Testing the Dutilleul syndrome: host use drives the convergent evolution of multiple traits in parasitic wasps

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Abstract

Common life-history aspects among independent lineages often result in the repeated evolution of suites of adaptive traits, or 'syndromes'. Such syndromes can be key avenues to understand relationships between morphological and ecological traits, but are rarely tested due to insufficient trait shift repetitions. We use a hyperdiverse lineage to investigate the evolution of a syndrome. Cryptine ichneumonid wasps that parasitize insects concealed in hard substrates display several traits that are putative adaptations to that end. Using a phylogenetic framework from a combined multigene molecular and morphological data set with 308 cryptine species, we tested whether these traits were part of a morphofunctional syndrome related to host use. Ancestral state estimations show multiple origins for six investigated traits, which are correlated to each other and to the use of deeply concealed hosts, suggesting adaptation. Putatively adaptive traits showed a much stronger link among themselves than with an assemblage of 49 other morphological traits. However, estimation of the order of evolution in adaptive traits showed no structured pattern. The results indicate that the challenge of attacking deeply concealed hosts induced the repeated evolution of a 'Dutilleul syndrome', named after the 'walker-through-walls' character from French literature. They also point towards a dynamic scenario in the evolution of complex functional systems. These findings highlight the power of morphology to illuminate poorly known aspects of natural history, and how hyperdiverse lineages can be used to understand the evolution of complex traits.

Introduction

Selective pressures exerted by the environment often affect multiple traits (e.g. Maina, 2000; Campbell, 2009; Trontelj *et al.*, 2012; Friedman *et al.*, 2016). A same environmental pressure may therefore connect a suite of adaptive traits into an evolutionary unit, or 'syndrome' (Dobzhansky, 1955; Mayr, 1963; Albert *et al.*, 1992). Syndromes drive a special interest in biology because they provide a framework for predictions about ecology and evolution. Syndromes have been reported and studied across several groups of organisms in

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various contexts, including carnivorous plants (Moran & Clarke, 2010), anole lizards in the Caribbean (Losos, 2011a), insular rodents (Adler & Levins, 1994) and lizards (Raia *et al.*, 2010), army ants (Brady, 2003) and butterflies (Legrand *et al.*, 2016). However, the mere co-occurrence of multiple traits in a given set of taxa is not necessarily indicative of a syndrome. Classical examples of syndromes such as pollination syndromes have been challenged in recent years (Ollerton *et al.*, 2009); at the same time, chance alone may repeatedly generate aggregated traits without an underlying ecological cause (Maddison & FitzJohn, 2015).

A rigorous evaluation of a syndrome, defined as a suite of connected traits evolving in response to a shared biological factor, requires repeated evolution of its traits. Evolutionary convergences, where similar traits are shared by different lineages, provide such

replications (Simpson, 1953; Losos, 2011b; Mahler *et al.*, 2017). However, the relative scarcity of convergent events at a macroevolutionary scale limits the possible statistical tests (Trontelj *et al.*, 2012; Mahler *et al.*, 2013). As a result, syndromes are rarely tested as a hypothesis of convergence of a suite of traits correlated due to a functional linkage (Ollerton *et al.*, 2009). Furthermore, the evolutionary origin of these syndromes remains poorly known. For example, do they follow a same pathway, with initial traits opening the gate for further adaptations, or do the various traits each evolve independently? The idea that certain traits can act as precursors for other changes has a long history in evolutionary biology (e.g. Vavilov, 1922; Brundin, 1976; Donoghue, 2005), but identifying the existence of such precursors is contingent on explicitly mapping their occurrence in a phylogenetic tree (Marazzi *et al.*, 2012).

To allow for objective tests of syndromes and their causes, we need model organisms with sufficient diversity to increase the likelihood of multiple events of convergent evolution affecting more than one trait. Hyperdiverse taxa such as parasitoid wasps could provide such context (Godfray, 1994), particularly clades with high rates of morphological homoplasy (Gauld & Mound, 1982). In this study, we focus on adaptations related to a dietary shift of parasitoid wasps to study the evolution of syndromes.

With 250 genera and over 2400 species distributed worldwide, Cryptini (Hymenoptera, Ichneumonidae, Cryptinae) are one of the most speciose groups of parasitoid wasps (Townes, 1970). Most of the species are specialized in attacking immature stages of moths, beetles and wasps (Gauld, 2006). These hosts are concealed to various degrees, from leaf rolls, twigs and vines to deep, hardened substrates such as clay nests and wood (Fig. 1). The latter pose several challenges to the parasitoids: (i) finding a suitable host, since deeply concealed pupae are not visible nor actively producing directly detectable acoustic or chemical cues; (ii) reaching the host through the thick, hard substrate; (iii) emerging from the substrate where they have developed (Quicke, 2015).

Wasps parasitizing such deeply concealed hosts display several features apparently related to this special habit (Quicke, 2015). The echolocation system called 'vibrational sounding' may be the most studied: wasps transmit a vibration to the substrate through their antennae and use hypertrophied mechanoreceptors located in their legs (the subgenual organ) to detect the concealed host (Henaut, 1990; Broad & Quicke, 2000; Vilhelmsen *et al.*, 2001; Otten *et al.*, 2002). Several species also use enlarged ovipositor muscles and an ovipositor tip reinforced with metal ion–protein complexes such as manganese, calcium and zinc to drill through the hard substrate (Quicke *et al.*, 1998, 2004). They can also chew their way out of the substrate using strong mandibular muscles and sickle- or chisel-shaped mandibles (Quicke, 2015).
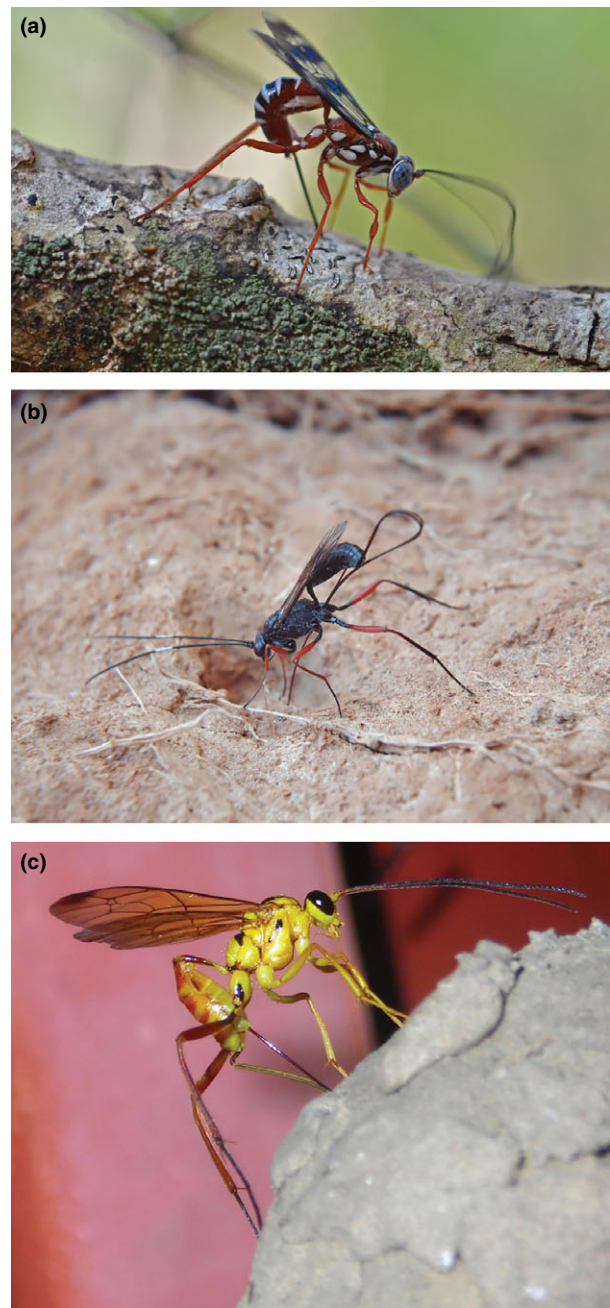

Fig. 1 Three species of cryptine wasps attacking hosts that are deeply concealed under hard substrates, each representing an independent evolution of this behaviour. (a) *Nesolinoceras ornatipennis* (Cresson); (b) *Stenarella domator* (Poda); (c) *Photocryptus pachymenae* (Cresson). Photographs by Max Padt, Axel Steiner and Suzana Rodríguez, used with permission.

All of these features may help wasps to exploit hosts through hard substrate, an attack to concealed prizes that is not unlike Marcel Aymé's short story about Dutilleul, the walker-through-walls (Aymé, 1943).

However, such a 'Dutilleul syndrome' remains to be tested: in spite of their putative functional importance, the adaptive significance of most of these morphological features is not established. Biological traits such as host location and oviposition have been extensively studied from a mechanistic, physiological point of view, or in a behavioural ecology framework (Godfray, 1994; Hanson & Gauld, 2006), but most of the available knowledge is derived from economically important species, and comparative studies are scarce. The vibrational sounding system was studied as an adaptation based on comparative data: Broad & Quicke (2000) related it to the use of deeply concealed hosts on ichneumonid wasps, and Laurenne *et al.* (2009) found that highly specialized antennal tips were associated with the use of wood-boring hosts in Cryptini. To our knowledge, no other study directly tested the other features as adaptations to the use of deeply concealed hosts.

To better understand the evolution of syndromes, we studied the convergent evolution of multiple traits related to the same ecological challenge: parasitizing hosts through hard substrates. First, we tested whether putative adaptations in cryptine wasps are associated with the use of deeply concealed hosts by mapping those traits onto a phylogeny. Then, we tested whether these traits have evolved in concert, as a functional unit, by comparing their evolution with that of other morphological traits. Finally, we identified the sequences of trait evolution to test whether the syndrome evolved according to a defined structure.

Materials and methods

Phylogenetic tree and morphological data

The phylogenetic framework was extracted from a recent revisionary work on Cryptinae (Santos, 2017). This is a maximum-likelihood tree based on molecular data from seven genes and 109 morphological characters, including 308 species from 181 genera of Cryptini (72.4% of the generic diversity of the group) and 62 outgroup taxa (Appendix S1). To account for phylogenetic uncertainty, all comparative analyses were conducted not only for the best tree but also for a collection of 100 bootstrap replicates made for the original analysis (Santos, 2017; and Appendix S1).

Six putative morphological adaptations for attacking deeply concealed hosts found in the literature were coded as binary traits (Fig. 2, Table 1; see Appendix S2 for complete matrix). Only females of each species were included; although sexual dimorphism in Cryptini is only moderate, males do not show the character states under investigation for this work. Intermediate states for the characters as defined here were absent or had very low prevalence, allowing for consistent binary coding.

Ancestral state estimation

Ancestral states for each of the discrete characters under study were estimated by first optimizing the characters under parsimony onto the reference tree using the 'change' command in TNT (Goloboff *et al.*, 2008). A maximum-likelihood approach was then used to estimate relative probabilities for each state using the 'ace' function of the *ape* package in R (Paradis *et al.*, 2004; R Core Team 2017). Both equal and unequal transition rate matrices were tested, and the difference in log likelihoods obtained under the two models compared against a chi-square distribution to determine whether the gain in likelihood justified the adoption of the more parameterized model. The unequal rate transition model (ARD, 'all rates different') was significantly better for every character ($P < 0.05$) and hence adopted in downstream analyses. To obtain a probability distribution of the number of state transitions, stochastic character mapping (Huelsenbeck *et al.*, 2003; Bollback, 2006) was implemented using the 'make.simmap' function in the *phytools* package (Revell, 2012). This function performs simulations of character histories taking into account the relative probabilities at each node, resulting in a population of alternative scenarios ('realizations' sensu Huelsenbeck *et al.*) from which frequency distributions can be summarized for the number of state transitions. For the present analyses, 10 000 simulations were conducted. The function 'densityMap' was then used to plot a tree with colour-coded probabilities of each state along the branches, as estimated from the collection of simulations.

Multiple trait evolution

To examine the relationships among the traits under study in a phylogenetic context, we used both phylogenetic logistic regressions (Ives & Garland, 2010, 2014) and Pagel's lambda (Pagel 1994). Pagel's method allows testing for correlated evolution without assumption of a predictive trait. Regression models were run in both directions (i.e. each trait tested as both predictor and response variables), except for the use of deeply concealed hosts itself, run exclusively as a predictor variable. Regressions were performed using the 'phyloglm' function in the *phylolm* package (Ho & Ane, 2014) in R, using 1000 bootstrap replicates. Pagel's method was implemented through the 'fitPagel' function in *phytools*. *P*-values were adjusted with a Benjamini–Hochberg correction (Benjamini & Hochberg, 1995) to account for multiple comparisons. This correction was performed to give our results extra robustness against type I errors, even though our analyses fit well the concept of 'planned comparisons', which usually do not require correcting for multiple comparisons (Keppel & Wickens, 2004).
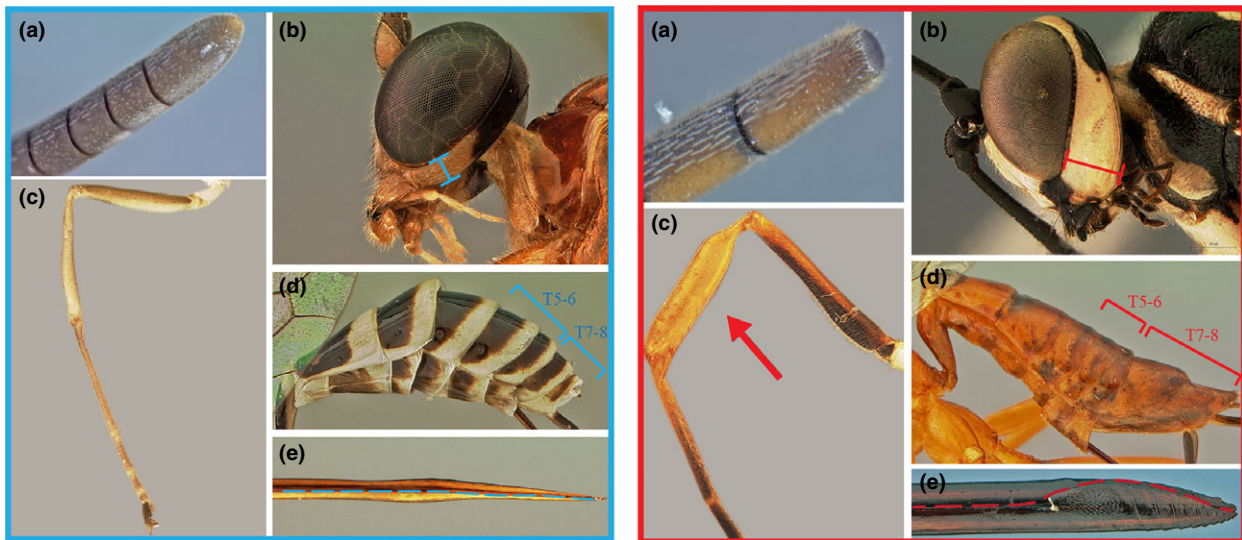
Fig. 2 Morphological traits coded for the analyses; in the left blue box, the 'unmodified', putatively ancestral state; on the right red box, putative adaptations to attack deeply concealed hosts. (a) antennal tip. (b) mandibular muscles. (c) fore tibia profile. (d) oviposition muscles. (e) ovipositor profile, on the right showing the ventral valve projected onto dorsal valve as clasping lobe.

Table 1 Morphological traits investigated as potential adaptations to locate and reach deeply concealed hosts, with respective diagnostic criteria and putative function.

Morphological trait	Description	Functional interpretation
Modified, hammer-like antennal tips	Tip of apical flagellomere flattened, with modified sensilla visible with light microscopy	Tapping substrate to produce vibrational sounding
Enlarged mandibular muscles	Ventral 0.5 of gena at least 1.5× longer than dorsal 0.5	Used by recently emerged adults to dig out of substrate
Enlarged fore tibia	Diameter over 0.25× length	Housing mechanoreceptor organs to detect vibrations
Enlarged apical tergites	Tergites 7–8 distinctly longer than T5–6	Housing stronger oviposition muscles
Stout, compressed ovipositor	At least 3× as long in dorso-ventral axis as in transverse axis	Drilling into hard substrates
Ovipositor ventral valve projected onto dorsal valve as clasping lobe	Ventral valve expanded in lateral view, covering most of dorsal valve profile	Stabilizing and strengthening ovipositor

Relationships among pairs of morphological traits were performed using the full cryptine data set (308 species). Each trait was also tested for correlation against host concealment itself, with species classified as 'using deeply concealed hosts' vs. 'weakly concealed hosts'. As hosts are unknown for many taxa, correlation among traits and host concealment was performed on a subsample for which hosts were known. Host records are missing for many cryptine species, especially in the tropics, although in many cases such records are available for closely related species. Examination of the extensive survey of Yu *et al.* (2012) shows that host types are conserved within genera. Therefore, in case of missing data, host records were extrapolated from cogeneric species whenever it was possible. Taxa were defined as attacking 'deeply concealed hosts' if at least one member of the genus was recorded as parasitoid of wood-boring insects or wasps that build nests made of clay. All terminal taxa from genera for which host records were unavailable (95 of 308 cryptine terminals) were then pruned from the phylogenetic tree, and the regression between host use and phenotypic traits was conducted with the remaining terminals.

The evolutionary module of adaptations was also tested by comparing the relationships between adaptive traits to the relationships of adaptive and nonadaptive traits. Under the hypothesis that the adaptive traits are part of a syndrome, or evolutionary module, their evolution should be more closely linked than with the rest of other morphological characters. In other words, an adaptive trait should better predict the evolution of another adaptive trait driven by the same environmental factor than a nonadaptive character. To test this hypothesis, we performed phylogenetic logistic regressions between the six discrete adaptive characters and all other 49 binary morphological characters from

Santos (2017). We then compared the Akaike information criterion of each model based on a same adaptive character between those using adaptive characters as predictors and those using nonadaptive characters as predictors.

To test whether putative adaptations arised following a defined structure during the evolution of each lineage, we examined all transitions of the adaptive traits from their primitive to derived states using ancestral state reconstructions. A structured evolution of a syndrome would require that some traits would consistently predate others. Every transition was therefore scored according to whether the other traits had already reached their derived state in the clade. This scoring was carried out for 1000 simulations of the 'make.simmap' function. The analysis highlighted whether adaptive traits appeared constantly before or after the diet shift or other adaptive traits, accounting for the uncertainty inherent to ancestral state reconstruction.

Results

Ancestral state reconstruction

Both parsimony optimizations and stochastic character mapping inferred multiple state transitions for all the investigated traits (Table 2, Fig. 3 and Fig. S1). Even under the conservative criterion of parsimony, the putative adaptive traits evolved independently 12–27 times, as optimized for the best tree, and reversals were frequent. Ancestral states estimated by maximum likelihood were generally unambiguous, attributing a probability 95% or higher to one state in almost all internal nodes. Stochastic character mapping always inferred considerably more transitions than the most parsimonious transitions, but the difference between the two methods varied among characters, from 3.3% more transitions in average for the enlarged oviposition muscles to 37.7% more for the modified antennal tips. Estimations for the 100 bootstrap trees confirmed these results of multiple transitions for all studied traits, although with more variation in the number of transitions depending on the topologies (Appendix S3).

Multiple trait evolution

Phylogenetic logistic regression showed significant results among almost all trait pairs (Table 3). Four comparisons returned nonsignificant relationships (trait a does not predict trait b), but in all these cases, the inverse comparison was upheld (trait b does predict trait a), showing that at least some connection between the traits does exist. These results were robust to the phylogenetic uncertainty: for 23 of these 26 comparisons, the results were significant with more than 95% of the bootstrap trees tested (Appendix S4). Using Pagel's (1994) method, models predicting covariance

Table 2 Summary of results for the ancestral state estimation.

Character	0:1	Mpr G	Mpr L	Simmap avg G	Simmap avg L
Modified antennal tips	295:64	15–19	3–7	21.2	9.1
Large mandibular muscles	294:65	13–15	0–2	15.2	0
Swollen fore tibia	299:60	12–15	1–4	15.3	2.1
Enlarged oviposition muscles	310:49	7–11	1–5	11.4	1.4
Stout ovipositor	296:63	19–23	4–8	23.4	11.9
Ovipositor lobe	298:61	9–10	2–3	12.4	2.5

0:1, number of taxa coded as 0 (unmodified state) and 1 (putative adaptation) for each trait. Mpr G, number times a character changed from state 0→1 (gains) under ACCTRAN and DELTRAN algorithms of the most parsimonious reconstruction. Mpr L, same as before with losses (1→0). Simmap avg G, average number of gains for the character under simulations performed with stochastic character mapping. Simmap avg L, same as before with losses.

among pairs of traits had also a better fit than uncorrelated models, with high significance (Appendix S4), for all pairwise comparisons.

The analyses of regression between phenotypic traits and the use of deeply concealed hosts *per se* also returned significant results for five of the six traits (Table 3), despite the considerably reduced sample ($N = 213$; see Material and Methods). In all analyses, the presence of strong ovipositor muscles, as indicated by enlarged apical tergites, was the trait with weakest relationships, specifically as a response variable.

The AIC values from models using adaptive characters as predictors were also significantly lower than those from models using nonadaptive characters as predictors ($t_{33.749} = -3.7937$, $P = 0.0006$; complete results in Appendix S5). Altogether, these results suggest that there is a stronger link among the evolution of the adaptive traits than with other morphological traits, supporting the hypothesis that the evolution of adaptive traits was driven by a same environmental factor and thus forming an evolutionary unit.

The estimation of the relative order of evolution of the traits showed no fixed pattern (Table 4, Appendix S6). The maximal and minimal frequencies of preceding occurrences of adaptive traits at the transition of another adaptive trait were of 21% and 57% for ovipositor muscles and antennae and for antennae and swollen tibiae, respectively.

Discussion

Hunting deeply concealed hosts

Our results confirm that multiple traits have evolved in correlation with the use of deeply concealed hosts by parasitoid wasps, apparently related to several functional demands including host location, oviposition and
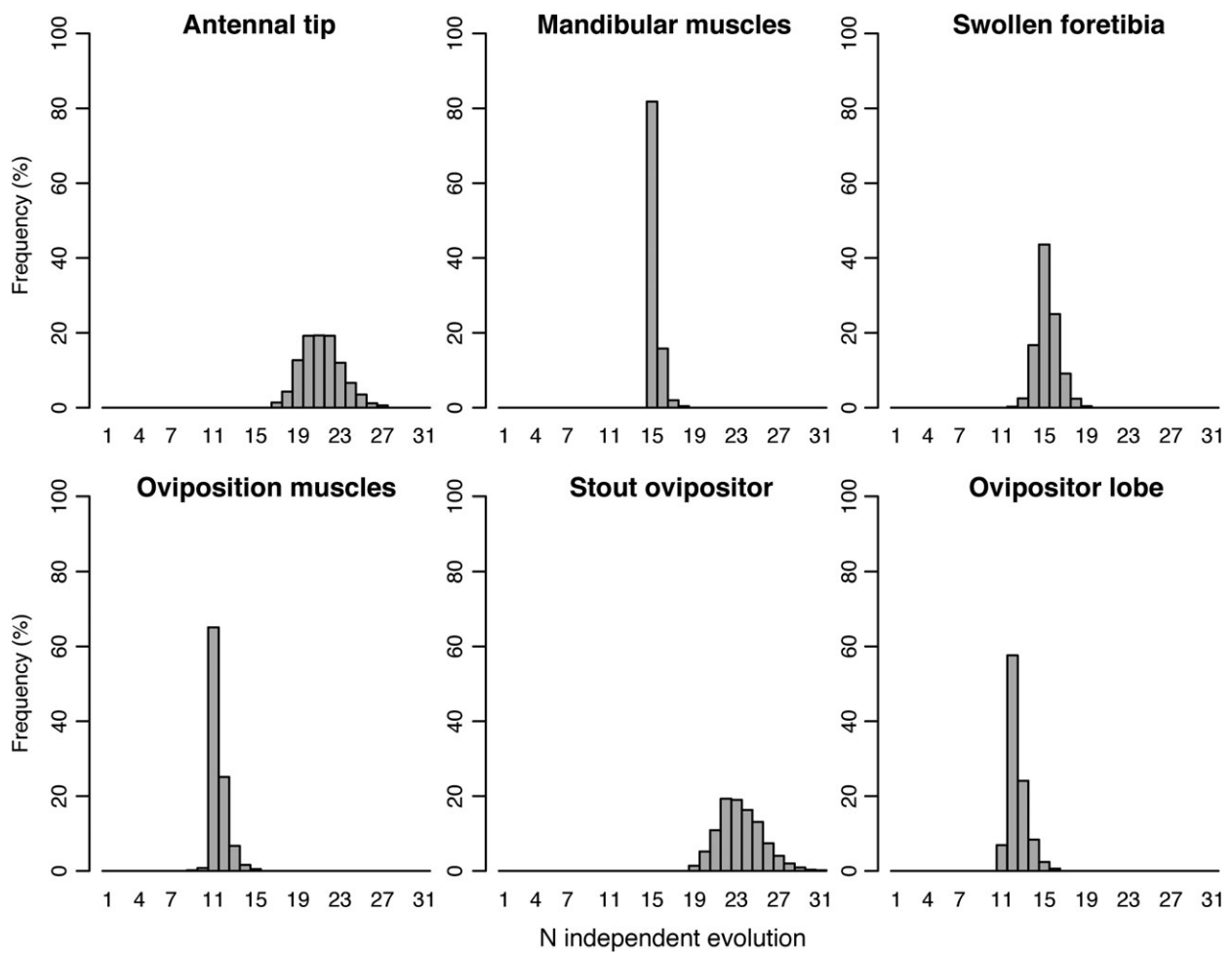
Fig. 3 Frequency distributions of alternative scenarios with different numbers of 0→1 transitions for binary traits under stochastic character mapping, as inferred by 10 000 simulations.

Table 3 Results of the phylogenetic logistic regression comparing pairs of phenotypic traits and comparing those traits to the use of deeply concealed hosts (DCH).

	Antennal tip		Mandible muscles		Swollen tibia		Oviposition muscles		Stout ovipositor		Ovipositor lobe	
	z	P	z	P	z	P	z	P	z	P	z	P
Antennal tip	–		0.040	0.0127*	0.466	0.0055	0.168	0.1218	1.377	0.0231	0.221	0.0231
Mandible muscles	1.369	0.0018*	–		1.141	0.0033*	0.268	0.0408	1.505	0.0033*	0.138	0.0055*
Swollen tibia	1.031	<0.0001*	0.385	0.0077*	–		0.631	0.0698	0.945	0.0018*	0.315	0.0033*
Oviposition muscles	0.792	0.0152*	0.126	0.0033*	0.435	0.0033*	–		1.368	0.0162*	0.561	<0.0001*
Stout ovipositor	0.99	0.0465	0.127	0.0273	0.600	0.0231*	0.274	0.1570	–		0.202	0.1058*
Ovipositor lobe	1.230	0.0033	0.097	0.0231*	0.543	0.0033*	2.468	0.0171*	1.315	0.0231*	–	
DCH	0.267	0.0120*	0.240	0.0140*	0.716	0.0127*	0.417	0.1234	1.502	0.0231	0.221	0.0231

Rows are predictor variables, and columns are response variables. Z-values are the ratio between the regression coefficient and the standard error, with higher values meaning stronger relationships. Asterisks next to the P-value indicate that the statistical significance was maintained in at least 95% of the bootstrap trees. P-values were adjusted with a Benjamini–Hochberg correction (Benjamini & Hochberg, 1995) to account for multiple comparisons. Nonsignificant relationships ($P > 0.05$) threshold are underlined.

Table 4 Percentage of the total number of transitions of a character (line) for which a second character (columns) had evolved previously or simultaneously. For example, comparison of line 1 (antennal tip) with column 3 (swollen tibia) shows that 40% of 0→1 transitions for the antennae occurred after or during state transitions for the tibia.

	Antennal tip	Mandible muscles	Swollen tibia	Oviposition muscles	Stout ovipositor	Ovipositor lobe
Antennal tip		0.34 ± 0.06	0.40 ± 0.06	0.21 ± 0.05	0.28 ± 0.06	0.4 ± 0.06
Mandible muscles	0.35 ± 0.05		0.44 ± 0.07	0.3 ± 0.04	0.39 ± 0.06	0.3 ± 0.04
Swollen tibia	0.57 ± 0.08	0.46 ± 0.07		0.33 ± 0.05	0.36 ± 0.07	0.47 ± 0.07
Oviposition muscles	0.29 ± 0.05	0.39 ± 0.05	0.34 ± 0.05		0.25 ± 0.04	0.44 ± 0.05
Stout ovipositor	0.39 ± 0.07	0.5 ± 0.08	0.46 ± 0.08	0.28 ± 0.06		0.34 ± 0.07
Ovipositor lobe	0.34 ± 0.06	0.33 ± 0.05	0.34 ± 0.05	0.3 ± 0.05	0.22 ± 0.05	

emergence from the substrate. Although we focused on cryptine wasps, due to the recent progress in their phylogeny (Santos, 2017), many of the adaptations studied here are not exclusive to this group. The vibrational sounding system was first detected on a different subfamily of wasps, the Pimplinae (Henaut & Guerdoux, 1982). Broad & Quicke (2000) investigated the occurrence of the vibrational sounding system across various groups of Ichneumonidae, and a similar system was also found in the Orussidae, a different family of Hymenoptera (Vilhelmsen *et al.*, 2001). Chisel-like mandibles are found in many insects digging through wood, including other families of wasps (Quicke, 2015). However, the present study is the first to investigate the character history of multiple traits with such a resolution within this hyperdiverse group. The estimation of 12–27 events of convergent evolution for each trait confirms that hyperdiverse groups are a good model to study patterns of convergent evolution, as these numbers are much higher than what was observed based on coarser samplings (Broad & Quicke, 2000). They also indicate that the selective pressure related to parasitizing deeply concealed hosts is strong enough to drive these drastic morphological changes, although the weaker relationships found for the presence of enlarged apical segments suggest that at least some taxa may be able to perforate hard substrate without particularly strong oviposition muscles.

In a group as diverse as parasitoid wasps, found in areas all continents and habitats, it is easy to understand how access to exclusive food resources can be a clear evolutionary advantage, even at the price of strong constraints.

The Dutilleul Syndrome of wasps

Based on our results, wasps seem to benefit from their special set of features to overcome the physical barrier protecting their food. The results of the phylogenetic logistic regression and the ancestral state reconstructions support the hypothesis that traits associated with the use of deeply concealed hosts are indeed part of a distinctive 'Dutilleul syndrome' that evolves as a unit in response to an ecological shift. This suite of traits evolves in concert in the cryptine tree and their presence is correlated with the use of deeply concealed hosts.

Considering the rather chaotic pattern observed among morphological characters for Cryptinae as a whole (Santos, 2017), the highly significant correlation observed among the features studied herein provides strong evidence of a link among these traits. Incidental correlation in trait occurrence among clades is likely when rates of morphological evolution are low (Maddison, 1990; Maddison & FitzJohn, 2015), and could result in within-clade pseudoreplication (Read & Nee, 1995; Grafen & Ridley, 1997; Maddison, 2000). Hence, regressions and correlations could be significant without a biologically relevant pattern. For this reason, we also compared the strength of these relationships against the relationships with 49 other morphological binary characters. Using the AIC of the different comparisons, we found an unambiguous link between the putative adaptive traits compared to the other traits. They form therefore a distinct evolutionary module, related to a same ecological shift: attacking deeply concealed hosts.

Estimation of the relative order of evolution of the traits showed inconclusive results, failing to demonstrate any structured pattern in the evolution of this syndrome. There are some cases in which a given adaptation tended to precede another, such as the swollen fore tibia, which tended to evolve after the modified antennal tip (57% of the times). However, with the maximum and minimum frequencies at 57% and 21%, respectively, there are no clear-cut 'rules' governing the order of evolution of these traits (absolute frequencies in Appendix S6). Statistical testing of the results is not straightforward because of the differing number of instances of evolution for each character (12–27). However, these observations clearly contradict the idea that some adaptations would always (or almost always) precede others (as represented by the concept of 'exaptation', sensu Gould & Vrba, 1982). Such a dependency was documented in a number of studies in a comparative framework, with phylogenetic patterns suggesting that the evolution of certain convergent traits is hierarchically contingent on the presence of precursor traits

(Maraun *et al.*, 2009; Marazzi *et al.*, 2012; Beaulieu *et al.*, 2013). In contrast, our results help to de-emphasize a 'key adaptations' approach in favour of a more dynamic and integrative scenario for morphological evolution in syndromes, pointing towards multiple viable pathways for the evolution of complex functional systems.

Testing syndromes as convergent evolution events

Syndromes are often the basis for biological predictions: by linking morphology to ecology, it becomes possible to infer the biology of poorly known organisms based on morphological cues (Rosas-Guerrero *et al.*, 2014). In our case, a few discrete traits provided decent estimators of the type of host use, enabling their use as proxies for biological attributes in larger data sets without loss in accuracy. A similar correlation between morphology and life history was identified in another group of ichneumonid wasps (Ichneumonidae: *Ichneumon*) linking antennal length to the use of hosts that pupate above vs. below ground (Tschopp *et al.*, 2013). For parasitic wasps, a clade with over 70 000 known species and host records still lacking for far too many taxa (Hanson & Gauld, 2006; Quicke, 2015), developing reliable biological predictions from morphological data can be transformative in the study of their ecology and evolution (Ricklefs & Miles, 1994; Barton *et al.*, 2011). This lack of knowledge, though, is not restricted to parasitoid wasps: the biology of species within hyperdiverse taxa is often poorly known. As those groups also possess the right conditions to develop syndromes, it is important to assess and to test such patterns in order to produce reliable predictions.

Predictable evolutionary convergence has been reported for many groups, often in the context of adaptive radiations in island-type ecosystems (Losos, 1992; Losos *et al.*, 1998; Rüber *et al.*, 1999; Blackledge & Gillespie, 2004; Gillespie, 2004). Documenting this phenomenon on a broader scale, however, has been rarer (Hollar & Springer, 1997; Hamilton *et al.*, 2001; Nikaido *et al.*, 2001; Moen *et al.*, 2016). Our results show that hyperdiverse groups such as parasitoid wasps can provide useful models to study this question at larger scale. In particular, predictability suggests a trend of evolution to follow similar paths according to specific constraints. This trend was difficult to verify in our case: we could not conclude whether host use constrained the morphology or the other way around. Besides, no one adaptation seemed mandatory to exploit deeply concealed hosts, nor consistently predated another adaptation. Evolution of the different lineages thus followed different paths towards a same syndrome. Whether this is an artefact of the overwhelming diversity of parasitoid wasps or a general trend will require further studies on different syndromes and other hyperdiverse models.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Maximum-likelihood tree used in the comparative analyses, followed by all 100 bootstrap replicates.

Appendix S2 Binary coding for the six phenotypic traits investigated and for host use. In each cell, '0' means either 'unmodified state' for phenotypic traits or 'not attacking deeply concealed hosts' for Biology; '1' means 'putative adaptation' and 'attacking deeply concealed hosts', respectively.

Appendix S3 Number of independent instances of evolution of each trait for all bootstrap replicates.

Appendix S4 Range of results of phylogenetic logistic regressions for all bootstrap replicates and of Pagel's (1994) method.

Appendix S5 Logistic regressions across putatively adaptive vs. nonadaptive traits.

Appendix S6 Complete results for analyses of timing of state transitions.

Figure S1 Ancestral state reconstruction based on stochastic character mapping. For each investigated trait, a density tree with the consensus of 10 000 simulated histories, with each iteration based on the relative probabilities for each state at each node, as estimated from a likelihood-based algorithm.