Phylogenetic Relationships among European *Polistes* and the Evolution of Social Parasitism (Hymenoptera: Vespidae, Polistinae)

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ABSTRACT

Cladistic analysis of the European species of *Polistes* is used to investigate the evolution of social parasitism in the genus. The three species of social parasites (formerly the genus *Sulcopolistes*) are all inquilines: lacking a worker caste, and dependent on usurping the colony of a host species to obtain a worker force. EMERY's Rule states that social parasites are more closely related to their hosts than to any other species. Previously published allozyme (CARPENTER *et al.*, 1993) and mtDNA (CHOUDHARY *et al.*, 1994) data did not support this hypothesis, but did not resolve relationships among the species of social parasites. Morphological characters are adduced which resolve the phylogenetic relationships among these three species, and the combination of the morphological and molecular data sets largely resolves the relationships among all nine European species. Cladistic optimization of traits associated with social parasitism on the resulting cladogram shows: (1) EMERY's Rule is rejected; (2) the scenario proposed by TAYLOR (1939) for the evolution of social parasitism is not supported either. The predatory behavior of the inquiline *P. atrimandibularis*, with separate "supply" and "nursery" nests, is evidently secondary, as is its initially passive invasion behavior.

RÉSUMÉ

La phylogénie des *Polistes* d'Europe et l'évolution du parasitisme social (Hymenoptera : Vespidae, Polistinae)

L'analyse cladistique des espèces de *Polistes* européennes est utilisée pour étudier l'évolution du parasitisme social dans le genre. Les trois espèces de parasites sociaux (autrefois le genre *Sulcopolistes*) sont toutes « inquilines » : elles n'ont pas de caste ouvrière et s'approprient celle de la colonie d'une espèce hôte. Le règle d'EMERY affirme que les espèces de parasites sociaux sont plus proches parents de leurs hôtes que de toute autre espèce. Des analyses basées sur les allozymes (CARPENTER *et al.*, 1993) et l'ADN mitochondrial (CHOUDHARY *et al.*, 1994) n'ont pas confirmé cette hypothèse, mais n'ont pas résolu non plus les relations entre les espèces parasites. L'addition de caractères morphologiques et la combinaison des données morphologiques et moléculaires ont permis de résoudre respectivement les relations phylogénétiques entre ces trois espèces, et entre les neuf espèces européennes. L'optimisation sur le cladogramme de traits associés au parasitisme social montre que : (1) le règle d'EMERY est réfutée ; (2) le scénario d'évolution du parasitisme social proposé par TAYLOR (1939) est également réfuté. Le comportement prédateur de l'inquiline *P. atrimandibularis,* qui maintient des nids séparés pour les provisions et pour le couvain, est à l'évidence secondaire, de même que son comportement d'invasion initiale passive.

CARPENTER, J. M., 1997. — Phylogenetic relationships among european *Polistes* and the evolution of social parasitism (Hymenoptera: Vespidae; Polistinae). *In*: GRANDCOLAS, P. (ed.), The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. *Mém. Mus. natn. Hist. nat.*, **173** : 135-161. Paris ISBN : 2-85653-508-9.

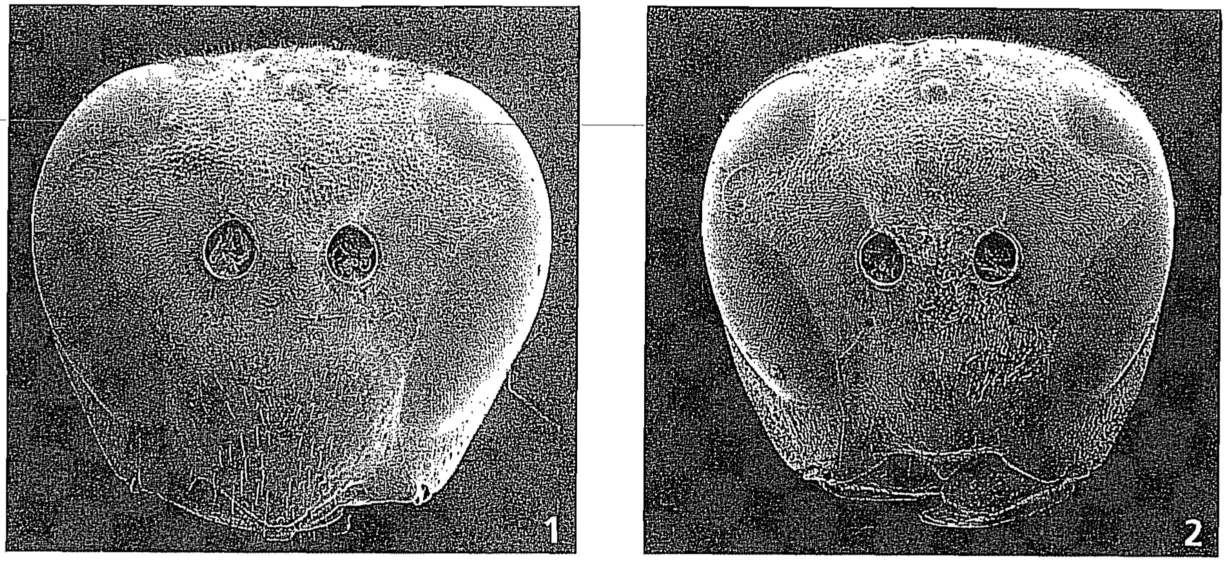
INTRODUCTION

The social parasites known as inquilines are among the most intriguing outcomes of evolution in paper wasps. Inquilines have no worker caste and cannot build nests; they must invade the colony of a host species and supplant the queen to obtain workers to rear their brood. Striking morphological differences occur between host and parasite (*cf.* Figs 1-2). This form of behavior is rare in paper wasps, having been found in just three species in one genus, *Polistes*. *Polistes* is a cosmopolitan genus, with more than 200 described species (CARPENTER, 1996b); the three social parasites (*atrimandibularis*, *semenowi* and *sulcifer*) are found only in Europe and the Mediterranean Region. The inquiline behavior has long been known (WEYRAUCH, 1937), but recent years have seen a profusion of studies, particularly by workers at the University of Florence (for a review see CERVO & DANI, 1996). These studies have revealed remarkable phenomena, such as simultaneous domination by *atrimandibularis* of several colonies of the host *biglumis*, only one of which serves for parasite brood rearing while the larvae of the other nests serve as a source of food (CERVO *et al.*, 1990c), or change in the composition of the chemical signature of *atrimandibularis* to match that of *biglumis* at the time of emergence of host workers (BAGNERES *et al.*, 1996). This wealth of new information has stimulated intense interest in evolutionary explanations of aspects of social parasitism.

In this paper I apply cladistic analysis to investigate the evolution of social parasitism in *Polistes*. I first review evolutionary explanations that have been advanced for the social parasites, and how cladistic tests may be constructed for such hypotheses. I then present the first cladistic analysis of interrelationships among the inquilines and related species to be based on morphology. These characters are also combined with previously published molecular data, and analyzed simultaneously. Behavioral features associated with social parasitism are optimized on the resulting cladogram, to test various evolutionary hypotheses.

EMERY's Rule

The classical explanation that applies to the origin of socially parasitic species is the hypothesis known as EMERY's Rule (after EMERY, 1909). EMERY's Rule is that social parasites are more closely related to their host species than to any other species. This is usually interpreted to mean that social parasites evolved directly from their hosts, either by sympatric speciation (*e.g.* WEST-EBERHARD, 1986; BUSCHINGER, 1986, 1990; BOURKE & FRANKS, 1991) or not (*e.g.* WILSON, 1971). Alternatively, social parasites may exploit similar recognition systems in closely related species (CARLIN, 1988). However, previous cladistic analyses do not support EMERY's Rule in *Polistes*. CARPENTER *et al.* (1993) presented an allozyme data set for the three species of social parasites, their four host species (see Table 1) and two outgroup species. The 27 loci were subjected to three different coding procedures, which led to different results for each method, but under none of the codings were the social parasites most closely related to their hosts. CHOUDHARY *et al.* (1994) analyzed a 386 base pair sequence from the mitochondrial 16S rRNA gene. Their cladistic results were less ambiguous, with two cladograms, differing only in the interrelationships among the social parasites. The social parasites were a monophyletic group. Thus, phylogenetic analysis of two independent sources of evidence, by rejecting close relationship of parasite to host, rejected EMERY's Rule.



FIGS 1-2. — Frontal view. 1: *Polistes dominulus*; 2: *Polistes atrimandibularis*. The magnification is 21x.

TABLE 1. — Host-parasite relations among European *Polistes* species. CERVO & DANI (1996) report experimental introduction of *atrimandibularis* into the nests of *nimphus*, but this is unknown to occur naturally.

Parasite	Host
atrimandibularis	*biglumis, gallicus*
semenowi	*dominulus, nimphus*
sulcifer	*dominulus*

TAYLOR's Scenario

EMERY's Rule also played a role in development of an evolutionary scenario for the origin and elaboration of social parasitism in wasps, that of TAYLOR (1939). TAYLOR observed a case of nest usurpation of the vespine species *Vespula vidua* by *V. squamosa*, then considered closely related. He then suggested a sequence of behavioral changes from free living to inquiline. The scenario consisted of four stages: (1) Intraspecific, facultative, temporary parasitism, (2) Interspecific, facultative, temporary parasitism, (3) Interspecific, obligate, temporary parasitism, (4) Interspecific, obligate, permanent parasitism.

Intraspecific nest usurpation thus evolved into inquiline behavior, with the loss of a worker force produced by the usurping queen. The existence of intraspecific nest usurpation was well known in vespines (JANET, 1903), as were inquilines (*e.g.* WEYRAUCH, 1937), and TAYLOR's scenario became generally accepted (*e.g.* WILSON, 1971; MATTHEWS, 1982; GREENE, 1991). The applicability of this hypothesis to polistine social parasites has been questioned by CARPENTER *et* *al.* (1993) and CHOUDHARY *et al.* (1994), who observed that whereas the first stage in TAYLOR's scenario was common in paper wasps, the second stage was rarely reported, and the third stage is unknown (see review in CERVO & DANI, 1996). Nevertheless, the general notion of evolution of usurpation into inquilinism was accepted.

Recent hypotheses

The recent increase in knowledge of the behavioral ecology of the inquilines has been accompanied by novel hypotheses on the evolution of features of their biology, some newly reported. Notable examples discussed by CERVO & DANI (1996) include observations on the distribution of parasites and length of the colony cycle in one host, timing of usurpation by the parasite, the tactics employed by the parasite in dominating the host queen, and the predatory behavior of *atrimandibularis*. These ideas are briefly summarized here.

The Florence group has shown that inquilines are moderately abundant at the foot of mountain ranges. The hosts nest mostly at low elevations, but *biglumis* nests high in the mountains (800-2000+ m in Italy; see CERVO *et al.*, 1990b). Obligate parasitism is suggested to have evolved from such a high altitude species (LORENZI & TURILLAZZI, 1986), because the colony cycle is short (four months, *vs.* six in the low altitude hosts), which is correlated with a high frequency of intraspecific usurpation. Synchronization of colony cycle, resulting in availability of suitable host nests (WCISLO, 1987), may also explain the limitation of inquiline behavior to temperate regions. Migratory behavior (between lowlands and mountain tops in both inquilines and hosts in Italy) may be related to the origin of obligate parasitism, whether through decreased kinship (CERVO & DANI, 1996) or through reduction in population size leading to enhanced parasitic tactics (WEST-EBERHARD, 1996).

Local nesting environment may also influence timing of invasion by the inquiline. Colonies at higher altitudes are invaded earlier in the colony cycle, in the middle of the period before worker emergence (pre-emergence phase), while those in the lowlands may be invaded early in the period after workers have begun to emerge (post-emergence phase). Inquilines tend to prefer larger nests in more advanced stages of development among available nests (CERVO *et al.*, 1993). Early invasion by *atrimandibularis* in *biglumis* nests may be an adaptation to the shortened colony cycle of the host, because usurpation while workers are emerging would entail delay in production of inquiline offspring, jeopardizing reproductive success at high altitudes (CERVO *et al.*, 1990c).

The inquilines differ in tactics employed during usurpation. In *sulcifer*, aggressive fighting generally leads to the expulsion or death of the host queen (SCHEVEN, 1958; DISTEFANO, 1969; TURILLAZZI *et al.*, 1990). Aggressive tactics, when invading hosts at low altitudes, may occur because the inquiline can afford to dispose of the host queen, and retain only individuals that contribute to the worker force (CERVO *et al.*, 1990b). The tactics of *semenowi* are also usually aggressive (SCHEVEN, 1958; CERVO *et al.*, 1990b; MEAD, 1991; ZACCHI *et al.*, 1996), but may be passive, with the host queen remaining on the nest (DEMOLIN & MARTIN, 1980). The tactics of *atrimandibularis* are variable. Initially it is passive, temporarily submissive when invading *biglumis* (CERVO *et al.*, 1990a), and the host queen of *biglumis* remains on the nest. When invading *gallicus* nests the host queen is expelled (CERVO *et al.*, 1992). But when invading colonies of *biglumis* later in the season *atrimandibularis* employs violent, fighting tactics (SCHEVEN, 1958). It also is more aggressive on the secondary nests that serve as food supply than on the primary nest (nursery nest) where brood is reared (CERVO *et al.*, 1990a). The tactical flexibility of *atrimandibularis* is thus correlated with characteristics of the invaded nest, such as number of foundresses present, length of colony cycle, and the point in the colony cycle where invasion occurs (CERVO *et al.*, 1990b; CERVO & DANI, 1996). The passive tactics of this inquiline may be considered unexpected in a generalist (*i.e.*, with several hosts; FISHER, 1984), but may be explained if *biglumis* is the original host of *atrimandibularis*, for which *atrimandibularis* has evolved specialized tactics (CERVO & DANI, 1996). Cohabitation of the inquiline and host queen may indicate an advanced form of parasitism, for example involving chemical control, or it may be a necessity if the inquiline is unable to inhibit ovarian development of host workers (CERVO & LORENZI, 1994), and so would be a less advanced type of parasitism.

The outstanding feature of the behavior of *atrimandibularis* is the ability to dominate more than one colony simultaneously (CERVO *et al.*, 1990c). Females of the other two species, once successfully established on a host nest, remain there, and depend entirely on the host workers to rear the parasite brood. Females of *atrimandibularis* engage in extensive extra-colonial activity, during which they usurp nests of the same host species, from which larvae and pupae are taken to the primary (nursery) nest and fed to the brood. This behavior occurs with either host species, and CERVO & DANI (1996) wonder whether it evolved originally on *biglumis* nests in response to the short colonial cycle of that species, due to a necessity for collaborating with host to increase fitness, or whether the behavior evolved independently of ecological conditions. This predatory behavior may represent a different pathway to obligate parasitism, for example as a form of cuckoo behavior, or it may be a secondary development, for example in response to reduced colony productivity in hosts (CARPENTER *et al.*, 1993).

Cladistic tests

Answers to questions such as those outlined in the preceding section require a cladistic context. The justification and a general framework for the use of phylogenetic information in evolutionary biology have been clearly stated by GRANDCOLAS *et al.* (1994). These authors outlined the correspondence between four types of phylogenetic patterns and the evolutionary processes that can be tested with these patterns. All are relevant to paper wasp inquilines, to greater or lesser degree, as will be seen.

The first correspondence concerns adaptation, which is tested by the phylogenetic pattern of polarity. That determining the direction of character change (polarity) is necessary to test whether a feature may be an adaptation is something that has long been understood by cladists (HENNIG, 1966; ELDREDGE & CRACRAFT, 1980). As formulated by CODDINGTON (1988, 1990), adaptation is apomorphic (derived) function, therefore the change from the primitive to the derived condition must be established. Direction of change is established by cladistic character optimization, or mapping onto a cladogram. I have applied optimization to the question of adaptation in various behavioral features in social wasps before (CARPENTER, 1987, 1988a; WENZEL & CARPENTER, 1994). In the present case, for example, the question whether the predatory behavior of *atrimandibularis* represents a novel pathway to inquilinism, or is secondary, is potentially answered by optimization showing the behavior to be ancestral, or derived.

The second correspondence concerns convergence, which is tested by the phylogenetic pattern of homology and homoplasy. Again, the pattern is established by optimization. Features shared by species and shown by optimization on a cladogram to be present in their common ancestor are most parsimoniously inferred to be homologous, that is, to have been inherited from their common ancestor (HENNIG, 1966). Convergence is demonstrated by homoplasy, that is, multiple independent occurrences of a feature on a cladogram. A pertinent example is inquiline behavior itself: is it homologous (CARPENTER *et al.*, 1993; CHOUDHARY *et al.*, 1994; CARPENTER, 1996a) or has it evolved as many as three times (WEST-EBERHARD, 1996)? If the most parsimonious optimization shows a single origin for this feature, arguments that it has evolved more than once are *ad hoc* (FARRIS, 1983), because there is then no positive evidence for multiple origins. Specifically, the claim that a behavior is "labile" and so prone to convergence is contradicted by showing that only a single origin is necessary to explain the evolution of that behavior.

The third correspondence is between evolutionary causality and relative phylogenetic appearance. Relations among features are often the object of study in comparative biology. The relative positions among two or more features shown by optimization on a cladogram may allow test of a causal relation. That is, the "time lag" (order of appearance) between origins of features may support or reject a suggested evolutionary progression based on the association of those features. I have previously applied this approach to testing a complex evolutionary scenario (CARPENTER, 1989, 1991, 1992). WEST-EBERHARD's (1978) model for the evolution of social behavior in wasps was tested by simultaneously optimizing the different behavioral features onto cladograms for social wasps. The relations among these features matched some of the stages in West-Eberhard's model, and did not correspond to others. In the case of the evolution of inquilines, a transition from intra- to interspecific usurpation and then obligate parasitism would correspond to part of TAYLOR's (1939) scenario.

The fourth correspondence is between adaptive radiation and differential cladogenesis. A feature suggested to promote diversification may be optimized onto a cladogram, and the relative diversity of sister-groups compared. If the feature in question is ancestral to the larger of two sister-groups, diversification occurred after the origin of the feature, according with the suggestion of adaptive radiation. In the case of social parasites, the question is whether inquiline behavior is associated with increased speciation.

All these questions on the evolution of social parasitism may thus be approached by cladistic optimization. What is required is a cladogram for the taxa in question, and knowledge of the distribution of behavioral features. This raises however the question as to the proper treatment of these features. Specifically, should the behavioral data be used during construction of the cladogram, or should they be optimized onto a cladogram constructed independently? That is, would inclusion of these features during cladistic analysis lead to bias or circularity (BROOKS & MCLENNAN, 1991)? KLUGE & WOLF (1993) have argued strongly that features to be interpreted phylogenetically should be used as evidence when inferring phylogeny, and behavioral and ecological features have indeed been treated successfully as characters, that is, as evidence of phylogenetic relationships (reviews in WENZEL, 1992; MILLER & WENZEL, 1995). DELEPORTE (1993) has pointed out that circularity is avoided as long as the cladogram is independent of the evolutionary hypothesis to be tested, not of the characters used. That is, the question is not choice of characters, rather it is the rationale that has been used to code the characters. Character polarity determined by the cladistic outgroup criterion is independent of hypotheses of direction of change according to an evolutionary model.

But some features are not typically treated as characters. As MICKEVICH & WELLER (1990: 139) put it: "Certain features of organisms are influenced by a large environmental component. The features influenced by environmental factors provide doubtful evidence for phylogenetic relationships". MICKEVICH & WELLER (1990), DELEPORTE (1993) and GRANDCOLAS *et al.* (1994) referred to such features as "attributes" and distinguished them from characters. Attributes are to be interpreted by optimization, rather than used in constructing cladograms. GRANDCOLAS (1993) considered attributes to be features for which a priori homology statements are so problematic that interpretation with reference to a pre-existing phylogeny is preferable. DELEPORTE (1993) and GRANDCOLAS *et al.* (1994) applied DE PINNA's (1991) distinction between primary and secondary homology, suggesting that cladogram construction proceeds only with characters, whose primary (*a priori*) homology may be confidently assessed, while attributes be interpreted, with homology assessed by optimization (secondary homology). However, the distinction between primary and secondary homology should not be maintained dogmatically, because the process of reciprocal illumination ("checking, correcting and rechecking," HENNIG, 1966) is an integral part of cladistics, and the critical test of homology is congruence with other characters. I suggest that logical justification for excluding some features from cladogram construction comes in the distinction between "traits" and characters made by NIXON & WHEELER (1990: 217). These authors defined traits as "attributes that are not universally distributed among comparable individuals within a terminal lineage" and characters as "found in all comparable individuals in a terminal lineage". In this terminology, traits are features that are variably distributed within any grouping (population, species or higher taxon) that is phylogenetically unresolved internally. So for example, features that vary within the genus *Polistes*, such as male clypeal ridges, would be considered traits when the genus *Polistes* is viewed a single terminal lineage. This same feature might diagnose a monophyletic group, and therefore be viewed as a character, if analysis of species within the genus is undertaken. Variable features within populations do not meet the constancy criterion for phylogenetically informative characters. Species are the terminal lineages that are phylogenetically unresolved by definition, because they consist of populations linked by tokogenetic (birth) relationships, to which cladistic analysis is not applicable. Features variable within species are therefore traits by definition. Traits only become phylogenetically informative when they become fixed in comparable semaphoronts (NIXON & WHEELER, 1990; DAVIS & NIXON, 1992), which at the level of species occurs by extinction of plesiomorphic states, that is, at speciation (NIXON & WHEELER, 1992). Features variable within species are precisely those for which *a priori* homology assessment is (by definition) problematic, and such traits should not be used to infer phylogenetic relationships.

To the extent, then, that the behavioral features associated with social parasitism in paper wasps are variable within species, they are best treated as traits. Evolutionary interpretation may be made by optimization on a pre-existing cladogram. Methodologically, the approach taken here will treat all the behavioral features as traits. It will be seen, however, that there are reasons for considering some of these features to be phylogenetically informative characters.

MATERIALS AND METHODS

Taxonomy

Some discussion of taxonomy is first warranted. The nomenclatural history of the European species of *Polistes* is quite tangled (Table 2). Nine species are currently recognized (see CARPENTER, 1996b), but four have been described within the past 100 years, and five have gone under more than one name in this century. The type species of the genus, *gallicus*, was misidentified in the revision by Kohl (1898), and this was followed by other authors until Day (1979). As a result, the older behavioral literature used the name *gallicus* (or *gallica*) for what is now known as *dominulus*, and *foederata* for what is now known as *gallicus*, including the landmark papers of Pardi (*e.g.* 1942), which first demonstrated dominance hierarchies in social insects. Numerous subspecies have also been described, but none are more than minor color variants, which do not deserve taxonomic recognition (Carpenter, 1996b, and see MacLean *et al.*, 1978; Gusenleitner, 1985; and below).

This nomenclatural instability has had its counterpart in the higher-level taxonomy of these species (Carpenter, 1996a). The distinctiveness of the social parasites was recognized on the basis of morphology before their behavior was known (Zimmermann, 1930). Discovery of social parasitism led to the generic separation of these three species - under two different names, first, but invalidly, as *Pseudopolistes* (Weyrauch, 1937) and then as *Sulcopolistes* (first as a subgenus, Blüthgen, 1938; then as a genus, Blüthgen, 1943). The latter name was generally used until I (Carpenter, 1990, 1991, 1996a; van der Vecht & Carpenter, 1990; Carpenter *et al.*, 1993) synonymized it with *Polistes*, on the grounds that recognition of *Sulcopolistes* rendered *Polistes* paraphyletic. Other generic (*Polistula*: Weyrauch, 1938) and subgeneric (*Leptopolistes*: Blüthgen, 1943) names have been proposed for the remaining European species, although they have not always been accepted (Richards, 1973). The misidentification of the type species of *Polistes* means that these other names are synonyms in any event. All of the European species, including the social parasites, are now placed in the subgenus *Polistes*

Table 2. — Taxonomic history of European *Polistes* species.

Author	Currently recognized species				
	biglumis	*dominulus*	*nimphus*	*gallicus*	*associus*
Saussure (1853)	*biglumis*			*gallica*	
Kohl (1898)	*dubia*	*gallica*	*opinabilis*	*foederata*	*associa*
Zimmermann (1930)	*dubia*	*gallica*	*opinabilis*	*foederata*	*chinensis*
Weyrauch (1937)	*dubia*	*gallica*	*opinabilis*	*foederata*	*chinensis* *associa*
Blüthgen (1938)	*kohli*	*gallicus*	*nimpha*	*foederatus*	*associus*
Weyrauch (1938)	*kohli*	*gallica*	*opinabilis*	*foederata*, *omissa*	*associa*
Weyrauch (1939)	*kohli*	*gallica*	*nympha*	*foederata*, *omissa*	*associa*
Blüthgen (1943)	*bimaculatus*	*gallicus*	*nimpha*	*foederatus*, *omissus*	*associus*
Blüthgen (1955)	*biglumis* *bimaculatus*				
Day (1979)		*dominulus*		*gallicus*	
Gusenleitner (1985)				*gallicus*	

Author	Currently recognized species			
	bischoffi	*semenowi*	*sulcifer*	*atrimandibularis*
Saussure (1853)				
Kohl (1898)		*semenowi*		
Zimmermann (1930)		*semenowi*	*sulcifer*	*atrimandibularis*
Weyrauch (1937)	*bischoffi*	*semenowi*	*sulcifer*	*atrimandibularis*
Blüthgen (1938)		*semenowi*	*sulcifer*	
Weyrauch (1938)	*bischoffi*	*semenowi*	*sulcifer*	*atrimandibularis*
Weyrauch (1939)	*bischoffi*	*semenovi*	*sulcifer*	*atrimandibularis*
Blüthgen (1943)	*bischoffi*	*semenowi*	*sulcifer*	*atrimandibularis*

sensu stricto (Carpenter, 1996a, 1996b). *Polistes* is the sole member of the tribe Polistini (Carpenter, 1993), which is the sister-group of the other Polistinae (Carpenter, 1991, 1993).

Morphological characters

Morphological characters for the European species of *Polistes*, and two outgroup species, are presented in Tables 3-4. Morphological terminology is as in Carpenter (1996a). All species were examined, including dissection of male specimens for study of genitalia. The literature was surveyed for characters to be examined, in particular keys, both published (*e.g.* Guiglia, 1972) and unpublished (Starr & Luchetti, 1993). These keys, however, are largely based on color characters, which may work well for identification in a limited part of a species' range, but generally show considerable variation over the entire range of widespread species. That was found to be true for the species studied here, particularly when material from, *e.g.*, Western Europe was compared to material from Scandinavia or Turkey. Color variation was therefore concluded to be microenvironmentally induced (see MacLean *et al.*, 1978), and was not included. Some of the morphological characters discussed in the literature were also found to be more continuously variable than implied by their inclusion in keys (for example, the characters used to separate *foederatus* and *omissus*, both now considered synonyms). The character states listed in Table 4 are those that could be consistently distinguished. Additivity of multistate characters was determined from observed nested similarity.

Tables 3-4 also include characters establishing monophyly of the ingroup, namely those establishing monophyly of the subgenus *Polistes sensu stricto* relative to the outgroups, both of which are species in the New World subgenus

Table 3. — Morphological characters for European *Polistes* species, and two outgroups. Multistate characters are treated as additive except for character 18. See Table 4 for Matrix.

1. Male antennae: tapered (0); coiled (1). This is a synapomorphy for the subgenus *Polistes sensu stricto* in Carpenter (1996a).
2. Male antennal apex: rounded (0); pointed (1). A number of other distinctions in shape of the terminal article of the male antenna have been made since the time of Kohl (1898), but do not appear to be tenable.
3. Scape: cylindrical (0); dorsobasally flattened (1).
4. Male interantennal ridge: raised (0); grooved (1).
5. Clypeal apex: convex (0); angular (1); broadly depressed (2). Depression of the clypeal apex diagnoses the inquilines, and is variable among the species, being more extreme in *sulcifer*.
6. Male clypeal rim: smooth (0); angulate rim (1). Interpretation of this character is complicated: it appears to be derived within the genus *Polistes* as a whole, in the European species, but then appears to have been lost in the group of species related to *gallicus* (see Fig. 3).
7. Male clypeal ridges: absent (0); present (1); extending to clypeal apex (2). The angulate, black rimmed margin of the clypeus seems to be an exaggeration of slight swellings commonly seen in males of the subgenus *Polistes sensu stricto*, and fully developed ridges are seen in some of the non-European species.
8. Male clypeal punctation: weak (0); macropunctures (1).
9. Male clypeal proportions: width > length to width = length (0); length > width (1). As the coding indicates, this character shows some continuous variation, which does not seem to lend itself to further partitioning.
10. Malar space: gena tapering (0); gena quadrate (1). The enlarged malar space is diagnostic of the inquilines.
11. Mandible: smooth (0); shallow groove (1); ridges pronounced (2); deeply grooved (3). Excavation of the external surface of the mandible is diagnostic of the inquilines, and is variable among the species, showing a morphocline in development. The groove is shallow in *atrimandibularis*, and *semenowi* and *sulcifer* are more similar to one another in having more perpendicular ridges, which are greatly exaggerated in *sulcifer*.
12. Male occiput: convex (0); straight (1). Temples convergent backwards is supposed to diagnose the species formerly placed in *Leptopolistes* (*viz.*, *associus*, *bischoffi* and *gallicus non auct.*) - but is found in non-European species of the subgenus *Polistes sensu stricto*.
13. Mesepisternal punctation: fine (0); clathrate (1). This is a synapomorphy for the subgenus *Polistes sensu stricto* in Carpenter (1996a).
14. Epicnemial carina: absent (0); present (1). This is a synapomorphy for the subgenus *Polistes sensu stricto* in Carpenter (1996a). However, it is reduced to traces in *bischoffi*.
15. Scutal hairs: short (0); elongate, much longer than an ocellus diameter (1). This character appears to vary, but some of this variation is evidently due to specimen wear.
16. Parameral spine: straight (0); lobed (1).
17. Aedeagal teeth: fine (0); robust (1).
18. Aedeagus medial lobes: small, sharp (0); large (1); square (2); pointed (3).

TABLE 4. — Morphological characters for European *Polistes* species, and two outgroups. Multistate characters are treated as additive except for character 18.

	111111111
Taxon	123456789012345678
exclamans	000000000000000111
dorsalis	000000000000000000
biglumis	101101000000111111
dominulus	111101010000110111
nimphus	101101100000110111
gallicus	101100101001110113
sulcifer	101121000130110112
atrimandibularis	101111010110110111
semenowi	101111000120110111
associus	101100201001110111
bischoffi	101100101001101111

Aphanilopterus, sister-group of *Polistes sensu stricto* (CARPENTER, 1996a). The two outgroup species included, *dorsalis* and *exclamans*, were selected because they were used in both the molecular analyses (CARPENTER *et al.*, 1993; CHOUDHARY *et al.*, 1994).

Cladistic Procedures

Cladistic analysis (HENNIG, 1966) was implemented with the computer program Nona (GOLOBOFF, 1996a). As pointed out elsewhere (CODDINGTON & SCHARFF, 1994; CARPENTER, 1996a), Nona implements a more stringent requirement for cladogram support than other available programs: cladograms are only reported if every branch is supported by all possible optimizations of at least one character. Programs such as Hennig86 (FARRIS, 1988) report cladograms with branches supported only by one of several possible optimizations for at least one character. Such optimizations can lead to the program reporting cladograms that are not in fact supported by the data, with branches supported by optimizations that cannot simultaneously coexist with other branches (examples are given in LORENZEN & SIEG, 1991; CODDINGTON & SCHARFF, 1994; WILKINSON, 1995; CARPENTER, 1996), even without missing values, which can also produce this misleading result (PLATNICK *et al.*, 1991). CODDINGTON & SCHARFF (1994) argued that branches supported only under some optimizations are desirable, but such "semistrict" support is at best ambiguous, if not misleading (NIXON & CARPENTER, 1996b).

The Nona program's implementation of "strict" support (NIXON & CARPENTER, 1996b) is incomplete, because the program does not optimize on multifurcations. Hence, it does not necessarily collapse all ambiguously supported branches. Several methods of collapsing such branches may be implemented with current programs (NIXON & CARPENTER, 1996b); with Nona, use of the "ksv" command to save cladograms in collapsed form, reading them back into Nona, and issuing the "best" command will filter out semistrict support. That method is employed here. Output from Hennig86 is also reported, for comparison. For both programs, exact calculations were made, using either the "mswap" command of Nona or the "ie" command of Hennig86.

Character weighting was employed as a check of the reliability of the results, both successive weighting as implemented in Hennig86, and implied weighting as implemented in the program Piwe (GOLOBOFF, 1996b). *A posteriori*, recursive character weighting checks the self-consistency of results: a cladogram based on reliable characters should imply weights that imply the same cladogram (see CARPENTER, 1988b, 1994; CARPENTER *et al.*, 1993).

In the simultaneous analyses of the morphological characters, allozymes and mtDNA sequences, the allozyme data were taken from tables 2-4 of CARPENTER *et al.* (1993), while the mtDNA data of CHOUDHARY *et al.* (1994) were provided by J. E. STRASSMANN. CHOUDHARY *et al.* (1994) reported 79 polymorphic sites, of which 55 were potentially informative, out of 386 sites sequenced. Their aligned sequences were converted to files for analysis by Nona and Hennig86 by the program Malign (WHEELER & GLADSTEIN, 1995); due to differences in interpretation of ambiguity codes, this resulted in 93 polymorphic sites (of which 43 were informative). This difference was irrelevant to the results, as analysis produced the same two cladograms reported by CHOUDHARY *et al.* (1994). The program Dada (NIXON, 1995a) was used to calculate the incongruence length difference (FARRIS *et al.*, 1994) among the character sets, and to determine whether these values were large, by performing the significance test of FARRIS *et al.* (1994). For the tests, 100 iterations were made using Hennig86 for cladogram calculations on the random matrix partitions.

Optimizations of the behavioral traits listed in the following section were calculated with the program Clados (NIXON, 1995b), which was also used to print results. The "allstates" command was used to check all possible optimizations at each node of the cladograms.

Behavioral Traits

Behavioral traits pertinent to social parasitism are listed in Table 5. These traits or attributes were compared among social parasites and their hosts in the discussions of the evolution of social parasitism by CERVO *et al.* (1990b) and CERVO & DANI (1996). As the scorings in Table 6 show, all of the variables are variable within species, aside from colony cycle length (which is known to vary intraspecifically; YAMANE, 1996). The questions that I will attempt to answer by optimization are stated for each trait below.

TABLE 5. — Behavioral traits for European *Polistes* species, related to social parasitism. Multistate trait 4 is treated as nonadditive. See Table 6 for Matrix.

1. FOUNDATION: haplometrosis (0); pleometrosis (1).
2. CYCLE LENGTH: long (0); short (1).
3. USURPATION: intraspecific (0); interspecific (1).
4. INQUILINISM: absent (0); parasitism (1); predation (2).
5. TIMING: pre-emergence (0); post-emergence (1).
6. USURPATION TACTICS: aggressive (0); passive (1).

TABLE 6. — Matrix of behavioral traits for European *Polistes* species, related to social parasitism. Multistate trait 4 is treated as nonadditive. A question mark denotes an unknown state, while a dash denotes an inapplicable trait. A asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism (1,2 for *atrimandibularis*). See Table 5 for list of traits.

Taxon	123456
exclamans	*00000
dorsalis	*0?0--
biglumis	010000
dominulus	10*000
nimphus	10*000
gallicus	000000
sulcifer	--11*0
atrimandibularis	--1$01
semenowi	--11**
associus	???0--
bischoffi	???0--

Colony foundation. Whether exclusively haplometrotic or also pleometrotic. The relation of this to origin of obligate parasitism is of interest (BUSCHINGER, 1986, 1990; CARPENTER *et al.*, 1993). As noted in CERVO & DANI (1996), while intraspecific usurpation occurs both in colonies with nest foundation by a single female (haplometrosis) and with multiple foundresses (pleometrosis), usurpation is less successful in pleometrotic colonies. Scorings for the outgroups, which are polymorphic, are drawn from the following references: for *dorsalis*, SPIETH (1948, cited as *fuscatus hunteri*), and STRASSMANN (pers. com.); for *exclamans*, STRASSMANN (1981). Note that even *biglumis* exhibits pleometrosis occasionally (LORENZI &

TURILLAZZI, 1986), although that is not scored here. The question is: did inquiline behavior originate in haplometrotic or pleometrotic ancestors?

Colony cycle length. Whether long or short. Factors influencing the extensive variation in this trait were reviewed by Yamane (1996). Is a short colony cycle derived, the minimal requirement for interpretation as an adaptation?

Usurpation. Whether it is intraspecific or interspecific. See CERVO & DANI (1996: table 5.1), for a list of *Polistes* species in which intraspecific usurpation has been reported. They also reported (CERVO & DANI, 1996: 104) observing two cases of interspecific usurpation in *dominulus*, and CERVO (pers. com.) has recently observed the phenomenon in *nimphus*. These two species are therefore scored as polymorphic. Is interspecific usurpation derived from intraspecific usurpation?

Inquilinism. Whether it is absent or present, and whether it is accompanied by predation. Unlike the other behavioral features discussed here, inquiline behavior as such does not show intraspecific variation. It is constant, and so may be treated as a character. WEST-EBERHARD (1996) nevertheless argued that it may have arisen in all three socially parasitic species independently, whether they form a monophyletic group or not. That is *ad hoc*, as pointed out above. But whether or not the predatory behavior of *atrimandibularis* is primitive or derived is a question of interest, and that behavior is found within one species, which also exhibits parasitic behavior like the other two inquilines. The feature is therefore treated as a trait, polymorphic for both parasitism and predation in *atrimandibularis*. What is the association between origin of inquilinism and transitions in usurpation?

Timing of invasion. Whether pre-emergence or post-emergence. Is the early timing of invasion by *atrimandibularis* derived, the minimal requirement for interpretation as an adaptation?

Usurpation tactics. Whether aggressive or initially passive. The scoring includes polymorphism within *semenowi*, which in one case has been observed to show passive tactics (DEMOLIN & MARTIN, 1980). Are the initially submissive tactics of *atrimandibularis* derived, the minimal requirement for interpretation as an adaptation?

RESULTS

Morphology

Analysis of the data in Tables 3-4 with Nona (using "ms 8") resulted in two cladograms; with Hennig86, 12 cladograms were reported. The length is 28, the consistency index is 0.85 and retention index is 0.84 (see FARRIS, 1989, for definition of the indices). The consensus tree for either set of cladograms is shown in Fig. 3; this tree shows the groups in common to all of the cladograms (such consensus trees are also referred to as "Nelson" or "strict"). Implied weighting, using the default weighting function of Piwe, resulted in the same two cladograms as reported by Nona. Successive weighting on the 12 cladograms reported by Hennig86 resulted in a report of six cladograms; their consensus is also Fig. 3.

The morphological characters do not completely resolve the interrelationships among the European species, as is the case with the two published molecular data sets. However, the morphological data do resolve interrelationships among the three socially parasitic species, unlike the molecular data sets. The morphological data set also allowed inclusion of all the European species, again unlike the molecular data sets, which could not include *associus* and *bischoffi*. This demonstrates that *gallicus* and *biglumis* are in fact not closely related. These two species were resolved as sister-groups by the mtDNA data and the independent allele coding of the allozyme data. The morphological characters show that *associus* and *bischoffi* are more closely related to *gallicus*.

Simultaneous analyses

None of the three available data sets completely resolves the interrelationships of the European species, but the combination of the three matrices does so. Simultaneous analysis of combined data, which has been called "total evidence" (KLUGE, 1989) is currently controversial in cladistics, with some authors arguing against combining data sets (*e.g.* BULL *et al.*, 1993; DE QUEIROZ, 1993; MIYAMOTO & FITCH, 1995). All such arguments are without force, as discussed in NIXON & CARPENTER (1996a). And a decisive argument justifies combining data sets

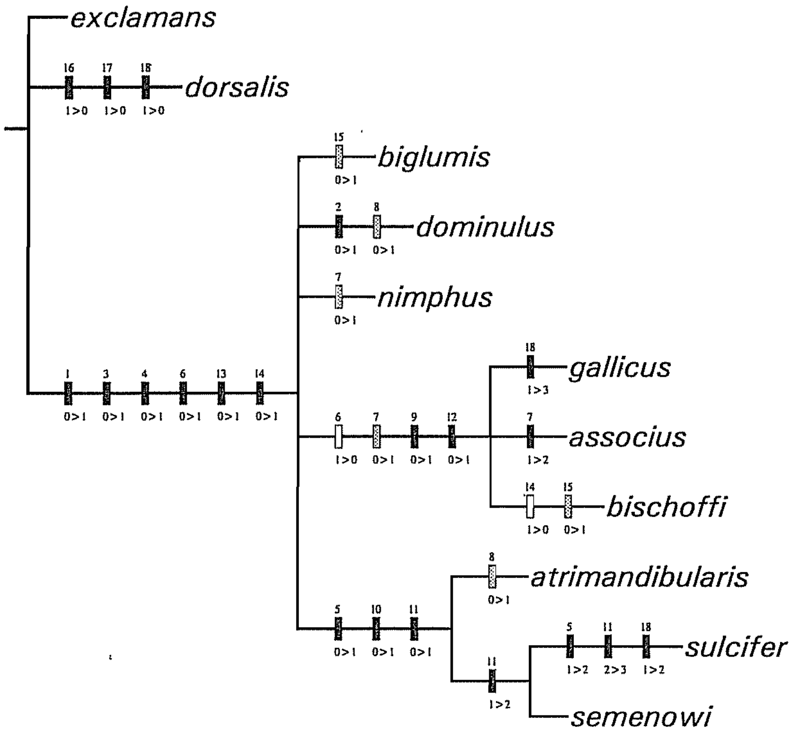


FIG. 3. — Consensus tree for cladograms reported after exact analysis of the character matrix in Table 4, by either Nona or Hennig86. This is also the consensus for the six cladograms resulting from successive weighting by Hennig86. Characters have been optimized by the default, "slow" transformation as implemented in Clados. Character numbers are above the hashmarks; state changes are shown below, with the respective primitive and derived conditions separated by a ">". Filled hashmarks denote unique origins, grayscaled hashmarks indicate convergent changes, and open hashmarks are reversals.

and determining the most parsimonious solution for all the data seeks the cladogram that is best supported and maximally explanatory for all the data. This approach maximizes information content and corroboration of the resulting hypothesis.

The morphological data from Tables 3-4 were combined with the allozyme data from CARPENTER *et al.* (1993) and the mtDNA data from CHOUDHARY *et al.* (1994). Three separate analyses of the combined morphological and molecular data were undertaken, corresponding to the three different coding schemes for the allozymes presented by CARPENTER *et al.* (1993: tables 2-4). The same cladogram resulted from analysis with Nona regardless of the allozyme coding scheme employed; it is shown in Fig. 4. This cladogram also resulted from implied weighting with Piwe. Hennig86 reported three cladograms regardless of which allozyme coding scheme was employed; these cladograms were stable to successive weighting. The consensus of the three cladograms is also Fig. 4. The three cladograms differed only in resolving relationships among *gallicus*, *associus* and *bischoffi*, based entirely on the possible optimizations for the numerous missing values found in the latter two species, hence three cladograms are not actually supported by the data.

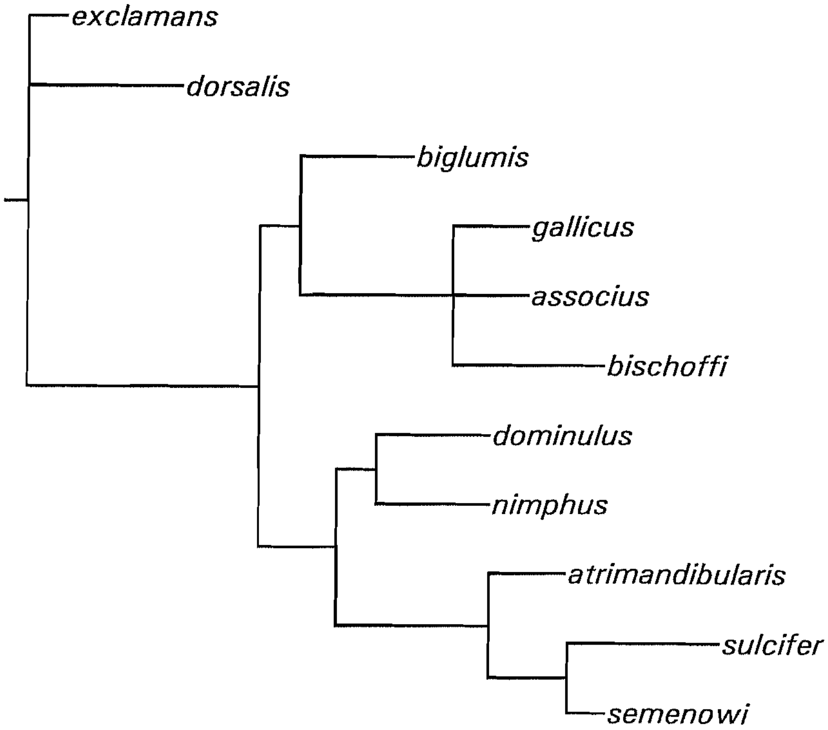


FIG. 4. — Cladogram resulting from simultaneous analysis of morphological and molecular data.

For the independent alleles coding from CARPENTER *et al.* (1993: table 2), analysis of 220 characters resulted in Fig. 4 with a length of 271, consistency index 0.83 and retention index 0.72. For the multistate locus coding from CARPENTER *et al.* (1993: table 3), analysis of 138 characters resulted in Fig. 4 with a length of 222, consistency index 0.90 and retention index 0.81. For the minimum turnover coding from CARPENTER *et al.* (1993: table 4), analysis of 148 characters resulted in Fig. 4 with a length of 229, consistency index 0.87 and retention index 0.77.

The results from incongruence length difference testing are as follows. For the independent alleles coding, the incongruence length difference is 3, and the percentage of 100 iterations reported by Dada as equaling or exceeding that value is 37. For the multistate locus coding, the incongruence length difference is 1, and the percentage of 100 iterations reported by Dada as equaling or exceeding that value is 83. For the minimum turnover coding, the incongruence length difference is 2, and the percentage of 100 iterations reported by Dada as equaling or exceeding that value is 75. The null hypothesis of congruence accordingly fails rejection by quite large margins for any combination of morphology, mtDNA and allozyme coding.

Optimizations

Optimization of the behavioral traits is shown in Figs 5-14. Changes are shown by hashmarks on the branches of the cladograms. All of the traits are mapped in Figs 5-6, which show two different, equally parsimonious optimizations. In Fig. 5, the traits are mapped

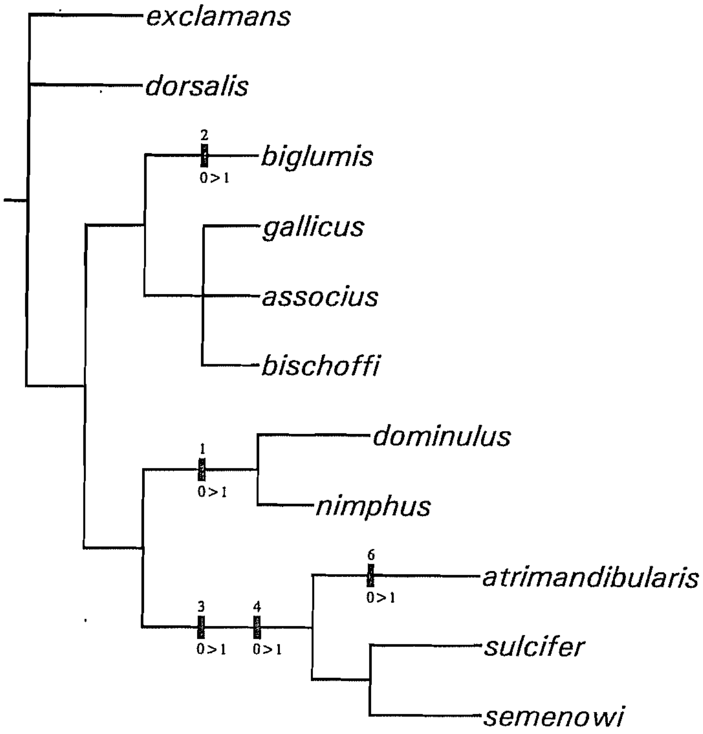


FIG. 5. — Cladogram showing optimization of behavioral traits related to social parasitism. The default, slow optimization, is shown. Plotting conventions as in Fig. 3.

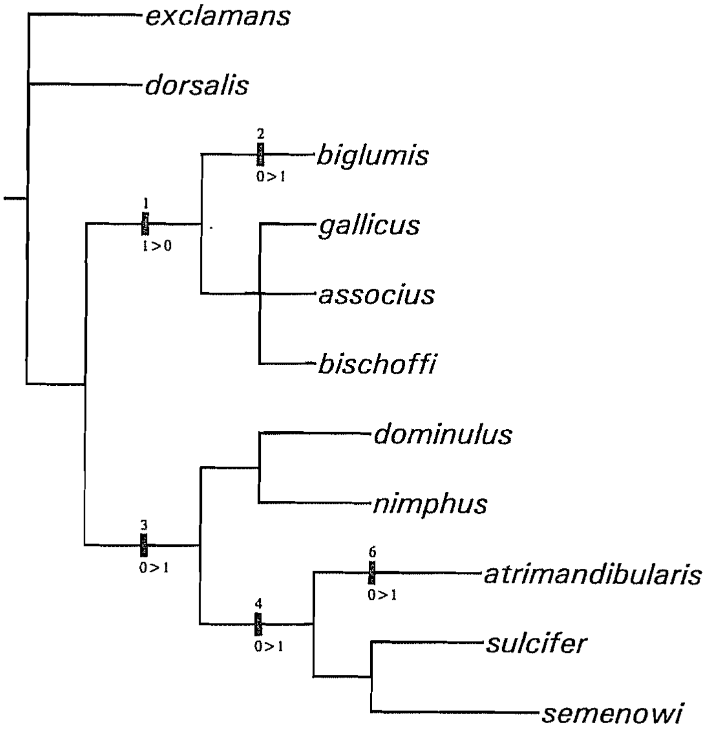


FIG. 6. — Cladogram showing alternative, equally parsimonious "fast" optimization. Plotting conventions as in Fig. 3.

according to the default optimization in Clados, "slow" transformation, which places changes toward the tips of the cladogram. This procedure is similar to delayed transformation (or "deltran", *e.g.* SWOFFORD & MADDISON, 1987). In Fig. 6, the traits are mapped according to the alternative, "fast" transformation of Clados, which places changes toward the root of the cladogram. This procedure is similar to accelerated transformation (or "acctran", SWOFFORD & MADDISON, 1987).

Optimization of the first trait, whether colony foundation is haplometrotic or pleometrotic, is ambiguous, and its placement is one difference among the two figures. The reason for this ambiguity is shown in Figs. 7-8, which show two possible placements for this trait. Because the trait is polymorphic in both of the outgroups, either state may be assigned to the common ancestor of the ingroup. Moreover, because the trait is inapplicable to the social parasites (which do not have colony foundation behavior), the optimization procedures, which treat inapplicable values as missing data, consider either state possible for them, and so the step in this trait could even be assigned to the common ancestor of the social parasites and their sister-group, *dominulus* + *nimphus*. The "squeeze missing data" optimization of Clados, which places changes so that the fewest number of taxa with missing values are included above the step, may be used to filter out such possibilities.

One other trait shows a similar difference in placement according to optimization: usurpation, whether it is intraspecific or interspecific. Figs 10-11 show the alternative slow and fast optimizations. Because the trait is polymorphic in *dominulus* and *nimphus*, either state can be assigned to their common ancestor, and thus to the common ancestor of the social parasites and their sister-group.

Mapping of the other four traits is the same regardless of the optimization procedure. Optimizations of the individual traits are shown in Figs 9 and 12-14. Fig. 13 shows no changes in timing of invasion. This trait is polymorphic in *sulcifer* and *semenowi*, therefore the only changes are parsimoniously placed within terminal lineages. Such changes are not mapped by Clados.

DISCUSSION

The social parasites in *Polistes* form a monophyletic group. They are thus not most closely related to any of their hosts, and EMERY's Rule is rejected. Both the morphological characters analyzed in this paper and mtDNA data (CHOUDHARY *et al.*, 1994) establish monophyly unequivocally, and combination of these data with allozyme data (CARPENTER *et al.*, 1993) lead to the same result. EMERY's Rule having been dispensed with, arguments that sympatric speciation was involved in the origin of the inquilines from their hosts are rendered moot in paper wasps.

This conclusion raises the issue of whether the inquiline behavior arose once, or several times. The parsimonious optimization of this behavior (Fig. 12) indicates a single origin. WEST-EBERHARD (1996) argued for the possibility of multiple origins despite monophyly of the inquilines. There is no evidence for this, but WEST-EBERHARD (1996: 315) stated: "The law of parsimony requires attributing the common features of a monophyletic group to their common ancestry only in the absence of biological evidence to the contrary. The evolutionary lability of facultative traits, and their propensity to reversals within a lineage as well as to rapid and parallel

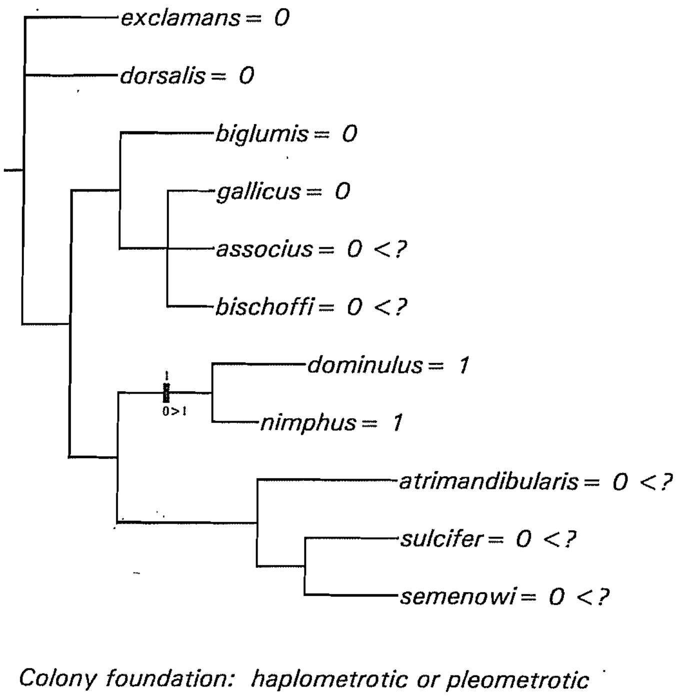


FIG. 7. — Cladogram showing slow optimization of colony foundation. Plotting conventions as in Fig. 3. States of each taxon are shown next to the taxon name, separated by an "=" sign. For taxa with unknown or inapplicable values, the state possible according to the optimization procedure is shown, with "< ?" written next to the state to indicate that the value is actually missing.

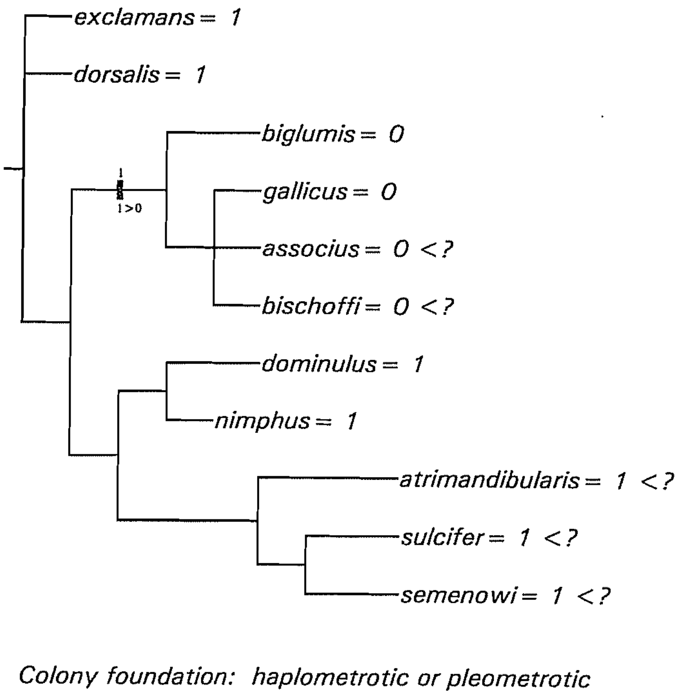


FIG. 8. — Cladogram showing fast optimization of colony foundation.

fixation in related species give reason at least to consider the possibility of multiple fixations of obligate parasitism in *Polistes*. Evolutionary lability of conditionally expressed traits means that it may sometimes be impossible confidently to track character "fixation" points using cladistics methods, because the character can come and go (change polarity) and rapidly become fixed rather than optional *between* the branching points of a cladogram (see also FRUMHOFF & REEVE 1994)".

Several points may be made to counter this argument. WEST-EBERHARD considered inquiline behavior to be evolutionarily labile. It is not: the social parasites are fixed for this feature; it does not vary in its expression within the species, nor is it found in other species. This observation also indicates the weakness in the argument of FRUMHOFF & REEVE (1994) cited by WEST-EBERHARD. FRUMHOFF & REEVE concocted a probabilistic model to show that inference of ancestral character states by optimization is highly error-prone. Their model may be rejected immediately as unrealistic (see general argument in FARRIS, 1983), but even if their approach is accepted, FRUMHOFF & REEVE failed to realize that observation of fixation for a character in a clade provides information on the evolutionary rate of change (SCHULTZ *et al.*, 1996), and specifically against the conclusion that a character has undergone a large amount of change. FRUMHOFF AND REEVE's argument is thus generally irrelevant to accuracy of ancestral conditions as inferred by optimization (SCHULTZ *et al.*, 1996).

Because inquilinism is not evolutionarily labile, there is no reason to entertain the *ad hoc* notion that it has arisen in parallel within a monophyletic group. Social parasitism indeed evidently arose from intraspecific usurpation (Figs 5-6, and see below), which may be considered a "phenotypic alternative" to independent nesting (WEST-EBERHARD, 1996). Even so, inquiline behavior became fixed at some point, and there is no necessity to postulate that event occurring more than once. Inquilinism is in this view really a character, providing evidence that the species showing the feature form a monophyletic group. This conclusion also applies to the morphological characters of the social parasites. The depressed clypeal apex, quadrate malar space and grooved mandible shared by the parasites are interpreted as synapomorphies in Figs. 3-4. These characters might be dismissed as evidence of phylogenetic relationship because they are considered to be adaptations to parasitism, involved in domination of the host during usurpation. WEST-EBERHARD (1996: 316) referred to these characters as "morphological accoutrements of parasitism" and suggests that in the inquilines these characters: "should not, of course, be taken as evidence that obligatory parasitism occurred prior to their speciation since these characteristics can be convergent (or parallel) developments".

Whether these features arose as adaptations or not, they became fixed, constant in distribution, restricted to the inquilines and occurring in no other species. These characters show no geographic variation whatsoever, contrary to the prediction of WEST-EBERHARD (1996: 313). There is no necessity for supposing this fixation to have occurred more than once, because the inquilines are a monophyletic group, as established by both morphology and molecular data (Fig. 4). Moreover, two of the characters show transformation series. The depression of the clypeal apex evidently evolved from slightly to broadly flattened (character 5 on Fig. 3), and the mandibular groove evidently changed from shallow to having pronounced ridges, to being deep

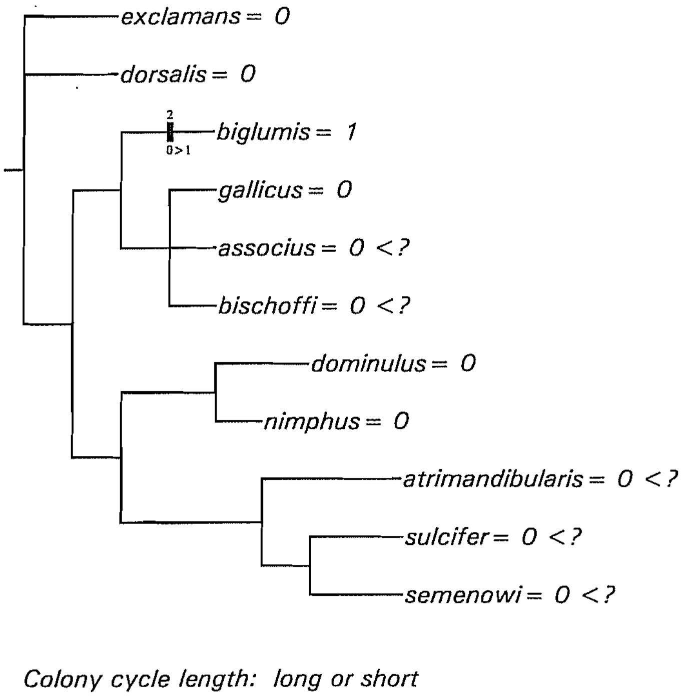


FIG. 9. — Cladogram showing optimization of colony cycle length.

(character 11 on Fig. 3). These transformations occurred as the inquilines speciated, and indicate that the common ancestor had the morphological accoutrements of parasitism. Therefore, presumably, it also had inquiline behavior.

The optimizations in Figs. 5-6 accord with the central idea underlying Taylor's (1939) scenario, but do not support the scenario as a whole. Interspecific usurpation evidently evolved from intraspecific usurpation (Figs 10-11). Intraspecific usurpation in *Polistes* is facultative and temporary (stage 1 in Taylor's scenario), and preceded the obligate and permanent usurpation of the inquilines (stage 4 in the scenario). But is unclear whether facultative and temporary interspecific usurpation preceded inquiline behavior. Temporary interspecific usurpation has been reported as a facultative behavior extremely rarely, but does occur in the sister-group to the social parasites (*dominulus* + *nimphus*). The optimization of this behavior is therefore ambiguous: inquiline behavior could have evolved directly from intraspecific usurpation (Fig. 10) or via an intervening stage of temporary interspecific usurpation (Fig. 11), which corresponds to stage 2 in the scenario.

In either case, the other stage in Taylor's scenario, which is obligate and temporary interspecific usurpation, does not correspond to the behavioral changes shown in Figs 5-6. Interspecific usurpation is either facultative and temporary, or obligate and permanent. Indeed, temporary interspecific usurpation has not been observed as obligate behavior. West-Eberhard (1996: 313) suggested: "In *Polistes* temporary obligate social parasitism, in which the usurper produces some worker offspring of her own, is expected to be rare or absent if [...] obligate (interspecific) parasitism originates in extreme climates with short nesting seasons, and invasion

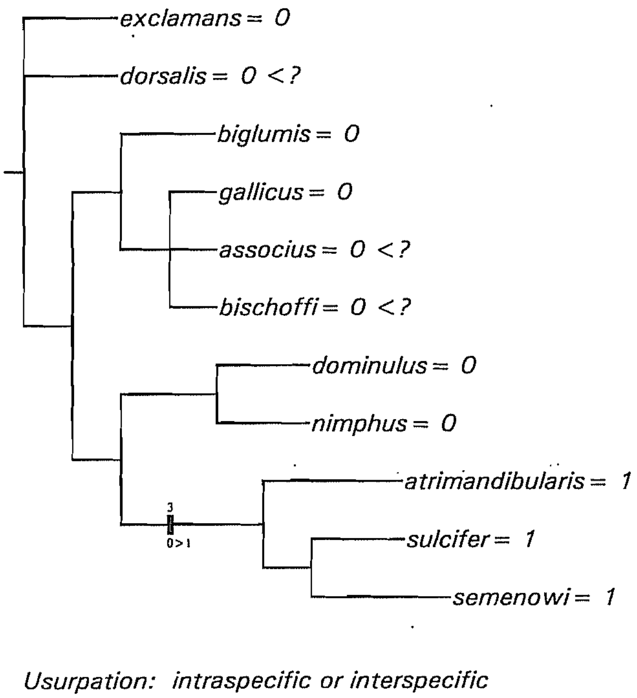


FIG. 10. — Cladogram showing slow optimization of usurpation.

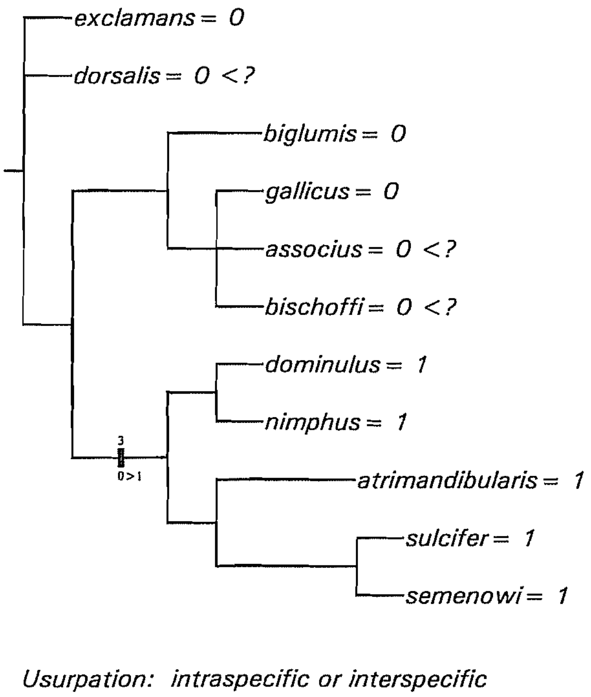


FIG. 11. — Cladogram showing fast optimization of usurpation.

occurs at about the time of first worker emergence [...] At that time temperate-zone *Polistes* females are already beginning to lay reproductive-producing eggs [...] Usurpers in such a species would soon produce reproductive offspring, not workers, and "temporary" parasitism may seldom occur". WEST-EBERHARD (1996: 314) concluded: "Temporary parasitism is not a necessary step in the transition from facultative to obligatory parasitism. Nor is facultative interspecific parasitism expected to be common [...] it may occur only when usurpers are running out of conspecific host colonies in a population where usurpation is the most frequently productive option – a transient situation expected to change rapidly toward obligate parasitism in the presence of suitable hosts".

The third stage of TAYLOR's scenario is thus unnecessary (as is also in fact the second).

What answers to the other questions posed about behavioral traits may be provided by the optimizations? Taking the traits in turn, whether the inquiline behavior originated in a haplometrotic or pleometrotic ancestor cannot be answered: the optimization is ambiguous (Figs 7-8). Given the intraspecific variation in this trait, the question may indeed be unanswerable.

A short colony cycle is evidently derived in *biglumis* (Fig. 9), and so is a candidate for being an adaptation. But whether this has anything to do with the evolution of inquiline behavior is not at all clear. As plausible as may be the notion that inquilines arose from an ancestor with a shortened cycle (LORENZI & TURILLAZZI, 1986; CERVO & DANI, 1996; WEST-EBERHARD, 1996), it is not evident whether that was indeed the condition of the primitive host. If host species were treated as a trait and optimized on the cladogram, *dominulus* may be inferred to have been the ancestral host for *semenowi* and *sulcifer*, but the ancestral host for inquilines as a

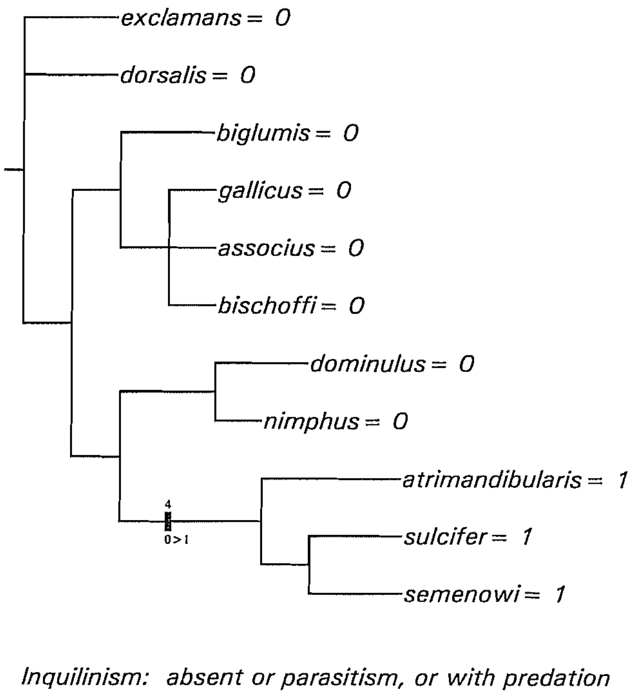
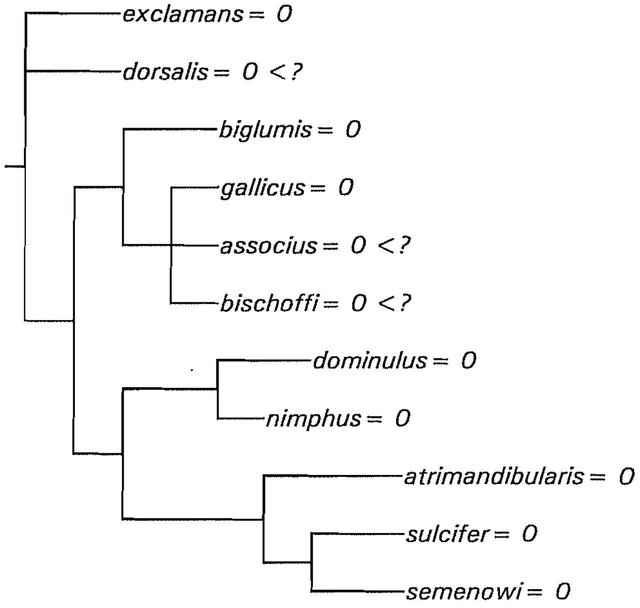
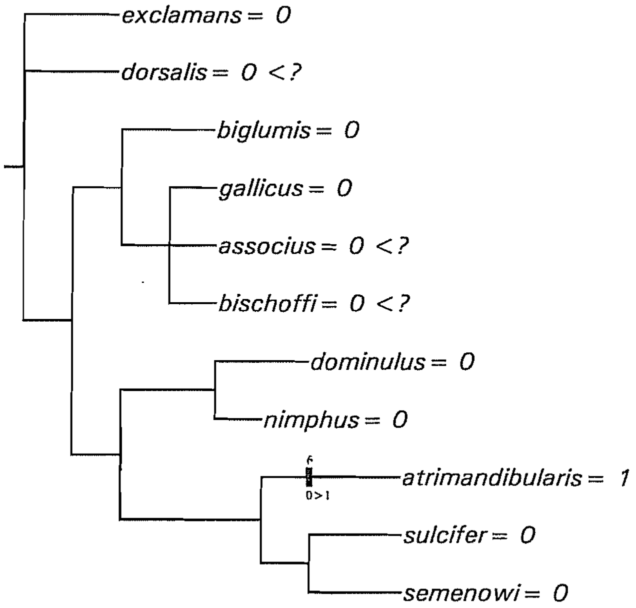


FIG. 12. — Cladogram showing optimization of inquilinism.



Timing of invasion: pre-emergence or post-emergence

FIG. 13. — Cladogram showing invariance of timing of invasion.



Usurpation tactics: aggressive or passive

FIG. 14. — Cladogram showing optimization of usurpation tactics.

whole could be *dominulus*, *gallicus* or *biglumis*. At least the possibility that the ancestral inquiline had a host like *biglumis* is not excluded.

The predatory behavior shown by *atrimandibularis* is evidently derived from parasitism (Fig. 12), occurring only within that species. It thus does not represent a different pathway to obligate parasitism; the behavior is a secondary development. This does not answer the question as to whether the behavior originated as an adaptation to the shortened colony cycle of its host species *biglumis* (CERVO & DANI, 1996), but leaves the possibility open. However, if predatory behavior is a specific adaptation to the host *biglumis*, that would not seem to accord very well with the notion that *biglumis* represents the primitive host for the inquilines (CERVO & DANI, 1996), or that parasitism arose in such a species (WEST-EBERHARD, 1996). The adaptation is not primitive in inquilines, it is derived within *atrimandibularis*.

The post-emergence timing of invasion shown by *semenowi* and *sulcifer* is evidently derived from pre-emergence invasion, arising separately within each of those species (Fig. 13). The pre-emergence timing of invasion shown by *atrimandibularis* is thus still a candidate for being an adaptation to the shortened cycle of its host *biglumis* (CERVO *et al.*, 1990c) – but it is a marginal candidate, being viable only if *biglumis* was the original host of the inquilines.

Finally, regarding the question of usurpation tactics, the passive tactics shown by *atrimandibularis* are evidently derived (Fig. 14), from primitively aggressive tactics. Initially passive behavior is thus specialized (CERVO & DANI, 1996). It seems a better candidate for an advanced form of parasitism than a prerequisite for parasitism – but, again, the conclusion of derived behavior does not fit very well with the notion that *biglumis* or something like it as the original host of the inquiline lineage.

In summary, the cladistic approach to the evolution of social parasitism in paper wasps provides decisive tests of the generalization known as EMERY's Rule, and TAYLOR's scenario for the origin of inquiline behavior. It provides answers to some of the questions posed on the evolution of various features of parasitic behavior, and is ambiguous on others. In terms of the framework for the use of phylogenetic information in evolutionary study developed by GRANDCOLAS *et al.* (1994), the present application illustrates all four of the phylogenetic patterns corresponding to tests of evolutionary processes. Adaptation is a possible explanation for features polarized as derived, such as the predatory behavior of *atrimandibularis* - although comparative functional studies remain to be done. Convergence is an unnecessary explanation for features optimized as derived once, like the origin of inquiline behavior. A causal connection is corroborated by association between particular traits, for example interspecific usurpation that is both permanent and obligate, showing no time lag in relative appearance. Various reasons may be advanced for such a connection (see WEST-EBERHARD, 1996), although tests may be difficult to formulate. And adaptive radiation, shown by differential cladogenesis, is a possible consequence of the origin of inquiline behavior. The inquiline clade, with three species, is not large, but is more diverse than its sister clade, *dominulus* + *nimphus*. Yet whether that difference is construed as impressive or not, the taxonomic context is incomplete. The European species of *Polistes* are not the only members of the subgenus *Polistes sensu stricto* (*sensu* CARPENTER, 1996a, 1996b). It is possible therefore that some of the African and Asian species of the subgenus are closely related to the *dominulus* + *nimphus* clade, similar to the situation of close relationship of *associus* and *bischoffi* to *gallicus*, which remained uninvestigated by the previous cladistic analyses based on molecular data. Further study of the phylogenetic relationships among the species of the subgenus is required to address this question. And this should be accompanied by more extensive study of the behavioral ecology of these species. As GRANDCOLAS *et al.* (1994: 671) concluded: "Finally, we submit the plea that more phylogenies are needed for comparative studies. Taxonomies should not be used for want of something better. Fruitful collaborative or integrated works should be carried out to achieve comparative studies".

ACKNOWLEDGEMENTS

The work of the behavioral ecologists centered at the University of Florence is saluted. I especially thank Rita CERVO for discussion of the behavior of the social parasites. I am grateful to Stefano TURILLAZZI for providing specimens of social parasites, Hikmet ÖZBEK for specimens of Turkish *Polistes*, and Fredrik RONQUIST, Bert GUSTAFSSON and Thomas G. T. JAENSON for Swedish specimens. Stephanie B. MINDLIN helped with the study of morphological characters. Joan E. STRASSMANN provided an electronic version of the mtDNA matrix. Rita CERVO, Pierre DELEPORTE, Philippe GRANDCOLAS and Mary Jane WEST-EBERHARD read the manuscript and made various suggestions for improvement. John WENZEL and Philippe GRANDCOLAS assisted with French translation. Finally, I thank Philippe GRANDCOLAS for organizing the symposium "Phylogenetic tests of evolutionary scenarios", thereby providing the impetus to complete this work.

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