. *D. cavus*); Vaud Com-mugny, no host, from bird nest (A, 1 female) (NMBE) (det. *D. cavus*). **Syria:** Damaskus, reared from *Galleria mellonella* (A, 2 females, 1 male) (BMNH) (det. *D. cavus*). **Tunesia:** Chaffar, reared from Lepidoptera pupa on olive (A, 1 female, 2 males) (BMNH) (previously unidentified specimens). **Turkey:** Tekirdag, reared from *Tenebroides mauritanicus* (A, 2 females) (BMNH) (det. *D. cavus*); Ankara, reared from *Galleria mellonella* (A, 9 females, 3 males) (BMNH) (det. *D. boarmiae*); Erzurun, no host, leg. Doganlar 25/06/1981 (1 female) (MDC) (det. *D. boarmiae*); Erzurun, labeled “*Apis mellifera*” (?), unclear if reared from *A. mellifera* or from *A. mellifera* beehive), leg. 18/05/1981 (1 male) (MDC) (det. *D. boarmiae*); Erzurun, no host, leg. H. Özrek (?) 29/08/1979 (1 female) (MDC) (det. *D. cavus*); Erzurun, labeled “Prunus mahaleb”, leg. Doganlar 13/07/1982 (1 female) (MDC) (det. *D. cavus*); Ankara, no host, leg. 15/08/1977 Kiliger (?) (2 females) (MDC) (det. *D. boarmiae*). **USA:** Ohio: Columbus, syntype of *Arthrolytus apatelae* (1 female) (USNM); West Virginia: Morgantown, syntype of *Arthrolytus pim-plae* (1 female) (USNM). **No location:** B. Cooke Coll. 84-52 (1 female) (BMNH) (det. *D. cavus*); labeled “aus Plettenberg Zucht 1972, H. Wolf” (6 females, 3 males) (BMNH) (det. *D. cavus*); reared from nest of *Dolichovespula norvegica*, leg. C. Nicholson, 1915 (A, 1 female) (BMNH) (det. *D. cavus*); reared from dipterous puparium under bark, labeled H.W. Miles collection, 1924 (2 females) (BMNH) (det. *D. cavus*); reared from puparium of *Calliphora* sp. (2 females, 1 male) (BMNH) (det. *D. cavus*); lectotype of *Pteromalus boarmiae* (A, 1 female) (BMNH); paralectotypes of *Pteromalus boarmiae* Walker (2 females) (BMNH) (det. *D. cavus* [?]); labeled “leg. Bock 1977” (1 female, 2 males) (ZMH) (det. *D. boarmiae*); lectotype of *Eupelmus cereanus* (A, 1 female) (MZUF); paralectotypes of *Eupelmus cereanus* (2 females, 5 males) (MZUF); syntypes of *Cleonymus clisiocampae*, labeled “Fitch’s Type”, “Semiotellus clisiocampae” (A, 1 female, 1 male) (USNM); syntypes of *Cheiropachus nigrocyaneus* (2 females) (USNM); syntype of *Pteromalus chionobae* (1 female) (USNM); lectotype of *Pteromalus gelechia* (1 male) (INHS); paralectotype of *Pteromalus gelechia*, labeled “lectoallotype” (A, 1 female), additional paralectotypes of *P. gelechia* (4 females, 4 males) (INHS); labeled “Collectio Ratzeburg [print]”, “Pt. Zelleri Psyche ...[illegible; Ratzeburg's hand?]”, “Zelleri R. [hand] det. Ratzeburg [print]”, “Zelleri R. [hand]” (1 male) (NMW) (det. *Pteromalus zelleri*).

**Biology.** The long host lists of *D. cavus* and *D. boarmiae* in such publications as Peck (1963), Krombein *et al.* (1979) and Noyes (2003) that summarize previously published records are unreliable for delimiting the true host range of *D. microgastri* for two reasons: (1) the parasitoid and host identifications have not been verified, and (2) earlier authors did not differentiate between *D. microgastri* and *D. lignicola*. Table 9 lists 38 verified host species based on label data of specimens we examined where the host species was identified or could be considered a distinct species (e.g., the listed tachinids). Based on this, *D. microgastri* is a polyphagous species that uses hosts from at least five insect orders, Diptera (3 families of Cyclorrhapha), Lepidoptera (10 families), Hymenoptera (5 families of “Symphyta” and Apocrita), Neuroptera and Coleoptera (one record each). Our list is more reliable, but is

still extraordinarily long, which shows *D. microgastri* can parasitize hosts from various orders and is truly polyphagous.

**TABLE 9.** Hosts of *Dibrachys microgastri*. Doubtful records from larval hosts are marked with an asterisk (\*).

host species	
<i>Tenebroides mauritanicus</i> (Linnaeus)	Coleoptera: Trogossitidae
<i>Calliphora</i> sp.	Diptera: Calliphoridae
<i>Protocalliphora</i> sp.	Diptera: Calliphoridae
<i>Stenopteryx hirundinis</i> (Linnaeus)	Diptera: Hippoboscidae
<i>Ocytata pallipes</i> (Fallén)	Diptera: Tachinidae
<i>Triarthria setipennis</i>	Diptera: Tachinidae
unidentified tachinid from <i>Acronicta psi</i> (Linnaeus)	Diptera: Tachinidae
unidentified tachinid from <i>Archips rosana</i> (Linnaeus)	Diptera: Tachinidae
unidentified tachinid from <i>Cydia pomonella</i> (Linnaeus)	Diptera: Tachinidae
<i>Apanteles longicauda</i> (Wesmael)	Hymenoptera: Braconidae
<i>Apanteles solitarius</i> (Ratzeburg)	Hymenoptera: Braconidae
<i>Cotesia glomerata</i> (Linnaeus)	Hymenoptera: Braconidae
<i>Glyptapanteles liparidis</i> (Bouché)	Hymenoptera: Braconidae
<i>Cephus</i> sp.	Hymenoptera: Cephidae
<i>Gilpinia hercyniae</i> (Hartig)	Hymenoptera: Diprionidae
<i>Gregopimpla inquisitor</i> (Scopoli)	Hymenoptera: Ichneumonidae
<i>Phygadeuon</i> sp.	Hymenoptera: Ichneumonidae
<i>Phytodietus griseanae</i> (Kerrich)	Hymenoptera: Ichneumonidae
<i>Vespula germanica</i> (Fabricius)	Hymenoptera: Vespidae
<i>Tyria jacobaeae</i> (Linnaeus)*	Lepidoptera: Arctiidae
<i>Eutromula pariana</i> (Clerck)	Lepidoptera: Choreutidae
<i>Coleophora</i> sp.	Lepidoptera: Coleophoridae
<i>Pectinophora gossypiella</i> (Saunders)	Lepidoptera: Gelechiidae
<i>Euproctis chrysorrhoea</i> (Linnaeus)	Lepidoptera: Lymantriidae
<i>Lymantria obfuscata</i> Walker	Lepidoptera: Lymantriidae
<i>Orgyia antiqua</i> (Linnaeus)	Lepidoptera: Lymantriidae
<i>Acronicta aceris</i> (Linnaeus)	Lepidoptera: Noctuidae
<i>Oeneis semidea</i> Say	Lepidoptera: Nymphalidae
<i>Hofmannophila pseudospretella</i> (Stainton)	Lepidoptera: Oecophoridae
<i>Pieris</i> sp.	Lepidoptera: Pieridae
<i>Galleria mellonella</i>	Lepidoptera: Pyralidae
<i>Pempelia genistella</i> (Duponchel)	Lepidoptera: Pyralidae
<i>Thaumatopoea pityocampa</i> (Denis & Schiffermüller)*	Lepidoptera: Thaumatopoeidae
<i>Kermania pistaciella</i> Amsel	Lepidoptera: Tineidae
<i>Cacoecia</i> sp.	Lepidoptera: Tortricidae
<i>Cydia pomonella</i> (Linnaeus)	Lepidoptera: Tortricidae
<i>Grapholita funebrana</i> (Treitschke)	Lepidoptera: Tortricidae
<i>Grapholita molesta</i> (Busck)	Lepidoptera: Tortricidae
<i>Lobesia botrana</i> (Denis & Schiffermüller)	Lepidoptera: Tortricidae
<i>Wesmaelius subnebulosus</i> (Stephens)	Neuroptera: Hemerobiidae

Only pupal stages of hosts appear to be used by *D. microgastri*, which implies they are restricted to holometabolous insects. Gontarski (1939) reported the use of cocooned Lepidoptera larvae, which are immobile, but this record is doubtful. Some museum material of *D. microgastri* was labeled with host records from Lepidoptera larvae, including *Tyria jacobaeae* (Arctiidae) and *Thaumetopoea pityocampa* (Thaumetopoeidae). These records are probably wrong or based on unrecognized hyperparasitism of Ichneumonoidea pupae on the lepidopteran larvae and therefore are marked as doubtful in the host list (Table 9).

*D. microgastri* is a facultative hyperparasitoid through parasitic Hymenoptera and Diptera. Facultative secondary hyperparasitism is common in ectoparasitic parasitoids (Askew & Shaw 1986). The record of parasitism of an Ichneumonidae pupa inside the puparium of the tachinid *T. setipennis* also demonstrates facultative tertiary parasitism for *D. microgastri*. Gordh (1981) stated that tertiary parasitism is always facultative.

Polyphagy of *D. microgastri* is also supported by our laboratory rearings on different species of Calliphoridae (Diptera) and on *Galleria mellonella* (Lepidoptera: Pyralidae), using parasitoids from a stock originally reared from tachinid puparia (Peters 2007). Although successful rearing in the lab can give information about a parasitoid's potential ability to use a host, this has to be considered with caution because it is known that parasitoids can use hosts that are normally outside their host range if no natural hosts are available and an artificial situation is created in a Petri dish (Godfray 1994). Accordingly, we only listed field host records in Table 9.

**Distribution.** *Dibrachys microgastri* is a cosmopolitan species. Noyes (2003) listed 57 countries for distribution. Those countries we confirmed or added through our examination of specimens are listed in Table 10.

**TABLE 10.** Geographic distribution of *Dibrachys microgastri*.

geographic region	country	geographic region	country	
Europe	Bulgaria	Asia	Afghanistan	
	Croatia		Cyprus	
	Czech Republic		India	
	France		Iran	
	Germany		Pakistan	
	Hungary		Syria	
	Italy		Africa	Algeria
	Moldova			Egypt
	Portugal			Eritrea
	Serbia			Morocco
	Switzerland		Tunesia	
Europe: Brit. Isles	England	North America	Canada	
Europa/Asia	Turkey		USA	
		Australia		
		New Zealand		

**Taxonomic remarks.** After morphological examination of females and males, morphometric analysis, and examination of name-bearing types, we consider *D. cavus*, *D. boarmiae* and *D. clisiocampae* to be synonyms. *Dibrachys cavus* and *D. boarmiae* have always been considered close (Graham 1969, Sharkov 1982) and their synonymy was said to be likely but was not formally stated by Zerova *et al.* (1986). *Dibrachys clisiocampae* was synonymized with *D. cavus* by Gahan (1938) but was re-established by Doganlar (1987).

Our analyses show the characters used to separate these three putative species are not reliable, including the three characters of the hypopygium used by Doganlar (1987) (Table 8). The other characters mentioned by Doganlar (1987) and Graham (1969) to separate *D. cavus* and *D. boarmiae* also proved to be intraspecifically variable. These characters were: “head breadth to length”, “eye height to breadth”, “eye margin emarginate or not” and the expression of the male gastral spot. Further characters such as the weakly colored discal cloud on the forewing in *D. boarmiae* was not observed in any specimen, and the shape of the wing stigma and differences in color are considered unsuitable for making taxonomic inferences (see Discussion).

We consider the senior synonym of *D. cavus*, *D. boarmiae* and *D. clisiocampae* to be *Dibrachys microgastri* (Bouché, 1834), which was originally described as *Diplolepis microgastri* but assigned to *Dibrachys* and listed as a possible synonym of *D. cavus* by Graham (1969). Vidal (2001) and Noyes (2003) listed the name as valid because Graham (1969) did not formally synonymize it. The original description includes a host record from *Cotesia glomerata* (= *Apanteles glomeratus*, *Microgaster glomeratus*) (Hymenoptera: Braconidae). *Cotesia glomerata* and other braconid species are commonly recorded host species for *D. cavus* (Noyes 2003; see also examined material and Table 9). Known hosts of *D. verovesparum* do not include Braconidae and although there is a single record of an *Apanteles* Förster (Braconidae) parasitoid of *D. lignicola* (see below), these species cannot be what Bouché (1834) described as *D. microgastri* because the original description states that the male is “stahlblau angelaufen” (tarnished steel-blue) which does not apply to either *D. verovesparum* or *D. lignicola*. The type material of *D. microgastri* is presumed lost (Graham 1969) and in order to resolve present nomenclatural instability we designate a neotype female for *D. microgastri*. The neotype was selected from the same host species, *Cotesia glomerata*, and the same geographic region, Northern Germany, as the type material used by Bouché (1834) in establishing *Diplolepis microgastri*. Although the name *D. cavus* has been widely used for almost a century, we deliberately refrain from requesting the International Commission on Zoological Nomenclature to set aside the lesser known name *D. microgastri* because *D. cavus* has often been confused with different species of *Dibrachys*, most notably *D. lignicola* and *D. braconidis*, and *D. cavus* as used in the literature has a highly ambiguous meaning. The adoption of *D. microgastri* thus underpins the changes associated with our redefinition of the species.

*Dibrachys elegans* is another new synonym of *D. microgastri*. The description of *Tritneptis elegans* by Szelényi (1981) contains a number of mistakes and ambiguous statements, which cause confusion or do not correspond to the holotype or the genus *Dibrachys* (e.g., funicle is used for flagellum, and “without any sign of notaulices”, “scutellum a little shorter than mesoscutum (1.0:1.9)”, and “ovipositor as long as a third of hind tibia” are stated). However, other parts of the description clearly show that this refers to the specimen that was examined by us as the holotype female. From our morphological examination and morphometric analysis there is no doubt that it is a female of *D. microgastri*.

In addition to the above synonymy, we confirmed all recorded synonyms of *D. cavus* and *D. clisiocampae* as synonyms of *D. microgastri* after examination of accessible type material. In the following we provide further information on these synonyms.

The type material of all of Ratzeburg’s taxa unfortunately is presumed lost. We examined a male (NMW) labeled “Collectio Ratzeburg” and “Pt. Zelleri Psyche ...” [illegible]. The latter is possibly written in Ratzeburg’s hand. *Pteromalus zelleri* Ratzeburg, 1848 was described based on a female reared from *Bombyx neustria* (Linnaeus) (= *Malacosoma neustria*) (Lepidoptera: Lasiocampidae). We therefore conclude that this male reared from *Psyche* sp. is not a type specimen of *D. zelleri*, though it probably is from Ratzeburg’s collection.

Despite the remarks of Novitzky in Graham (1969: 810), we follow the conclusions of Kurdjumov (1913) who stated that *D. vesparum* (Ratzeburg, 1852) is a synonym of *D. boucheanus* and hence a synonym of *D. microgastri*. Kurdjumov (1913) reported that he examined the then still existing type material of Ratzeburg. Graham (1969: 810) mentioned some specimens he received from Z. Bouček that were reared from *Dolichovespula saxonica* (Fabricius) (Hymenoptera: Vespidae) and that he suspected might be “the true *vesparum*”. We include these specimens in the type material of our new species *D. verovesparum* and do not consider they are conspecific with *D. vesparum* because the original description of the latter states: (1) gaster as long as head and mesosoma, and (2) body “ölgrün” (oilgreen). A black body without green metallic coloration and a short gaster (always shorter than head plus mesosoma) are two diagnostic characters of our new species and we thus consider *D. vesparum* as a synonym of *D. microgastri*. Vespidae are not only hosts of our new species, but are also within the confirmed host range of *D. microgastri* (Table 9), which supports our conclusion.

The original description of *Cheiropachus nigrocyaneus* Norton, 1869 states “3 specimens bred”. The examined 2 specimens are in bad condition (e.g., heads missing), which makes species assignment difficult though they clearly belong to *Dibrachys*. Because this name was already synonymized with *D. clisiocampae* by Girault (1916b: 408) and with *D. cavus* by Gahan (1938: 211) we consider it a synonym of *D. microgastri*.

We examined the lectotype male and paralectotypes (one female labeled “lectoallotype” and 4 females and 4 males labeled paratypes) of *Pteromalus gelechia* Webster, 1883. There is no doubt about the synonymic status of this species.

The original description of *Pteromalus chionobae* Howard, 1889 states that it was based on 2 specimens reared from *Oeneis semidea* (Lepidoptera: Nymphalidae). The single examined female syntype is in bad condition (without head and gaster separated), but it can be assigned to *D. microgastri* with high certainty.

We examined a syntype of *Arthrolytus apatela* Ashmead, 1893 that again is in very bad condition (head, gaster and forewings missing). From our examination of the remaining mesosoma it can be assigned to *Dibrachys*, but not to species. However, we consider *A. apatela* a synonym of *D. microgastri* based on Girault (1916a; 1916b) and Gahan (1938).

One female syntype of *Arthrolytus pimplae* Ashmead, 1894 was examined. It was reared from *Pimpla inquisitor* (= *Gregopimpla inquisitor*) (Ichneumonidae) and we base this host record for *D. microgastri* on this specimen.

In addition to the above synonymy, Graham (1956) transferred *Pteromalus perversus* Walker, 1835 to *Dibrachys* and subsequently listed it as a questionable synonym of *D. cavus* (Graham 1969) based on one male from the Walker collection that he considered was the type (probably holotype). Walker (1835) had erroneously described this male as a female in the original description. Unfortunately, we were unable to locate this specimen in the BMNH or elsewhere (e.g., HDOU). We did examine a male labeled “perversus? see type” by Graham (BMNH), which Graham (1969: 811) stated was “extremely close” to the probable holotype of *D. perversus*. This is a male of *D. microgastri* and suggests that the missing holotype male of *D. perversus* was also a specimen of *D. microgastri*. However, the original description by Walker (1835) does not provide any useful information further to the brief notes given by Graham (1969). Graham (1969) did not formally synonymize *D. perversus* with *D. cavus* and because we could not locate the probable male holotype of *D. perversus* we prefer to treat the name as valid, but as a *nomen dubium* in our list of valid species (see Appendix).

### ***Dibrachys lignicola* Graham, 1969**

(Figs 7b, 7e, 8b, 8e, 9b, 9e)

*Dibrachys (Dibrachys) lignicola* Graham, 1969: 810, holotype female in HDOU (Type HYM: 1283) (examined by Peters).

*Dibrachys (Dibrachys) goettingenus* Doganlar, 1987: 202–203, holotype female in IFUG (examined by Peters); **syn. n.**

**Diagnosis.** *Both sexes.* Eyes large, eye height greater than 2.0x POL. Head and mesosoma with distinct metallic coloration (Figs 7b, 7e, 8b, 9b).

*Female.* Gaster short and eyes broad, gaster length equal to or less than 4.05x eye breadth (Figs 6, 7b, Table 7) and shorter than head plus mesosoma. Eyes broad and oval, eye height equal to or less than 1.6x eye breadth, outer margin never distinctly emarginate (Fig. 7b). Stigmal vein long compared to marginal vein, marginal vein mostly less than 2.0x stigmal vein (1.57–2.05, but only 2 of 47 > 2.0) (Fig. 8e). Mesoscutum never bluish. Mouth narrow, head breadth greater than 2.0x mouth breadth (Fig. 7e).

*Male.* Scape and pedicel apically with distinct lobe on outer side (Fig. 9e). Gastral spot distinct (Fig. 9b).

**Description.** FEMALE (Figs 7b, 7e, 8b, 8e). Body length 2000–3000  $\mu\text{m}$ .

*Head* (Figs 7b, 7e). Eyes large and usually oval, with outer margin rarely only very slightly emarginate; eye 1.38–1.60x as high as broad; eye height 2.11–2.68x POL. Level of lower margin of antennal toruli at level of lower ocular line. Clypeus distinctly striate vertically, though less distinct towards lower margin. Lower face only moderately receding. Mouth narrow, head breadth 2.10–2.55x mouth breadth; mouth breadth 2.38–2.92x malar space. POL 1.55–2.11x OOL. First anellus ringlike, second anellus slightly longer than broad; first funicular segment slightly longer than broad, second to fifth quadrate, and sixth slightly transverse; flagellum 0.63–0.77x head breadth.

*Mesosoma* (Fig. 8b). Mesoscutum and scutellum slightly convex in lateral view. Mesoscutum 0.51–0.61x as long as broad. Reticulation coarse, slightly coarser than in *D. microgastri*, 10.7–14.9 meshes/200  $\mu\text{m}$  in anterior part of mesoscutum. Marginal rim of scutellum only moderately turned upwards. Plicae straight or weakly curved; median carina weak or interrupted.

*Wings* (Fig. 8e). Wings hyaline; stigmal vein long, marginal vein only 1.57–2.05x stigmal vein; submarginal vein 1.74–2.24x marginal vein.

*Metasoma* (Fig. 7b). Gaster shorter than head plus mesosoma; massive and broad, moderately pointed; length 3.54–4.05x eye breadth. Tergites smooth, weakly alutaceous and with some strong hairs in apical half of gaster.

*Color* (Figs 7b, 7e, 8b). Head with distinct metallic coloration, usually dark green. Antenna varying from brown to dark brown, in general slightly darker than in *D. microgastri*. Mesosoma with distinct metallic coloration,



but never blue or almost black, mostly with distinct tinge of bronze or gold, especially on scutellum; ventral surface black with tinge of blue. Venation of wings light brown. Coxae concolorous with mesosoma. Trochanters, femora and tibiae usually yellow or light brown, rarely brown, generally lighter than in *D. microgastri*. Tarsi yellow, last two segments of metatarsus sometimes darker. Gaster brown to dark brown, shiny.

**MALE** (Figs 9b, 9e). Similar to female except as follows. Smaller, body length 1500–2000 µm.

**Head.** Eye height 2.19–2.62x POL. Scape and pedicel apically with distinct lobe on outer side (Fig. 9e).

**Color** (Fig. 9b). Mesoscutum and scutellum always distinctly metallic green or dark green, rarely with a slight tinge of blue; bronze on scutellum mostly indistinct. Coxae dark brown, sometimes at least in part concolorous with mesosoma. Gaster with distinct light testaceous spot on ventral side of anterior segments, the spot also visible in dorsal view.

**Material examined. England:** Berkshire, Slough, reared from *Crataerina pallida* pupae by Woodroffe 1951 (A, 5 females) (BMNH) (det. *Dibrachys* sp.); Farnham, reared from Diptera puparium (A, 2 females) (BMNH) (det. *D. cavus*); Hampshire (Hants), reared from dead *Larix* trunk (A, 5 females, 2 males) (BMNH) (det. *D. boarmiae*). **France:** Sollies Pont, reared from pupae of *Cydia pomonella* (A, 2 females, 1 male) (BMNH) (det. *D. cavus*). **Germany:** Hamburg, reared from puparia of *Triarthria setipennis*, leg. R. Peters March 2006 (6 of numerous females A, and numerous males) (ZMH); Hamburg, stock HRL, laboratory rearing on *Calliphora vomitoria* (20 of numerous females A, and numerous males) (ZMH); Hamburg, reared from *Ocytata pallipes*, leg. R. Peters (numerous females and males) (ZMH); Hamburg, stock HRL II (numerous females and males, including specimens in Figs 7–9); Hessen: Bad Arolsen, host *Ornithomya avicularia*, leg. K. Staiber March 2005 (2 females, 1 male, all dead inside host puparium) (ZMH); Göttingen, reared from *Gilpinia hercyniae*, holotype of *Dibrachys goettingenus* (A, 1 female) (IFUG); paratypes of *D. goettingenus*, same data as holotype (all 3 females A, 1 male) (IFUG); paratypes of *D. goettingenus*, same data as holotype (A, 2 females) (BMNH). **Ireland:** Dublin, Harold's Cross, 22.viii.1954, on a wooden post in garden at 14, Clareville Road, holotype of *Dibrachys lignicola* (1 female A) (HDOU); paratypes of *Dibrachys lignicola*, same data as holotype (all 5 females A, 1 male) (BMNH); Dublin, Harold's Cross, paratype of *D. lignicola*, in house (A, 1 female) (BMNH). **Italy:** Tuscany, reared from *Phryxe caudata* on *Thaumetopoea pityocampa* (A, 8 females, 1 male) (BMNH) (det. *Dibrachys* sp.); Conca del Re Castrovillari, NP of Pollino, reared from *Phryxe caudata* associated with *Thaumetopoea pityocampa* (1 female) (ZMH). **Morocco:** Mamora, reared from *Apanteles* sp. on *Lymantria dispar* (2 females, 1 male) (BMNH) (det. *D. cavus*). **Switzerland:** Vaud Bonvillars, ex bird nest (A, 2 females) (NMBE) (det. *D. cf. goettingenus*). **USA:** California, Riverside, reared from tachinid puparium (A, 6 females, 5 males) (BMNH) (det. *D. cavus*). **(Former) Yugoslavia:** no host (1 female) (BMNH) (det. *D. cavus*).

**Biology.** Noyes (2003) listed only a single lepidopteran host record for *D. lignicola*, though also one hymenopteran species for *D. goettingenus* based on Doganlar (1987). Our study shows *D. lignicola* uses pupae of Diptera (Tachinidae, Hippoboscidae) in addition to Hymenoptera (Diprionidae, Braconidae) and Lepidoptera (Tortricidae) (Table 11). We added to the records in Noyes (2003) several other countries that are in the range of distribution of *D. lignicola* (Table 11). The record from North America (USA) is a single record and needs confirmation. There are only two records from Africa (Algeria (Noyes 2003), Morocco). The Moroccan record from *Apanteles* sp. cocoons is extraordinary because it is the only record from parasitic Hymenoptera, though we frequently found this species in the puparia of two earwig parasitoids (Diptera: Tachinidae) (Table 11). The recorded host species show no obvious similarities, but the revised taxonomy and key to species might help to identify further aspects of this species' biology in the future.

**Distribution.** See Table 11 for confirmed records.

**Taxonomic remarks.** The establishment of *D. goettingenus* by Doganlar (1987) was most probably made only because the description of *D. lignicola* by Graham (1969) is incomplete. Graham only mentioned the lobe on the scape in males and makes no statement about a lobe on the pedicel. Doganlar used the lobe on both the scape and pedicel as the main diagnostic character for his *D. goettingenus*. Doganlar was unable to check the character for *D. lignicola* males because Graham's collection was not accessible to him. It is now part of the NHM collection and we examined the type series of *D. lignicola*, which showed that male paratypes have a distinct lobe on both the scape and pedicel. Further differences mentioned by Doganlar (1987: 203) to distinguish the two species proved unreliable. The ratio of eye height to eye breadth in females varies more strongly than indicated by Doganlar and also the difference in the POL to OOL ratio was not confirmed.

Though males of *Dibrachys lignicola* and *D. microgastri* are easily distinguished by the structure of the scape and pedicel, females are difficult to differentiate. The diagnostic characters used by Graham (1969) and Doganlar

(1987) to separate the females of the two groups, the ratios of eye height to breadth, mouth breadth to malar space, and gaster length to length of head plus mesosoma, proved to overlap in our morphometric analysis. The separation of *D. lignicola* and *D. microgastri* females is only possible using the characters given in our key (see also Fig. 6 and Table 7), though there is still no single character known to completely separate females of the two species. If the identification is in doubt one should simply try another specimen of these gregarious parasitoids, if accessible.

**TABLE 11.** Hosts and geographic distribution of *Dibrachys lignicola*.

country	host species	
Germany	<i>Triarthria setipennis</i>	Diptera: Tachinidae
	<i>Ocytata pallipes</i>	Diptera: Tachinidae
	<i>Ornithomya avicularia</i>	Diptera: Hippoboscidae
	<i>Gilpinia hercyniae</i>	Hymenoptera: Diprionidae
France	<i>Cydia pomonella</i>	Lepidoptera: Tortricidae
Italy	<i>Phryxe caudata</i>	Diptera: Tachinidae
Switzerland		
former Yugoslavia		
England	<i>Crataerina pallida</i>	Diptera: Hippoboscidae
Ireland		
Morocco	<i>Apanteles</i> sp.	Hymenoptera: Braconidae
USA (California)	Tachinidae sp.	Diptera: Tachinidae

***Dibrachys verovesparum* Peters & Baur sp. n.**

(Figs 7c, 7f, 8c, 8f, 9c, 9f)

**Diagnosis.** *Both sexes.* Eyes small, eye height equal or less than 2.0x POL (Figs 7c, 9c). Head and mesosoma black without metallic coloration or only with slight tinge of bronze, brown or green (Figs 7c, 7f, 8c, 9c, 9f).

*Female.* Gaster shorter than head plus mesosoma (Fig. 7c). Eyes oval, eye height less than 1.6x eye breadth, outer margin never distinctly emarginate (Fig. 7c). Mouth broad, head breadth equal to or less than 2.0x mouth breadth (Fig. 7f).

*Male.* Scape and pedicel apically without lobe on outer side (Fig. 9f). Gastral spot distinct (Fig. 9c).

**Description.** FEMALE (Figs 7c [holotype], 7f, 8c, 8f [paratype no. 15]). Body length 1780–2650 µm.

*Head* (Figs 7c, 7f). Eyes small and oval, outer margin not emarginate; eye 1.32–1.57x as high as broad; eye height 1.69–2.00x POL. Level of lower margin of antennal toruli at level of lower ocular line. Clypeus striate vertically, indistinctly reticulate in its median part. Lower face distinctly receding. Mouth broad, head breadth 1.75–2.00x mouth breadth; mouth breadth 2.47–3.04x malar space. POL 1.71–2.20x OOL. First anellus small and ring-like, second anellus distinctly transverse rectangular, 1.5x broader than long; first funicular segment longer than broad, second to sixth almost quadrate; flagellum 0.68–0.77x head breadth.

*Mesosoma* (Fig. 8c). Mesoscutum flat, scutellum slightly convex in lateral view. Mesoscutum 0.51–0.60x as long as broad. Reticulation of pronotal collar, mesoscutum, scutellum and frenum fine, 13.1–17.0 meshes/200 µm in anterior part of mesoscutum. Marginal rim of scutellum distinctly turned upwards. Plicae distinct, weakly curved; median carina distinct or interrupted.

*Wings* (Fig. 8f). Wings hyaline; marginal vein 1.43–2.07x stigmal vein; submarginal vein 2.06–2.37x marginal vein.

*Metasoma* (Fig. 7c). Gaster shorter than head plus mesosoma; broad, oval and not distinctly pointed; length 3.50–4.61x eye breadth. Tergites not very smooth and not very shiny, weakly alutaceous, especially in apical half of gaster and with few, but distinct and strong hairs; sternites without hairs.

*Color* (Figs 7c, 7f, 8c, 8f). Head and mesosoma black, without metallic coloration, sometimes with slight tinge of brown or bronze on face, vertex, mesoscutum, scutellum and axillae. Antennal segments varying from light brown to brown, flagellum usually slightly darker than scape and pedicel. Venation of wings usually pale brownish.

Legs light brown, metafemur brown; coxae brown, proximal parts sometimes concolorous with mesosoma. Gaster dark brown.

**MALE** (Figs 9c, 9f [paratype no. 11A]). Similar to female except as follows. Smaller, body length 1340–2050  $\mu\text{m}$ .

**Head.** Eye height 1.55–1.92x POL. Level of lower margin of antennal toruli slightly above lower ocular line. Scape and pedicel apically without lobe on outer side.

**Metasoma** (Fig. 9c). Gaster almost circular.

**Color** (Figs 9c, 9f). Head black or sometimes with tinge of bronze and green a little more distinct than in females. Antennae usually completely light brown. Gaster with distinct light testaceous spot on ventral side of anterior segments, the spot also visible in dorsal view.

**Material examined.** Holotype female. **Germany:** Schwarzwald, Eschbach, reared from *Dolichovespula saxonica*, labeled leg. R. Gauss, leg. 3.ii.1966, ex *Dolichovespula saxonica* det. R. Gauss, *Dibrachys* sp. [prope *vesparum* (Ratz.)] Zd. Bouček 1968; det. R. Peters 2009. Deposited at SMNS.

Paratypes. **Austria:** S.E. Styria, coll. 30.v.82 CIBC, ex *Sphecophaga vesparum* in *V. saxonica*, labeled *Dibrachys* (?) *vesparum* (Ratz.) det. Z. Bouček, 1984 (7 females (NHM no. 1–7)) (BHNH). **England:** London, no host, labeled Syn. *Pteromalus vitripennis*, det. Bouček 1977, paralectotype of *D. boarmiae* (1 female) (BMNH) (det. *D. boarmiae*, transferred to *D. verovesparum*). **Germany:** all specimens from Schwarzwald, Eschbach; coll. 2.ii.1966, ex *Dolichovespula saxonica* (P.) det. R. Gauss, labeled M.W.R. de V. Graham coll. BMNH (E) 1995-489 (1 female (NHM no. 8), 1 male) (BMNH); leg. 4.ii.1966, ex *Dolichovespula saxonica* det. R. Gauss, *Dibrachys* sp. [prope *vesparum* (Ratz.)] Zd. Bouček 1968 (1 female) (SMNS); leg. 7.ii.1966, ex *Sphecophaga vesparum* Curt. det. R. Gauss, *Dibrachys vesparum* (Ratz.) det. R. Gauss (3 females, 3 males, including paratype no. 11A) (SMNS); leg. 7.ii.1966, ex *Sphecophaga vesparum* Curt. det. R. Gauss, *Dibrachys* spec. nahe *vesparum* (Rtz.) det. Z. Bouček (8 females, 2 males, including paratype no. 15) (SMNS); leg. 21.ii.1966, ex *Sphecophaga vesparum* Curt. det. R. Gauss, *Dibrachys* sp. [prop. *vesparum* (Ratz.)] Zd. Bouček 1968 (3 females, 3 males [1 female, 1 male in SMNS; 1 female, 1 male in NMBE; 1 female, 1 male in ZMH]); ex *Sphecophaga vesparum* Curt. det. R. Gauss, *Dibrachys vesparum* (Ratz.) det. R. Gauss (4 females, 4 males) (SMNS); ex *Sphecophaga vesparum* Curt. det. R. Gauss, *Dibrachys vesparum* (Ratz.) det. Z. Bouček (1 female [paratype 12, not used for morphometric analysis], 1 male) (SMNS).

**Biology.** The host species of *D. verovesparum* are *Dolichovespula saxonica* (Hymenoptera: Vespidae) and *Sphecophaga vesparum* (Curtis) (Hymenoptera: Ichneumonidae), a primary parasitoid of Vespidae. Further collection of vespidae nests is necessary to increase our knowledge on life history of this species.

**Distribution.** Europe. Germany, Black Forest; Austria, Styria; England.

**Etymology.** From the Latin *verus*, meaning “true”, and *vesparum*; referring to the material in Graham (1969: 810) that he considered might be the “true” *D. vesparum*, which we interpret as a new species (see under “Taxonomic remarks” for *D. microgastris*).

**Taxonomic remarks.** Our interpretation of the name *D. vesparum*, which was described originally from females reared from a wasp nest, is discussed under *D. microgastris*. Based on the original description we do not think *D. vesparum* is conspecific with our new species.

## Discussion

The results of this study can provide information to refine the selection of characters for taxonomic analysis of other Pteromalidae. Qualitative characters often include the color of weakly sclerotized body parts like antennae, eyes, legs and gaster (e.g., Graham 1969). We consider these too variable, being influenced by body size, age, host, and preservation medium, and thus they should not be used for species identification. An exception is the color of the head and mesosoma, which are highly sclerotized. The coloration of these was found to be consistent and could be used as a diagnostic character, which is why we used it in the diagnosis of *D. verovesparum*.

Another example of a variable character is the shape of the stigma of the forewing. Shape of the stigma can not only vary in one species, but can even be different between the two forewings (Baur, unpublished) and thus is an unsuitable character for taxonomic inferences. This is also true for a number of morphometric characters that have been used before. Measurements taken of such characters as head length or temple length (Graham 1969, Doganlar

1987) vary decisively with only slight changes of position. These characters were not used in this study and should be avoided in future studies. Overall size differences may also not be used to separate parasitoid species because of differences in host size and quality or in the degree of superparasitism. Intraspecific differences in size are a typical phenomenon in parasitoids and especially in idiobionts like most Pteromalidae (Godfray 1994).

## Acknowledgements

For loans, information and giving access to material the authors thank Luca Bartolozzi, Zoological Museum “La Specola”, University of Florence (Italy); Gavin Broad, Natalie Dale-Skey Papilloud, John Noyes, Andrew Polaszak and Suzanne Ryder, The Natural History Museum, London (UK); Miktat Doganlar, Mustafa Kemal University, Antakya-Hatay (Turkey); Michael Gates, United States Museum of Natural History, Washington D.C. (USA); Lars Krogmann, Staatliches Museum für Naturkunde Stuttgart, Stuttgart (Germany); Darren Mann and James Hogan, Hope Department, Oxford University, Oxford (UK); Stefan Schmidt, Zoologische Staatssammlung München, Munich (Germany); Stefan Schütz and Julian Heiermann, Institut für Forstzoologie der Universität Göttingen, Goettingen (Germany); Paul Tinerella, Illinois Natural History Survey, Urbana, Illinois (USA); Dominique Zimmermann, Naturhistorisches Museum Wien, Vienna (Austria); and László Zoltán, Hungarian Natural History Museum, Budapest (Hungary). We acknowledge Karl Staiber (Bad Arolsen) and Jörg Roloff (Nützen) for collecting bird nests from which *Dibrachys* spp. were reared. SYNTHESYS funded the stay of RSP at the NHM. Furthermore, we thank Gary Gibson, two anonymous reviewers, and Elsa Obrecht (Bern) for useful comments on the manuscript, and Rudolf Abraham (Hamburg) for starting the studies on life history and taxonomy of *Dibrachys*.

## References

- Anderson, T.W. (2003) *An introduction to multivariate statistical analysis*. Wiley, New York, 752 pp.
- Ashmead, W.H. (1888) On the chalcideous tribe Chiropachides. *Canadian Entomologist*, 20 (9), 172–176.
- Ashmead, W.H. (1893) Descriptions of new parasitic Hymenoptera bred by Prof. F.M. Webster. *Bulletin of the Ohio Agricultural Experiment Station, Technical Series*, 1, 159–165.
- Ashmead, W.H. (1894) Descriptions of new parasitic Hymenoptera. *Transactions of the American Entomological Society*, 21, 318–344.
- Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. In: Waage, J. & Greathead, D. (Eds.), *Insect parasitoids*. Academic Press, London, pp. 225–264.
- Baur, H. (2002) The power of multivariate statistical methods in the taxonomy of Pteromalidae (Hymenoptera: Chalcidoidea). In: Melika, G. & Thurocz, C. (Eds.), *Parasitic wasps: Evolution, systematics, biodiversity and biological control*. Agriinform, Budapest, pp. 73–81.
- Blanchard, E.E. (1938) Un nuevo enemigo de la oruga del duraznero. *Revista Chilena de Historia Natural*, 41, 178–180.
- Bouček, Z. (1965) A review of the Chalcidoid fauna of the Moldavian S.S.R. with descriptions of new species (Hymenoptera). *Acta Faunistica Entomologica Musei Nationalis Pragae*, 11, 5–38.
- Bouček, Z. (1974) On the Chalcidoidea (Hymenoptera) described by C. Rondani. *Redia*, 55, 241–285.
- Bouček, Z. & Heydon, S.L. (1997) Chapter 17. Pteromalidae. In: Gibson, G.A.P., Huber, J.T. & Woolley, J.B. (Eds.), *Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera)*. NRC Research Press, Ottawa, pp. 541–692.
- Bouček, Z. & Rasplus, J.-Y. (1991) *Illustrated key to West-Palaearctic genera of Pteromalidae (Hymenoptera: Chalcidoidea)*. Institut National de la Recherche Agronomique, Paris, 140 pp.
- Bouché, P.F. (1834) *Naturgeschichte der Insekten, besonders in Hinsicht ihrer ersten Zustände als Larven und Puppen*. Berlin, 216 pp.
- Claude, J. (2008) *Morphometrics with R*. Springer, New York, 318 pp.
- Delucchi, V. (1955) Notes sur les ptéromalides. *Mémoires de la Société Royale Entomologique de Belgique*, 27, 171–175.
- Doganlar, M. (1987) Hypopygia of most Nearctic and Palaearctic species of *Dibrachys* Foerster, key to most species of the genus, and descriptions of three new species (Hymenoptera, Pteromalidae). *Spixiana*, 10, 191–206.
- Fitch, A. (1856) Report on the noxious, beneficial and other insects. *Transactions of the New York State Agricultural Society*, 15, 409–459.
- Förster, A. (1856) *Hymenopterologische Studien. 2. Chalcidiae und Proctotrupii*. Aachen, 152 pp.
- Frison, T.H. (1927) List of the insect types in the collections of the Illinois State Natural History Survey and the University of Illinois. *Bulletin of the Illinois State Laboratory of Natural History*, 16, 137–309.
- Gahan, A.B. (1938) Notes on some genera and species of Chalcidoidea (Hymenoptera). *Proceedings of the Entomological Society of Washington*, 40, 209–227.

- Gahan, A.B. (1942) Descriptions of five new species of Chalcidoidea, with notes on a few described species (Hymenoptera). *Proceedings of the United States National Museum*, 92, 41–51.
- Gibson, G.A.P. (1997) Morphology and terminology. In: Gibson, G.A.P., Huber, J.T. & Woolley, J.B. (Eds.), *Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera)*. NRC Research Press, Ottawa, pp. 16–44.
- Girault, A.A. (1916a) New miscellaneous chalcidoid Hymenoptera with notes on described species. *Annals of the Entomological Society of America*, 9 (3), pp. 291–308.
- Girault, A.A. (1916b) The North American Species of *Dibrachys* (in the North American Sense – *Coelopisthoidea* Gahan) with a note on *Uriella* Ashmead. *The Canadian Entomologist*, 48, 408–409.
- Godfray, H.C.J. (1994) *Parasitoids – Behavioural and evolutionary ecology*. Princeton University Press, Princeton, New Jersey, 488 pp.
- Gontarski, H. (1939) Zur Biologie der Schlupfwespe *Dibrachys cavus* (Walk.). *Zeitschrift für Morphologie und Ökologie der Tiere*, 35, 203–220.
- Gordh, G. (1981) The phenomenon of insect hyperparasitism and its taxonomic occurrence in the Insecta. In: Rosen, D. (Ed.), *The role of hyperparasitism in biological control: A Symposium*. University of California Division of Agricultural Science, pp. 10–18.
- Graham, M.W.R.d.V. (1956) A revision of the Walker types of Pteromalidae (Hym., Chalcidoidea). Part 2 (including descriptions of new genera and species). *Entomologist's Monthly Magazine*, 92, 246–263.
- Graham, M.W.R.d.V. (1969) The Pteromalidae of North-Western Europe (Hymenoptera, Chalcidoidea). *Bulletin of the British Museum (Natural History). Entomology, Supplement*, 16, 1–908.
- Howard, L.O. (1889) The Hymenopterous parasites of North American Butterflies including a section upon the miscogasters by C.V. Riley. In: Scudder, S.H. (Ed.), *The Butterflies of the Eastern United States and Canada, with special reference to New England*. Cambridge, Massachusetts, USA, pp. 1869–1911.
- Janzon, L.-A. (1986) Morphometric studies of some *Pteromalus* Swederus species (Hymenoptera: Chalcidoidea) with emphasis on allometric relationships, or: Are ratios reliable in chalcid taxonomy? *Systematic Entomology*, 11, 75–82.
- Jolicoeur, P. (1963) The multivariate generalization of the allometry equation. *Biometrics*, 19, 497–499.
- Klimov, P.B., Lekveishvili, M., Dowling, A.P.G. & Oconnor, B.M. (2004) Multivariate analysis of morphological variation in two cryptic species of *Sancassania* (Acari: Acaridae) from Costa Rica. *Annals of the Entomological Society of America*, 97, 322–345.
- Klingenberg, C.P. (1996) Multivariate allometry. In: Marcus, L.F., Corti, M., Loy, A., Naylor, G.J.P. & Slice, D.E. (Eds.), *Advances in morphometrics*. Plenum Press and NATO Scientific Affairs Division, New York, pp. 23–49.
- Krombein, K.V., Hurd, P.D., Smith, D.R. & Burks, B.D. (1979) *Catalog of Hymenoptera in America North of Mexico. Volume 1. Symphyta and Apocrita (Parasitica)*. Smithsonian Institution Press, Washington D.C., 1198 pp.
- Kurdjumov, N.V. (1913) Notes on Pteromalidae (Hymenoptera, Chalcidoidea). *Russkoe Entomologicheskoe Obozrenie*, 13, 1–24.
- Kusevska, M. (1977) Morphological characteristics of *Dibrachys fuscicornis* Walk. (Hym., Pteromalidae) and his activity in relation to *Euproctis chrysoorrhoea* L. (Lep., Lymantriidae) as a host. *Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium*, 10 (6), 45–56.
- Newman, E. (1863) Parasites and hyperparasites. *Zoologist*, 21, 8609–8610.
- Norton, E. (1869) American Hymenoptera. *Transactions of the American Entomological Society*, 2, 321–368.
- Noyes, J.S. (2003) *Universal Chalcidoidea Database*. Available from <http://www.nhm.ac.uk/entomology/chalcidoids/index.html> (accessed 10 February 2010).
- Peck, O. (1963) A catalogue of the nearctic Chalcidoidea (Insecta: Hymenoptera). *The Canadian Entomologist, Supplement*, 30, 1–1092.
- Peters, R. (2007) Interaktionen zwischen Wirten und Parasitoiden: Nahrungsnetzstruktur, Wirtsspektren und Wirtsfindung am Beispiel der Arten aus Vogelnestern. Ph.D. thesis. University of Hamburg, Germany. Available from <http://www.sub.uni-hamburg.de/opus/volltexte/2007/3234/pdf/DissertationPeters.pdf>
- Peters, R.S. & Abraham, R. (2010) The food web of parasitoid wasps and their non-phytophagous fly hosts in birds' nests (Hymenoptera: Chalcidoidea, and Diptera: Cyclorrhapha). *Journal of Natural History*, 44, 613–626.
- Pimentel, R.A. (1979) *Morphometrics. The multivariate analysis of morphological data*. Kendall/Hunt, Dubuque, Iowa, 276 pp.
- Polaszek, A., Manzari, S. & Quicke, D.L.J. (2004) Morphological and molecular taxonomic analysis of the *Encarsia meritoria* species-complex (Hymenoptera, Aphelinidae), parasitoids of whiteflies (Hemiptera, Aleyrodidae) of economic importance. *Zoologica Scripta*, 33, 403–421.
- R Development Core Team (2010) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Ratzeburg, J.T.C. (1844) *Die Ichneumonen der Forstinsekten in entomologischer und forstlicher Beziehung*. 1. Berlin, 224 pp.
- Ratzeburg, J.T.C. (1848) *Die Ichneumonen der Forstinsekten in entomologischer und forstlicher Beziehung*. 2. Berlin, 238 pp.
- Ratzeburg, J.T.C. (1852) *Die Ichneumonen der Forstinsekten in entomologischer und forstlicher Beziehung*. 3. Berlin, 272 pp.
- Rencher, A.C. (2002) *Methods of multivariate analysis*. Wiley Series in Probability and Statistics, New York, 708 pp.
- Reyment, R.A., Blackith, R.E. & Campbell, N.A. (1984) *Multivariate morphometrics (2nd edition)*. Academic Press, London, 233 pp.

- Rondani, C. (1876) Il nemico della tignuola della cera (*Galleria cereana*). *Bollettino del Comizio Agrario Parmense*, 9, 38–41.
- Sharkov, A.V. (1982) The pteromalid *Dibrachys boarmiae* (Walker) (Hymenoptera, Pteromalidae), new to the USSR. *Entomologiceskoe obozrenie*, 61, 620–625.
- Sharkov, A.V. (1983) A new species of the genus *Dibrachys* (Chalcidoidea, Pteromalidae) from the vicinity of Odessa. *Zoologicheskij Zhurnal*, 62 (3), 452–453.
- Sorensen, J.T. & Footitt, R. (1992) *Ordination in the study of morphology, evolution and systematics of insects. Applications and quantitative genetic rationals*. Elsevier Science, Amsterdam, 426 pp.
- Szelényi, G. (1981) New genera and species of Pteromalidae (Hymenoptera: Chalcidoidea) collected in the Hungarian National Park, Hortobágy. *Acta Zoologica Academiae Scientiarum Hungaricae*, 27, 399–406.
- Thomson, C.G. (1878) *Hymenoptera Scandinaviae. Tom. V. Pteromalus (Svederus) continuatio*. Lund.
- Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S (fourth edition)*. Springer, New York, 495 pp.
- Vidal, S. (2001) Entomofauna Germanica. Band 4. Verzeichnis der Hautflügler Deutschlands. Chalcidoidea. In: Dathe, H.H., Taeger, A. & Blank, S.M. (Eds.), *Entomologische Nachrichten und Berichte Beiheft 7*, pp. 51–69.
- Walker, F. (1835) Monographia Chalciditum. *The Entomological Magazine*, 2, 476–502.
- Wang, X.-H. & Lester, P.J. (2004) A preliminary study of the usefulness of morphometric tools for splitting the *Monomorium antarcticum* (Smith) complex (Hymenoptera: Formicidae), New Zealand's most common native ants. *New Zealand Entomologist*, 27, 103–108.
- Webster, F.M. (1883) Observations of the angoumois grain moth and its parasites. *Report of the Illinois State Entomologist*, 12, 151–152.
- Yang, Z. (1996) *Parasitic wasps on bark beetles in China* [In Chinese with English summary]. Science Press, Beijing, China, 363 pp.
- Zerova, M.D., Seregina, L.Y. & Tsybulskh, A.I. (1986) The systematic position and host-parasite relations of *Dibrachys cavus* (Hymenoptera: Pteromalidae). Part I. *Verstnik Zoologii*, 2, 7–16.

#### APPENDIX. Synopsis of valid species in *Dibrachys* Förster.

- Dibrachys* (*Allodibrachys*) *affinis* Masi, 1907  
*Dibrachys* (*Dibrachys*) *braconidis* (Ferrière & Faure, 1925)  
*Dibrachys* (*Dibrachys*) *confusus* (Girault, 1916)  
*Dibrachys* (*Dibrachys*) *crassiscapus* Sharkov, 1983  
*Dibrachys* (*Dibrachys*) *fuscicornis* (Walker, 1836)  
*Dibrachys* (*Allodibrachys*) *hians* Bouček, 1965  
*Dibrachys* (*Allodibrachys*) *kojima* (Ishii, 1938)  
*Dibrachys* (*Dibrachys*) *koraiensis* Yang, 1996  
*Dibrachys* (*Dibrachys*) *lignicola* Graham, 1969  
*Dibrachys* (*Dibrachys*) *maculipennis* Szelényi, 1957  
*Dibrachys* (*Dibrachys*) *microgastri* (Bouché, 1834)  
*Dibrachys* (*Dibrachys*) *palandoekenus* Doganlar, 1987  
*Dibrachys* (*Dibrachys*) *pelos* Grissell, 1974  
*Dibrachys* (*Dibrachys*) *perversus* (Walker, 1835), *nomen dubium*  
*Dibrachys* (*Dibrachys*) *relativus* Doganlar, 1987  
*Dibrachys* (*Dibrachys*) *verovesparum* Peters & Baur, 2011  
*Dibrachys* (*Allodibrachys*) *yunnanensis* Yang, 1996