

Zeitschrift: Contributions to Natural History : Scientific Papers from the Natural History Museum Bern

Herausgeber: Naturhistorisches Museum Bern

Band: - (2009)

Heft: 12/3

Artikel: Morphology-based taxonomy is essential to link molecular research to nomenclature

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DOI: <https://doi.org/10.5169/seals-787027>

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Morphology-based taxonomy is essential to link molecular research to nomenclature

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The authors contributed equally to this work.

ABSTRACT

Contrib. Nat. Hist. 12: 1295–1315.

Biodiversity research is experiencing a heightened tension between molecular and traditional taxonomy. The solution is to combine the two approaches into integrative taxonomy. Morphology-based alpha taxonomy (MOBAT) is essential to link molecular research to botanical and zoological nomenclature because it frequently is the only discipline that can allocate taxonomically valid names by analyses of name-bearing specimens (types). For highly similar species, numerical character descriptions often are inevitable.

MOBAT, especially numerically-based species identification and verification, faces a crisis caused by a dramatic decline of human and financial resources. Taking current advances in ant research as an example, we expose what taxonomists can do to enhance the reputation of MOBAT, and what non-taxonomists can do to promote biodiversity research ¹.

¹ Submitted on 29 September 2006. The extensive literature published between dates of submission and publication of this paper could not be included, but the main conclusions presented still apply. Also note that we have in the meantime further developed some of the ideas presented here, in the following two papers:

Schlick-Steiner, B.C., Seifert, B., Stauffer, C., Christian, E., Crozier, R.H. & Steiner, F.M. (2007): Without morphology, cryptic species stay in taxonomic crypsis following discovery. — *Trends in Ecology & Evolution* 22: 391–392.

Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E. & Crozier, R.H. (2010): Integrative taxonomy: a multi-source approach to exploring biodiversity. — *Annual Review of Entomology* 55: 421–438.

Keywords: Biodiversity research, integrative taxonomy, molecular analyses, morphology-based alpha taxonomy, numerically-based species identification and verification, ants

What inventorying biodiversity is about

To inventory the diversity of life is a priority objective of systematic biology (Wheeler 1995, Cracraft 2002). With every recognized species the true dimensions of organismic variety take shape. Biodiversity research rests upon the reliable characterization and demarcation of species, which makes them distinguishable from any others, and upon their unambiguous labelling according to the international codes of nomenclature (ICZN 1999, ICBN 2000). The more species we uncover, the more details are needed to grasp a species' uniqueness, and, as a consequence, the more difficult it becomes to allocate correct names.

Current tension between molecular research and traditional taxonomy

Gadgets which spit out correct species labels for any living being at the touch of a button (Janzen 2004) will remain a dream, at least for the near future. Recently however, presenting it as a ready-to-use silver bullet, Hebert & al. (2003) reanimated the term "DNA barcoding" (originally coined by Arnot & al. 1993). In its current meaning, DNA barcoding is a large-scale screening of a mitochondrial (mt) DNA reference gene in order to assign unknown individuals to species and to sift out new species. A series of follow-up articles and case studies have been published since (over 40 publications known to the authors, as of September 2006, references available on request). Some authors even demanded that "DNA taxonomy" should use DNA not additionally to, but instead of morphological methods (Tautz & al. 2002, 2003, Markmann & Tautz 2005). DNA barcoding has received an enormous echo ranging from popular media (e.g., The Times: Hendersen 2005) to top-ranking science journals (e.g., Nature: Blaxter 2003). Reasons for this may be its advertized and indeed impressive simplicity and virtue, and the familiarity of the term "barcoding" in today's supermarket world (cf. Sperling 2003, Moritz & Cicero 2004).

A series of general problems currently afflicts work with (mt)DNA on several levels, including data acquisition, analysis, interpretation and, finally, linking to collateral data (Kuhner & Felsenstein 1994, Lake 1994, Philippe & Forre 1999, Bensasson & al. 2001, Dean & Ballard 2001, Nichols 2001, Besansky & al. 2003a, Funk & Omland 2003, Harris 2003, Ballard & Whitlock 2004, Kocher 2004, Seifert & Goropashnaya 2004, Bergsten 2005, Lorenz & al. 2005, Hurst & Jiggins 2005, Margelevičius & Venclovas 2005, Binladen & al. 2006). These problems question (mt)DNA as a sole approach. Several authors point

out that single-locus DNA barcoding falls short of its claimed role as panacea (Sperling 2003, Moritz & Cicero 2004, Will & Rubinoff 2004, DeSalle & al. 2005, Hurst & Jiggins 2005, Meyer & Paulay 2005, Prendini 2005, Rubinoff & Holland 2005, Vences & al. 2005, Will & al. 2005, Brower 2006, Cognato 2006, Gompert & al. 2006, Nielsen & Matz 2006, Rubinoff & al. 2006). Other authors refer to the intellectual one-sidedness of DNA taxonomy (Dunn 2003, Lipscomb & al. 2003, Scotland & al. 2003, Seberg & al. 2003, Seberg 2004, Wheeler 2004, Ebach & Holdredge 2005b, Prendini 2005).

The solution: integrative taxonomy

In our opinion, molecular analyses are merely a single, powerful, yet supplementary tool in the toolbox of systematic biologists (Steiner & al. 2005, Brower 2006, Nielsen & Matz 2006). Years before barcoding became popular, DNA methods proved to be powerful in the discovery and characterization of cryptic species (e.g., Pinto & al. 1997, Beresford & Cracraft 1999, Ryan & Ayres 2000, Moon-van der Staay & al. 2001, Roca & al. 2001) and in determination routines (Baker & Palumbi 1994, DeSalle & Birstein 1996, Van Bortel & al. 2000, Wells & Sperling 2001, Floyd & al. 2002). Molecular analyses, however, cannot replace the other tools of the taxonomist (Ebach & Holdredge 2005a, Fisher 2006). We agree with Scotland & al. (2003) and Smith (2005) that contrasting molecular research and traditional taxonomy is counterproductive and concur with those who call for an integrative approach to taxonomy (Miller & al. 1997, Dunn 2003, Mallet & Willmott 2003, Quicke 2004, Wheeler 2004, Dayrat 2005, DeSalle & al. 2005, Schander & Willassen 2005, Will & al. 2005, Caesar & al. 2006, Dasmahapatra & Mallet 2006, Fisher 2006, Nielsen & Matz 2006, Rubinoff & al. 2006). In our own research we have taken advantage of the integrative approach to tackle problems in ant taxonomy (Schlick-Steiner & al. 2003b, 2005, Schlick-Steiner & al. 2006a, b, Steiner & al. 2006a, c; Excursus 1).

Why morphology is the essential name-allocator in integrative taxonomy

Notwithstanding all considerations on heuristic and intellectual pros and cons of the molecular and the traditional approaches, we believe that morphology-based alpha taxonomy (MOBAT) is still the basis of taxonomy, not least for practical reasons. Taxonomic work rests in large part upon a comprehensive comparison of any (potentially) new species with related established species.

This comparison is not generally possible via molecular avenues. Extraction of DNA from dried and even more so from historical vouchers – which may date back as far as to Linnaeus (1758) – is still in its infancy (e.g., Quicke & al. 1999, Dean & Ballard 2001, Hajibabaei & al. 2005), despite some recent advances (e.g., Phillipps & Simon 1995, Townson & al. 1999, Junqueira & al. 2002, Goldstein & DeSalle 2003, Hajibabaei & al. 2006). DNA extraction is destructive to specimens in various degree – curators might accept sampling from large-bodied type specimens, but likely not from tiny ones. Proper long-term preservation of DNA from freshly collected vouchers, which would be mandatory if DNA taxonomy took over, is still largely unexplored (cf. Quicke & al. 1999, King & Porter 2004).

MOBAT is irreplaceable to link all other disciplines of integrative taxonomy to the botanical and zoological nomenclature. Only this method allows non-destructive investigation of type material against the background of written and pictorial information accumulated over 250 years of biosystematic research.

Not only types, but also other, partly historical vouchers must be identifiable at any time for a wide range of biological fields (Kühnelt 1974, Francoeur 1976, Alberch 1993, Brooke 2000, Schlick-Steiner & al. 2003a, Wheeler 2003, Suarez & al. 2005, Steiner & al. 2006c). Most vouchers can exclusively be morphologically identified in order to connect them to existing knowledge about the respective group of organisms and to integrate new observations into a general context (Brower 2006). In cases of morphologically highly similar species, numerically-based species identification and verification have proved to be powerful tools in various taxa. If we depreciate the role of morphology in taxonomy and biology in general, we run the risk that nobody can reliably tell (or check) to which organisms certain phylogenetic, biological or ecological data relate (cf. Franz 2005).

The crisis of MOBAT

Traditional, morphology-centred taxonomy currently faces a crisis (Buyck 1999, Brooke 2000, Godfray 2002, Hopkins & Freckleton 2002, Thiele & Yeates 2002, Besansky & al. 2003b, Scotland & al. 2003, Scoble 2004, Wheeler 2004, Wheeler & al. 2004): The average age of specialists is increasing, their total number declining (Excursus 3) – as is the number of research positions available – and the amount of funding is insufficient. Taxonomy can hardly keep pace with the steady flow of new species uncovered by molecular methods (cf. Cognato & Caesar 2006), and at the same time unknown species are going extinct at an ever increasing speed. Morphology-based routine determination

struggles with similar problems – who is still able to identify all the newly established species unerringly? This situation is largely caused by indifferent attitudes in society and in the educational systems (Schander & Willasen 2005). Campaigns like that of DNA barcoding get publicity and funding (Wheeler 2004, Ebach & Holdredge 2005b, Rubinoff & Holland 2005) and thus tie up working capacity. Brower (2006) aptly warns that "if resources are cannibalised from systematics to support molecular parataxonomy, systematic training and research programmes will languish, the loss of systematic expertise will be accelerated, and the framework of natural history to which DNA barcodes are intended to link will be impoverished".

MOBAT is widely reputed to be old-fashioned, the metaphoric equivalent of dusty museum collections (Brooke 2000). Experiences in our immediate working environments suggest that there often is a stark contrast between how people perceive molecular research and morphology. In the molecular lab, trouble-shooting has the aura of an intellectual exercise, as time- and money-consuming as it may be. We seem never to hear people express real unease which could ultimately lead to a change of research direction. In contrast, many colleagues perceive morphological work as extremely tedious, especially when it boils down to morphometrics. It is regarded as the province of hapless drudges lost in the methodologies of the past that are not productive of "real" science, worthy of publication.

We feel that – polemically phrased – in today's scientific world much of the general research effort is channelled by what resembles advertising strategies and public relation campaigns; these are characterised by, among other things, buzz-words suggestive of "splashy" publications in posh journals, ready for release at the press conference (cf. Sperling 2003).

What to do about the crisis?

The crisis of taxonomy requires immediate attention. Only thus can biodiversity research effectively leverage the decisive role of MOBAT. This cannot be achieved by taxonomists themselves without institutional-level measures toward resolution of the crisis. Universities should consider MOBAT in their syllabi, both by direct training and image building. Decision makers of grant agencies must change funding policies – to our knowledge and experience it is currently very difficult to raise funds for projects that aim to solve taxonomic problems via morphological means. Leaders of research groups should explicitly include MOBAT in their research programmes and have young scientists educated in this field of research. Research institutions must augment

job opportunities for which young MOBAT researchers can apply. Editors and referees of high-ranking, non-taxonomic biology journals must realise that MOBAT is an issue to be seriously considered in the "Methods" section of articles. Museums and other institutions housing large voucher-specimen collections must continue and increase their efforts to achieve a fresh, non-dusty image while fostering serious, basic taxonomic research – molecular and morphological approaches are by no means mutually exclusive.

There is, however, a lot taxonomists can and should do themselves. MOBAT researchers complain about their inferiority in the ranking of biosciences but are unaware of their own partial responsibility for this situation. Modernization (in the best sense of the word) is required!

MOBAT researchers should become more outgoing and ready to contribute to overcoming the threatening secession of traditional taxonomy and molecular research. Integrative taxonomy is superior to solely morphological studies, and all partners of multilateral collaboration benefit strongly from the others' views.

At least in cases of highly similar species, there often is no alternative to the numerical description of characters on a standardized basis (Excursus 2) if MOBAT aims to establish testable hypotheses or test hypotheses derived by other means. This is established for various taxa (e.g., lilies: Fisher 1936, gentians: Greimler & Dobes 2000, oaks: Ishida & al. 2003, corals: Knowlton & al. 1992, starfishes: Flowers & Foltz 2001, mussels: Claxton & al. 1997, mites: Klimov & al. 2004, grasshoppers: Tatsuta & al. 2000, beetles: Alvarez & al. 2005, flies: Cazorla & Acosta 2003, ants: Seifert 2002, fishes: Barluenga & al. 2006, reptiles: Glor & al. 2003, birds: Cicero 2004, mammals: Bühler 1964) but remains to be explored for others. Only then will MOBAT operate at the same cognitive level as modern molecular biology. How can taxonomists allocate a name to a recognized species in nature if they are unable to testably demonstrate that a type specimen belongs to this entity and not to another, highly similar one? Comparative drawings and (z-stack) photos of specimens are a valuable contribution, but such pictures are not a test of the hypothesis unless they cover all the intraspecific variability. Many intuitively operating MOBAT workers have a keen sense of different morphological types and quite reliably distinguish species by hidden probability calculations performed in the background of their mind. Such abilities are most valuable because they produce instantly a provisional order out of the large diversity found in many groups of organisms. Nevertheless, even the most ingenious of these taxonomists has little chance to capture very delicate features without comprehensive data analysis. MOBAT researchers must accept the challenge and steadily improve their means of data acquisition and analysis. Taxonomy looks back

to a long tradition, in contrast to young disciplines like molecular research which experience methodological improvements on a monthly basis, but even in this venerable field, there still is much room for improvement (cf. Seifert 2002, Alonso & al. 2006, Moder & al. 2007). In the end, this also concerns the development of faster means of data acquisition, potentially involving semi-automatic systems.

The demand for making taxonomic resources available at a mouse click is justified (Agosti & Johnson 2002, Bisby & al. 2002, Godfray 2002, Scoble 2004, Wheeler 2004, Wheeler & al. 2004, Polaszek & al. 2005; Excursus 4). However, we should consider potential misuse when going online (e.g., Lee 2002), keep in mind the ultimate goal of a biodiversity inventory, and reflect whether technophily might lead to a further marginalization of taxonomy (Orr 2002, Scotland & al. 2003, Wheeler 2004). In our opinion, adequate efforts will yield results comparable to the handy high-end facilities common in present-day molecular technologies.

Finally: Side-effects of MOBAT

The task of morphology-based taxonomy and species identification involves working with "one's own" favorite organisms; this constitutes heuristic opportunities for formulating and testing hypotheses (Wheeler 2004), also for higher-level (beta) taxonomy. The merits of traditional taxonomic work for gaining evolutionary-biological insight are well recognized (Brower & Judd 1998, Wilson 2000, Lipscomb & al. 2003, Scotland & al. 2003, Raven 2004). In fact, warning bells should ring when the mantra of instant identification through DNA analysis is intoned. Even if and when these approaches become refined to such a degree that all inherent problems are resolved: Won't this ultimately result in a further decline in the number of biologists who know their organisms (May 2004, Raven 2004, Ebach & Holdrege 2005b)? As Gotelli (2004) argues for ecology, any such approach cannot substitute experts who have devoted their entire professional careers to species identification and taxonomy. Scotland & al. (2003) radically state that "taxonomic specialists worth their salt know that there are no quick answers to the inventory shortfall and to claim otherwise ... is pie in the sky".

Excursus 1: Integrative approach reveals cryptic diversity in *Tetramorium* ants.

Background: Ants of the *T. caespitum/impurum* complex are among the most widespread and abundant ants in open habitats of the Palaearctic region. They exert significant ecological influence by collecting seeds, engaging in trophobiotic relationships with sap-feeding insects, feeding on carrion, and active hunting (Seifert 1996). Two species have successfully established invasive populations in the Nearctic region (Schlick-Steiner & al. 2006a, Steiner & al. 2006c). The *T. caespitum/impurum* complex has challenged taxonomy for a long time (e.g., Kutter 1977, Seifert 1996).

Example: Capturing biodiversity within the complex was a monumental task and was only achieved by an international collaboration of scientists from 14 research institutions, by combining high-precision morphometrics, qualitative male-genitalia traits as well as mitochondrial (mt)DNA, semiochemistry and ethological methods. The integration of contributions to evolutionary biology, sociobiology and biogeography/phylogeography uncovered an unexpectedly high degree of cryptic biodiversity within the *T. caespitum/impurum* complex. Schlick-Steiner & al. (2006a) revealed that the complex encompasses at least nine species instead of four as formerly believed, including the five cryptic species *Tetramorium* spp. A–E (Fig. 1).

Perspective: The remaining problem is that although the species *T. spp.* A–E have been comprehensively characterized, among others by morphometric characters, it is currently not possible to allocate names complying with the ICZN. A taxonomic decision on species A–E will require the revision of about 50 names which come into question for Palaearctic *Tetramorium* species (Bolton 1995a). This will entail assessment of the name-bearing specimens via high-precision morphometrics and numerical evaluation as shown in Excursus 2. The study is ongoing, but progress is slow because only one of the authors of Schlick-Steiner & al. (2006a) is able to focus mainly on MOBAT.

Conclusion: Integrating molecular and morphological methods is the most powerful approach to solve intricate problems in biodiversity research.

Excursus 2: Allocation of name-bearing specimens to sibling species of ants.

Background: The ant subgenus *Coptoformica* comprises 11 species with differing biology; due to minor interspecific morphological differences but pronounced intraspecific variation, however, the described taxa sum nearly tripled (Seifert 2000). Allocating taxonomically valid names to the recognized species in nature, i.e., names in line with the principle of priority of the ICZN

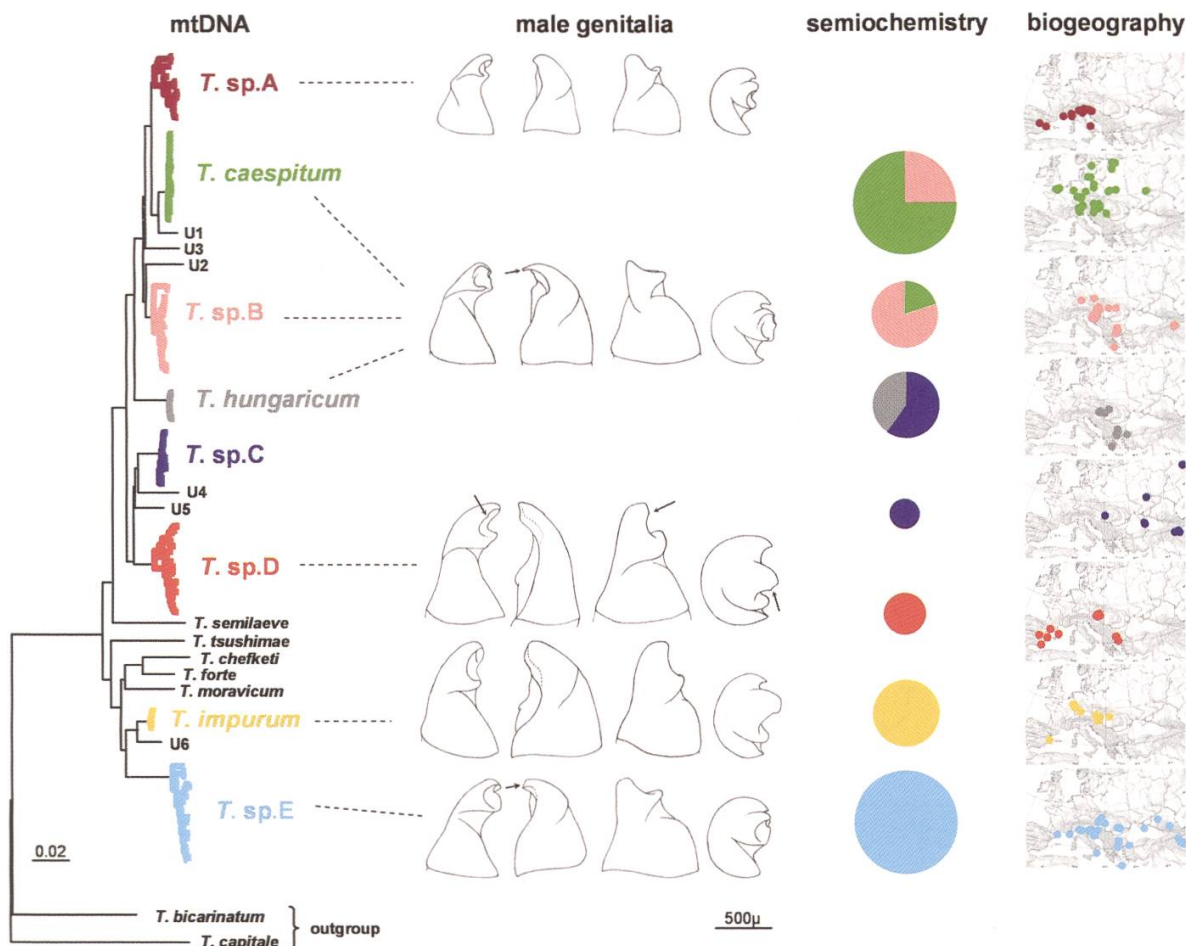


Fig. 1: Cryptic diversity of the *Tetramorium caespitum/impurum* complex: Integrated analysis of, among others, mitochondrial DNA (mtDNA), male genitalia, semiochemistry and biogeography revealed that the complex encompasses at least nine species instead of four as formerly believed (*T. caespitum*, *T. hungaricum*, *T. tsushimae*, *T. impurum*), including the five cryptic species *Tetramorium* spp. A–E. For details see Schlick-Steiner & al. (2006a).

(1999), required analyses of the name-bearing (type) specimens. Six taxa proved especially intricate.

Example: Efforts to allocate the six types based on subjective impression failed. Molecular analyses are not possible as the types are dry historical voucher-specimens. However, a discriminant analysis using high-precision morphometric data of four characters (Seifert 2000, and unpubl. data) clearly showed that *Formica naefi* KUTTER, 1957, *F. tamarae* DLUSKY, 1964 and *F. goesswaldi* KUTTER, 1967 are junior synonyms of *F. foreli* BONDROIT, 1918, whereas *F. rufomaculata* RUZSKY, 1895 is a junior synonym of *F. pressilabris* NYLANDER, 1846 (Fig. 2).

Perspective: Correct name allocation to cryptic species will become even more important in the future because our records of highly similar species are increasing, not only from the tropics and from marine biomes, but also from well-investigated terrestrial faunas of temperate zones (Excursus 1).

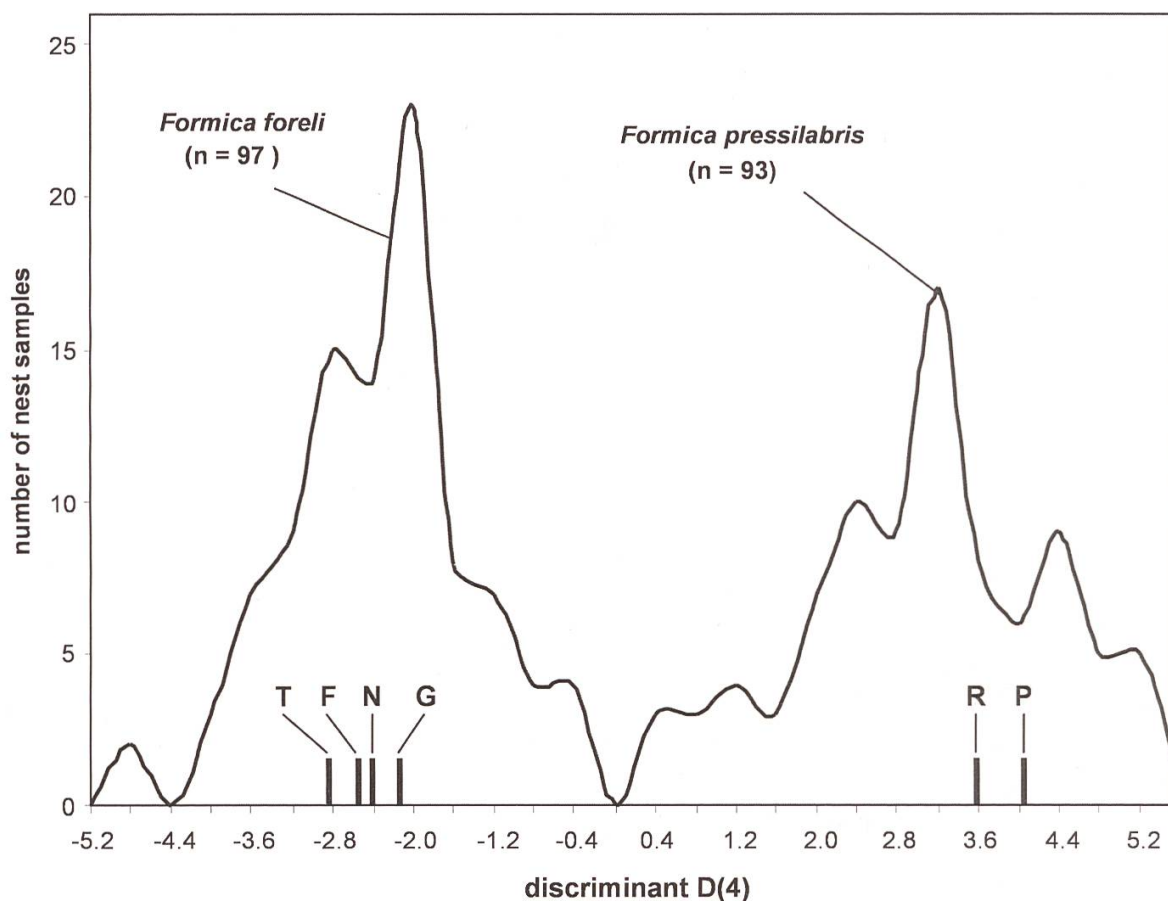


Fig. 2: Separation of nest samples of *Formica foreli* BONDROIT, 1918 (97 samples) and *F. pressilabris* NYLANDER, 1846 (93 samples) by discriminant analysis using four morphometric characters. Position of type specimens indicated: T = *F. tamarae* DLUSSKY, 1964; F = *F. foreli* BONDROIT, 1918; N = *F. naefi* KUTTER, 1957; G = *F. goesswaldi* KUTTER, 1967; R = *F. rufomaculata* RUZSKY, 1895; P = *F. pressilabris* NYLANDER, 1846.

Conclusion: MOBAT is the only way to allocate taxonomically valid names by analysis of name-bearing specimens. For highly similar species, numerical character descriptions are inevitable.

Excursus 3: The current working capacity of MOBAT in European ant research.

Background: Ants are prime model organisms in an exceptionally wide range of biological fields including evolutionary biology, biodiversity research, biogeography, community ecology, conservation biology, invasion biology and sociobiology. Having the model organism identified at species level is crucial for most investigations.

Example: A recent census revealed that MOBAT researchers constitute a marginal minority of 5.2% among the 210 European myrmecologists (Tab. 1). This number includes those who contribute to taxonomy only occasionally – just 1.4% of myrmecologists focus mainly on morphology-based ant taxon-

Country	Myrmecologists	MOBAT myrmecologists			
		main		occasional	
		total	numerical	total	numerical
Austria	6			1.5	0.5
Belgium	12			0.5	
Bulgaria	1				
Czech Republic	2				
Denmark	17				
Estonia	1				
Finland	15				
France	21			0.5	
Germany	42	1	1	0.5	
Greece	2				
Hungary	3			1	0.5
Italy	7			1	
Netherlands	1				
Poland	5				
Romania	3			0.5	
Russia	6			0.5	
Slovakia	1				
Spain	11			1	
Sweden	3				
Switzerland	33	1		0.5	
Turkey	3				
Ukraine	1	1			
United Kingdom	14			0.5	0.5
total	210	3	1	8	1.5
	100 %	1.4 %	0.5 %	3.8 %	0.7 %

Tab. 1: Census of the current working capacity of MOBAT in European ant research. The survey was performed to assess the working potential of MOBAT in relation to other fields of myrmecology in Europe, as of May 2005, by directly communicating with group-leaders as well as by screening the literature collections of the authors and personal homepages. Despite great care to include all myrmecologists, we cannot claim completeness; the number of MOBAT myrmecologists, however, can be regarded as precise. We counted as "myrmecologists" graduated scientists at European research institutions (universities, museums and others) with research activities in ant research. As a subgroup of these we counted MOBAT workers. Further, as a subgroup of the latter we assessed the number of taxonomists performing numerically-based species identification and verification – under "numerical". MOBAT myrmecologists were classified as either mainly or occasionally working in this field. Those included under "occasional" were subjectively grouped according to their documented output and the time they apparently spend on taxonomy. The manpower of each occasional taxonomist was scored 0.5. Scientists exclusively doing molecular systematics as well as those exclusively working in higher-level (beta) taxonomy were included in the sum of myrmecologists but were not counted as MOBAT myrmecologists.

omy. The actual working capacity of MOBAT using numerically-based species identification and verification is even lower, totaling 1.2%. As a consequence, the small fraction of active, morphology-based ant-taxonomists is heavily overburdened with determination services for the rest of the myrmecological community. From 2001 to 2005 the last author has written 170 determination reports on about 3,800 ant samples containing some 20,000 specimens for 106 persons and institutions in 29 countries all over the world. Another figure likewise illustrates the dimension of the task ant taxonomists have to cope with: between 31 December 1993 and 8 September 2006 the number of recognized ant species has increased by at least 2,378, or 24.9 % (Bolton 1995b, Agosti & Johnson 2005).

Perspective: The problem of a decreasing portion of expert taxonomists applies to most taxa (cf. Hopkins & Freckleton 2002). We are unaware of other detailed censuses, but for some taxa the situation might even be worse than for ants, including economically important taxa such as mushrooms (Basidiomycota, Buyck 1999), mosquitoes (Culicidae, Besansky & al. 2003b) and bark beetles (Scolytinae, Bright 1992).

Conclusion: The working capacity of MOBAT and even more so of MOBAT applying numerically-based species identification and verification is currently infinitesimal.

Excursus 4: Morphology-based Cyber Identification Engine for *Tetramorium* ants.

Background: It is self-evident that the world wide web is suitable for identification tasks. Wheeler (2004) lists "sophisticated interactive identification keys" among the seven immediate information-technology opportunities taxonomists should make use of. Nash (2005) reviewed the particular utility of the web to the myrmecologist. However, the number of such morphology-based facilities is still low.

Example: Recently, Steiner & al. (2006b) presented the first version of a morphology-based identification engine for ants of the *Tetramorium caespitum/impurum* complex in the www (Fig. 3). Using discriminant analysis, the facility allows the workers of nine very similar species to be discriminated (Excursus 1). The identification engine includes verbal and graphic character definitions as well as an entry mask for morphometric data. Upon data entry, probability values for the sample's membership to each of the nine species are returned.

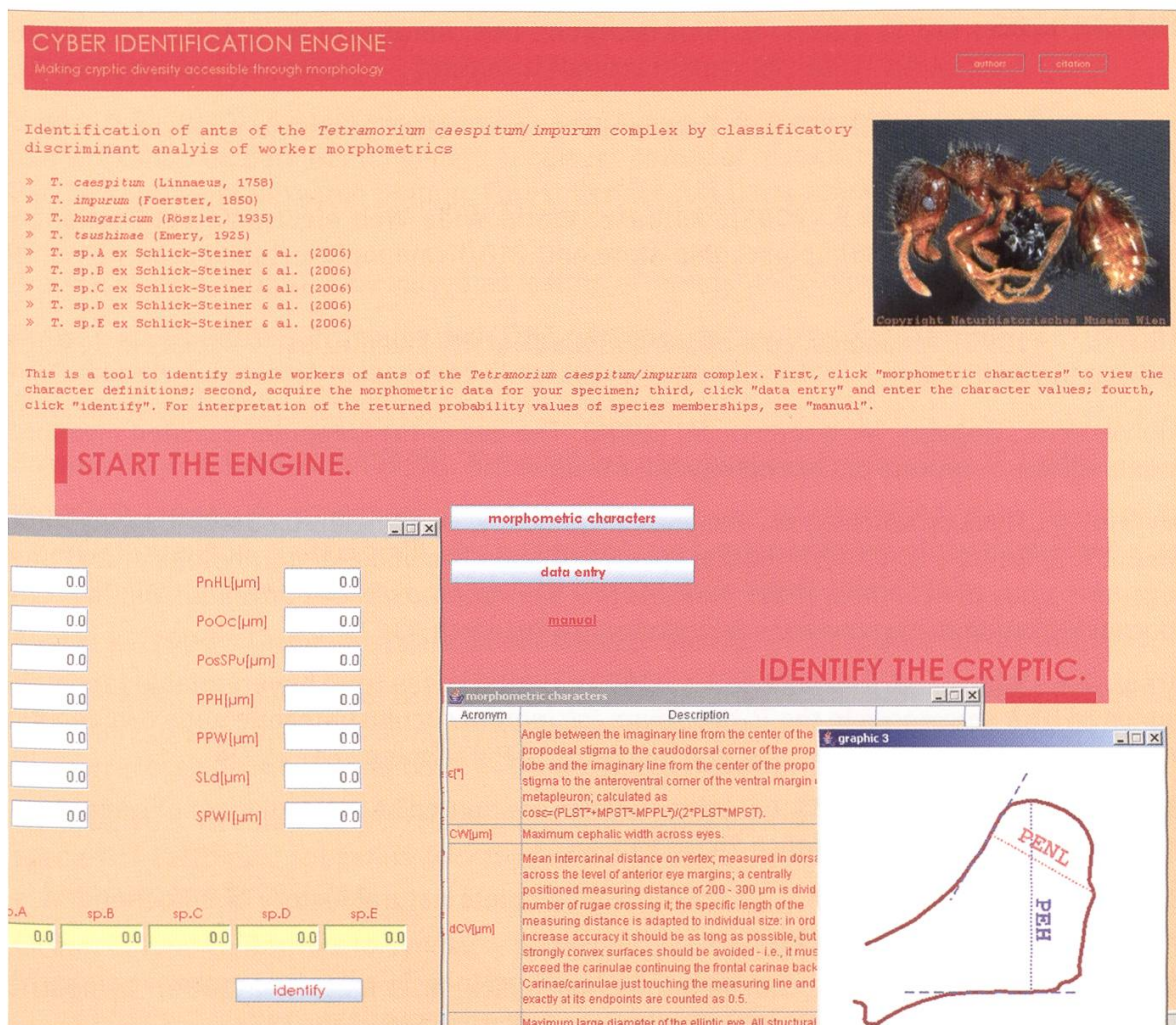


Fig. 3: Screenshot of the morphology-based cyber identification engine for workers of nine species of the *Tetramorium caespitum/impurum* complex (<http://homepage.boku.ac.at/h505t3/DiscTet>).

Conclusion: As part of the necessary modernization of data acquisition and analysis in MOBAT, the interactivity of the internet can be harnessed.

Acknowledgements

Our thanks go to the editors for inviting us to contribute to the Konrad Thaler memorial volume; to all those myrmecologists who helped us with the census; to A.V.Z. Brower, E. Christian, C. Stauffer, J.C. Trager, and H. Zettel for constructive comments on earlier versions of the manuscript; and to M. Stachowitsch for a linguistic revision.

We gratefully dedicate this paper to the memory of Konrad Thaler.

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