

Evolution of the courtship phenotype in the bird of paradise genus *Parotia* (Aves: Paradisaeidae): homology, phylogeny, and modularity

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Received 5 February 2007; accepted for publication 11 October 2007

Birds of paradise (Aves: Paradisaeidae) exhibit extreme differences among taxa in courtship-related form (i.e. courtship phenotype). In the genus *Parotia*, the courtship phenotype is organizationally modular and this property may play an important role in the evolution of phenotypic disparity among taxa. The present study investigates variational aspects of phenotypic modularity in the *Parotia* by examining the structure and composition of courtship form in a comparative context. First, a module-based model of male display-phenotypes is compiled for four biological species to facilitate phenotypic comparison. Models are constructed using data from existing phenotype ontologies and associated video-vouchers. Next, a phylogenetic analysis of display-phenotype data is performed using a matrix of 47 etho-phenotypic characters coded for eight *Parotia* and out-group taxa. Analysis yields one tree, length 60 (CI = 0.83; RI = 0.85). The results demonstrate variation among taxa to be greater at higher-levels of phenotypic integration (i.e. among display-modules) than at intermediate and lower-levels (i.e. among phase- and element-modules). Three display-modules and five of six phase-modules were present in the common ancestor and complexity has increased through time as the display-modules became dissociated into subunits that diverged independently. The history of *Parotia* evolution involves numerous instances of duplication and divergence of etho-phenotypic modular components and likely reflects the same processes that have contributed to the pronounced phenotypic disparity within the entire bird of paradise radiation. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **94**, 491–504.

ADDITIONAL KEYWORDS: disparity – display behaviour – dissociation – divergence – duplication – ethology – phylogenetic analysis – sexual selection.

INTRODUCTION

The birds of paradise (Aves: Paradisaeidae) are a clade of lek-breeding corvid passerines that have radiated into an array of wildly divergent forms throughout New Guinea, a few nearby islands, and parts of north-eastern Australia (Gilliard, 1969; Nunn & Cracraft, 1996; Frith & Beehler, 1998; Cracraft & Feinstein, 2000; Barker *et al.*, 2004). The most prominent differences among species are in traits associated with courtship (i.e. ornamental plumage and complex, often bizarre, display behaviours) (Fig. 1). Differences in form among species

(i.e. phenotypic disparity) are so extraordinary that the approximately 38 biological species (88 phylogenetic species) have been placed into 14–20 genera (Gilliard, 1969; Cracraft, 1992; Frith & Beehler, 1998).

Paradisaeid display-phenotypes are exceptional, even among lekking birds. Most striking are the ways that courting males transform themselves from typical bird-like forms into unusual geometric abstractions, flower-like puffs of colour, or even peculiar ballerina-like dancers on the forest floor (Frith & Beehler, 1998; Scholes, 2006; Fig. 1). Overall diversity is impressive and the degree of disparity in colour, shape, size, and behaviour among lineages is astonishing and representative of some of the most extreme among vertebrates.

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Figure 1. Inter-specific disparity in the male display-phenotypes of ten species in the family Paradisaeidae. A, king of Saxony bird of paradise (*Pteridophora alberti*). B, red bird of paradise (*Paradisaea rubra*). C, king bird of paradise (*Cicinnurus regius*). D, Carola's Parotia (*Parotia carolae*). E, Wilson's bird of paradise (*Diphyllodes respublica*). F, blue bird of paradise (*Paradisaea rudolphi*). G, twelve-wired bird of paradise (*Seleucidis melanoleuca*). H, superb bird of paradise (*Lophorina superba*). I, Goldies' bird of paradise (*Paradisaea decora*). J, black sicklebill (*Epimachus fastuosus*). Photographs used in (A–G) and (I) are provided by Tim Laman. Photographs in (H) and (J) are by the author.

Phenotypic differentiation among species, and the pace at which diversification has occurred, has confounded systematic and evolutionary explanation for decades (Stonor, 1938; Mayr, 1941; Mayr, 1945; Rand & Gilliard, 1967; Gilliard, 1969; Diamond, 1972; Schodde, 1976; Sibley & Ahlquist, 1985; Christidis & Schodde, 1992; Nunn & Cracraft, 1996; Frith & Beehler, 1998; Cracraft & Feinstein, 2000). At the heart of the issue is that the birds of paradise are a relatively recent radiation of macroevolutionary proportion. In other words, the 'gaps' in form among closely related lineages are extreme; differences among species are on the order of that seen within all Passerines and comparable with that among the higher-nonpasserine orders as well. Therefore, when examining patterns of phenotypic evolution within the Paradisaeidae, there are usually many unique (apomorphic) characters within lineages and few obvious shared derived (synapomorphic) characters among them. It appears that the pace of within-lineage phenotypic evolution has exceeded lineage bifurcation, even though phylogenesis has been quite rapid (Nunn & Cracraft, 1996; Frith & Beehler, 1998).

An important question to ask therefore is how this happened? How have so many closely-related lineages come to be so different from one another? How can we understand the historical pathways that have led to such pronounced phenotypic diversity? How can the great disparity, or 'gaps' in form, among lineages be explained given how little we know about macroevolution in strongly sexually selected systems?

One approach is to examine macroevolutionary patterns of phenotypic evolution at a finer scale, a scale in which the disparity among taxa is not as great as within the entire paradisaeid clade and homology is easier to discern. To a certain extent, evolutionary processes occurring at intermediate scales should mirror what has taken place within the entire radiation, but be more straightforward to reconstruct, because the disparity among taxa is not as great. Furthermore, given the well-known difficulties of researching birds of paradise in the wild, acquiring the data needed to evaluate evolutionary patterns associated with courtship is simply more feasible within a more narrowly defined framework.

Good candidates for study at this intermediate scale are the species in the genus *Parotia*. This group

consists of four polytypic biological (or ten phylogenetic) species endemic to the montane forests of mainland New Guinea (Gilliard, 1969; Schodde & McKean, 1973; Cracraft, 1992; Frith & Beehler, 1998). Like most birds of paradise, male *Parotia* are under the influence of strong sexual selection by female choice (Pruett-Jones & Pruett-Jones, 1990), and the bizarre display-related characteristics of the adult males are the traits that define the genus (Frith & Beehler, 1998).

Parotia males are mostly jet-black, jay-sized birds with a suite of bizarre plumage ornaments, such as the three elongate wire-like and racket-tipped feathers that protrude from behind each eye, the large patch of iridescent feathers of the upper breast, and the unusual body feathers on the upper flanks that extend beyond the torso (Fig. 1D; Schodde & McKean, 1973; Frith & Beehler, 1998; Scholes, 2006, 2008a). Males perform a series of complex courtship displays on terrestrial display territories (Schodde & McKean, 1973; Frith & Frith, 1981; Pruett-Jones & Pruett-Jones, 1990; Scholes, 2006, 2008a). Through a series of recent field-based studies, I have characterized structure and composition of courtship of four species in great detail, making the genus the most comprehensively studied group of birds of paradise with respect to the details of courtship-related ethophenotypic form (Scholes, 2006, 2008a, 2008b).

The most significant finding of the recent research on the *Parotia* is that the components of phenotype comprising courtship are modular in form and organization (Scholes, 2006, 2008a, 2008b). In other words, *Parotia* courtship phenotypes exhibit organizational modularity (*sensu* Eble, 2005). Organizational modularity refers to the state of being modular (Eble, 2005), and organizational modules are the 'building-blocks' of phenotype complexity (Raff, 1996; Wagner, 1996). Four hallmarks of organizational modularity are: (1) hierarchical organization; (2) recurrence of the same set of elements in space or time; (3) temporal or spatial discreteness relative to other similar units; and (4) stereotypy of form (West-Eberhard, 2003). These properties are characteristic of the components that make up the courtship phenotypes in the *Parotia* (Scholes, 2006, 2008a, 2008b).

Modularity of *Parotia* courtship phenotypes is important because it is a property of organismal design that fosters the evolution of phenotypic dispar-

ity (Raff, 1996; West-Eberhard, 2003). Modularity is thought to enhance evolvability and promote complexity by facilitating the origin of novelty through the reuse and reorganization of existing parts (Raff, 1996; Wagner, 1996; Wagner & Altenberg, 1996; Prum & Dyck, 2003; West-Eberhard, 2003). As a concept, modularity plays a central role in macroevolutionary theory because it unites the processes of development and evolution (West-Eberhard, 2003; Schlosser & Wagner, 2004). This connection exists because, in addition to being building-blocks, modular units are also the characters and homologs that unite phenotypes through evolution (Raff, 1996; Wagner, 1996; Eble, 2005). This aspect of modularity has been called variational modularity and describes the condition of varying in modular fashion (Eble, 2005). Variational modularity results from the operation of several unique evolutionary processes that operate on phenotypic development (Raff, 1996), including the recurrent event sequences that produce behavioural phenotypes at a temporal scale that extends beyond individual growth and maturation (Wenzel, 1993; West-Eberhard, 2003). Fundamental features of variational modularity are: (1) the existence of units that occur with the same structure and location in different individuals of the same species or higher taxon (i.e. homology, including iterative homology) and (2) the ability to be duplicated, deleted, re-expressed and/or re-used (co-opted) as a unit (i.e. dissociability) (Roth, 1994; Raff, 1996; Prum & Dyck, 2003; West-Eberhard, 2003).

To help understand the evolution of disparity in courtship form within the birds of paradise, the present study examines the genus *Parotia* in a comparative framework. The goal is to explore patterns of similarity (and dissimilarity) within a relatively complete sample of male display components previously described (Scholes, 2006, 2008a). Because *Parotia* courtship phenotypes exhibit the hallmarks of organizational modularity, the present study investigates whether they also exhibit the features of variational modularity (i.e. homology and dissociability of component units)? To do this, two complementary analyses are employed. First, the results of earlier studies (Scholes, 2006, 2008a, 2008b) are used to assemble a schematic model of the display phenotypes for the four biological species in which all components (i.e. organizational modules) are fully vouchered with supporting photographic and permanently archived video data. The model is used as a heuristic tool for comparing display-related components among species. Next, to evaluate homology of components, a phylogenetic analysis of display-phenotype data is performed using 47, fully vouchered, characters extracted from the phenotype ontologies assembled in previous studies (Scholes, 2006, 2008a, 2008b). The purpose of this

analysis is to test hypotheses of putative homology in a cladistic framework via congruence with other homologs (Patterson, 1982; de Pinna, 1991) and to do so in a character-transparent way that is uncommon for ethologically based data (i.e. via comprehensive use of archived video vouchers for character argumentation and homology assessment). The purpose of the cladistic analysis is to provide a preliminary phylogenetic hypothesis for interpreting patterns of evolutionary diversification at the level of the entire display-phenotypes described in the first analysis. The overarching goal, however, is to understand the evolutionary patterns and mechanisms that characterize the radiation in display form within the genus as a means to understanding the patterns and mechanisms operating within the entire paradisaeid radiation.

MATERIAL AND METHODS

DISPLAY PHENOTYPE MODELS

This analysis provides a directly comparable visual overview of the complex display-phenotypes for four biological species (*Parotia wahnesi*, *Parotia lawesii*, *Parotia sefilata*, and a generalized *Parotia carolae*), which can be compared directly with one another (Fig. 2). These species were chosen because they span the majority of phenotypic diversity within the genus. Data used to build the models shown in Figure 2 come from the hierarchical-structure courtship phenotype (CP) 'anatomies' available in Scholes (2006, 2008a, and 2008b). These studies provide basic phenotype ontologies that name the components of each behaviour and outline how those parts are inter-related. The ontology framework is enhanced with supporting evidence in the form of comprehensive photographic ethograms and permanently archived video-vouchers available online via the Macaulay Library sound and video catalogue at the Cornell Laboratory of Ornithology (Scholes, 2006, 2008a). Catalogue numbers for the video-vouchers corresponding to each of the major display modules depicted in Figure 2 are given in Table 1. Vouchers can be viewed online as streaming video clips by going to the Macaulay Library's sound and video catalogue website (<http://www.animalbehaviorarchive.org>) and searching for the desired catalogue number.

To build the models shown in Figure 2, data were extracted from the male display components of each species' CP. The branching tree-like ontology structure diagrams were reformatted to illustrate the structure and composition of the primary display and phase-level units as a visual module-based format. Elements and versions (except for versions of the ballerina dance) were omitted for simplicity. Grey rounded boxes represent display-modules and coloured

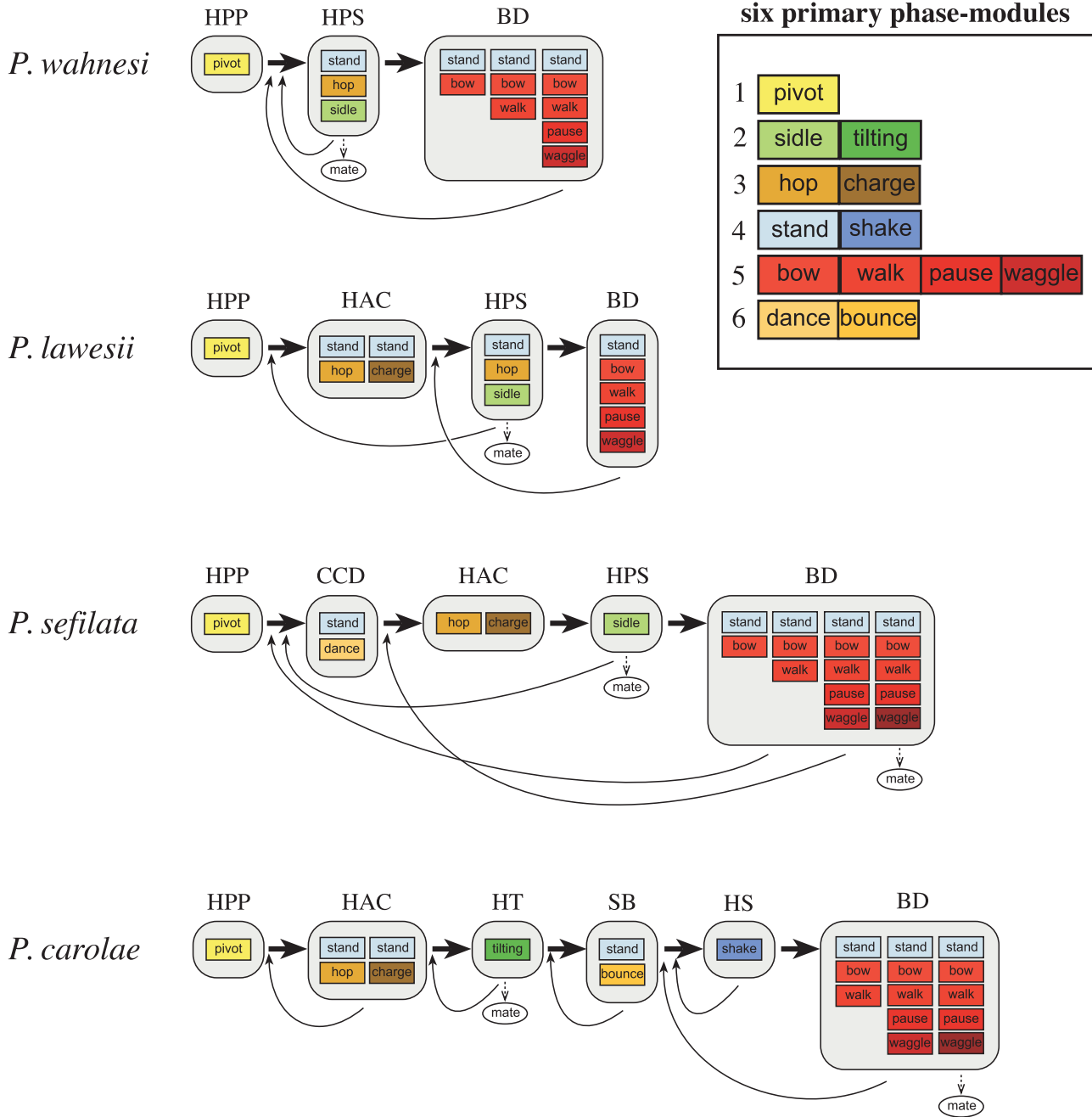


Figure 2. Structure and composition of male display-phenotypes for four species in the genus *Parotia*. An etho-phenotypic model showing the organizational structure of major modular units is given for each species. Shaded octagonal-boxes denote displays (abbreviated names are above), coloured rectangles denote phases, and versions are depicted as columns of phases (not labelled). Arrows indicate the sequence of events among display-modules. The sequence of occurrence for phase-modules reads from top to bottom. Rounded 'boxes' indicate where in the sequence mating occurs and serves as a comparative landmark. The key on the upper right shows the colour coding for the primary phase-modules. HPP, horizontal perch pivot; HPS, horizontal perch sidle; HAC, hops-across-court; CCD, court clearing dance; HT, head tilting; SB, swaying bounce; HS, hop and shake; BD, ballerina dance.

Table 1. Primary display-phenotype modules and associated Macaulay Library (ML) sound and video catalogue numbers for the voucher clips that represent them (data from Scholes, 2006, 2008a, 2008b)

Module name	ML video catalogue numbers (video_#)			
	<i>Parotia wahnesi</i>	<i>Parotia lawesii</i>	<i>Parotia sefilata</i>	<i>Parotia carolae</i>
HPP	45964, 45965	45944, 45945	46126	21680
HPS/HT	45966–45968	45946, 45947	46127	21681
Stand	45966	45946	46127	NA
Hop	45966	45946	46127	NA
Sidle/head tilting	45966–45968	45947	46127	21681
HAC	NA	45942, 45943	46125	21682–21684
Stand	NA	45942	46125	21683
Hop/charge	NA	45942, 45943	46125	21682–21684
CCD/SB	NA	NA	46121	21685–21688
Stand	NA	NA	46121	21685–21688
Bounce/dance	NA	NA	46121	21685–21688
HS	NA	NA	NA	21689–21692
BD	45954–45958	45931–45933	46116–46119	21693–21696

Clips can be viewed online (<http://www.animalbehaviorarchive.org>) by using the quick search field to locate an individual catalogue number (note: catalogue numbers in this search field should be prefaced with 'video_' followed by the number). Multiple clips can be returned through an advanced search of the video catalogue using the range of numbers given. HPP, horizontal perch pivot; HPS, horizontal perch sidle; HT, head tilting; HAC, hops-across-court; CCD, court clearing dance; SB, swaying bounce; HS, hop and shake; BD, ballerina dance. Sub-components are in italics beneath the display they are a part of. In some instances, the specified subcomponent is included within larger clip showing multiple components. NA means that the module is not a component of that species' display phenotype.

rectangular boxes represent phase-modules. Arrows indicate the sequence of occurrence for depicted modules. The sequence of occurrence for phase modules reads from top to bottom. White boxes show where in the sequence mating occurs and serve as a comparative landmark of sorts. All phase-level units are given a unique colour and putative variational modules among species (i.e. homologs; orthologs) are given similar colours of differing shades.

PHYLOGENETIC ANALYSIS

Six ingroup taxa are included in the phylogenetic analysis: two taxa from the *P. carolae* complex (populations from Mt Stolle and Crater Mountain), *P. sefilata*, *P. wahnesi*, *P. lawesii* and *Parotia helenae*. Although not definitively diagnosed, the Mt Stolle population of *P. carolae* is probably *Parotia (carolae) clelandiae*, but the Crater Mountain population possibly represents a new member of the complex (E. Scholes, unpubl. data). Analysis is based on a total of 47 behavioural characters (Table 2). Character coding and descriptions are provided in the Appendix, which is available in the Supplementary material. Characters come from detailed video-analysis of the courtship and mating ethology of wild birds collected from five localities in Papua New Guinea and Papua (formerly

Irian Jaya), Indonesia between 2000 and 2004 (Scholes, 2006, 2008a, 2008b). Characters were extracted directly from the hierarchical models of each species' courtship phenotype (i.e. phenotype ontologies; Scholes, 2006, 2008a, 2008b). For the most part, characters used in the analysis are at the level of phases and their component elements. This analysis uses characters that come from male courtship only.

Both populations of *P. carolae* described in a previous study (Scholes, 2006) were coded separately. One taxon used in this analysis, *P. helenae*, has not been previously described with a courtship phenotype ontology and so characters were coded directly from video instead of directly from an ontology. The total amount of video data for this species was not comparable with other species, but it was sufficient to adequately assess the presence or absence of most of the characters used in the present study.

Missing characters are scored in the matrix with a question mark. Autapomorphic characters are included because they may prove to be phylogenetically informative with the addition of more data and/or more taxa. Furthermore, the aim of the phylogenetic analysis is to describe and understand the evolution of the *Parotia* display-phenotype, including all independent evolutionary events occurring within lineages. A potential problem with the coding scheme

Table 2. Data matrix of character states in the Appendix (online Supplementary material)

Taxa	Characters																						
	1			2			3			4													
<i>Parotia lawesii</i>	0	1	1	0	1	1	0	1	1	1	0	0	1	1	2	3	4	5	6	7	8	9	
<i>Parotia helenae</i>	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0
<i>Parotia wahnesi</i>	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0
<i>Parotia sefilata</i>	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	1
<i>Parotia carolae-Stolle</i>	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	0	1
<i>Parotia carolae-Crater</i>	1	1	1	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1
<i>Lophorina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pteridophora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

used here is that multiple characters coded from the details of a specific behaviour may not be independent of one another, potentially exaggerating the level of character support for a particular node. However, this type of coding was used to maximize evolutionary information summarized in the phylogenetic result and also because it is most appropriate for the level of character analysis under consideration (i.e. elements of larger phenotypic units). Furthermore, it is not uncommon for characters treated as independent in phylogenetic analyses have subtle degrees of dependence (i.e. bases within a codon).

Monophyly of the genus *Parotia* is unambiguous and the ingroup taxa were designated as monophyletic for the analysis. The sister group to the *Parotia* is unknown, but the two taxa chosen as outgroups here, *Lophorina* and *Pteridophora*, have been hypothesized to be possible sister taxa (Frith & Beehler, 1998). Of the 47 characters, 44 were binary and three were multistate. Multistate characters were treated as unordered. All characters were equally weighted. Searches were run using PAUP* 4.0b10 (Swofford, 1999) using the exhaustive search option. Bootstrap, jackknife, and Bremer branch support analyses were performed. Bootstrap and jackknife analyses were run using 1000 replicates. Bremer decay indices were calculated using TREEROT, version 2 (Sorenson, 1999).

RESULTS

COMPARISON OF DISPLAY PHENOTYPE MODELS

Figure 2 illustrates the organizational structure of male display phenotypes for the four taxa at two hierarchical levels. At the most inclusive level, Figure 2 shows the configuration of displays both within and among species. Octagonal-boxes represent the putative display modules (Scholes, 2006, 2008a, 2008b). At a lower level, Figure 2 illustrates the occurrence and distribution of the phases that comprise display modules. Phase modules are represented by rectangular bracket-boxes of different colours. Below, I describe the patterns of display and phase module configuration among the four focal species as highlighted in Figure 2.

At the level of displays (i.e. octagonal-boxes), the number of modules among species varies two-fold, from three in *P. wahnesi* to six in *P. carolae*. Two displays, horizontal perch pivot and ballerina dance, are common to all four species. The horizontal perch side is found in three species: *P. wahnesi*, *P. lawesii*, and *P. sefilata*; however, it is less complex in *P. sefilata* (i.e. composed one phase-module, see below). Although different in aspects of form and given a unique name, *P. carolae* is also hypothesized to have an horizontal

perch sidle display-module, called head tilting, which is indicated by the darker shade of green. The hops-across-court display is found in all species, except *P. wahnesi*. *P. sefilata*, and *P. carolae* have a display that, although quite distinct from one another and given different names, are nevertheless hypothesized to be the same module based on unique similarities in form (see below and character 35 in the Appendix). In *P. sefilata*, this display is called the court clearing dance and, in *P. carolae*, it is called the swaying bounce. Finally, *P. carolae*, has one display-module not found in any other species: the hop and shake.

At the lower organizational level depicted in Figure 2, the phase level, display-modules are comprised of six types of phase-modules: (1) horizontal perch pivot; (2) sidle/head tilting; (3) hop/charge; (4) stand/hops and shake; (5) the various ballerina dance phases; and (6) dance/bounce. There are four distinct ballerina dance phases, but they are lumped into one colour-type for simplicity in the diagram. Five of six phase-module types are present in all species, yet the total number of phase-modules within each species (including those repeated in different contexts) ranges from 13 (*P. lawesii*) to 22 (*P. carolae*). In other words, with just one exception (i.e. dance/bounce), the phenotype of all four species is comprised of the same set of components (at the level of phase-module organization) even though the complexity among species varies with respect to the total quantity of display-modules present (Fig. 2).

Differences in complexity among species therefore are due to two factors: (1) number of times a given phase-module occurs throughout the display-phenotype and (2) where within the sequence it occurs. For example, in *P. wahnesi*, the stand and hop phase-modules exist only within in the horizontal perch sidle display but, in *P. lawesii*, the same two phases occur as independent entities forming the hops-across-court display-module. Hence, in *P. lawesii*, the hop phase-module occurs three times (including the charge as a form of hop) compared with one in *P. wahnesi*. Differences in phase-module occurrence also explain the majority of differences in the complexity of the ballerina dance among species. Different versions of the ballerina dance have different phase-module compositions so that the total number of ballerina dance phase-modules among species differs. For example, *P. lawesii* has just one ballerina dance version, the stationary waggle, and therefore has just one bow phase within the entire ballerina dance phenotype. By contrast, *P. sefilata* has four ballerina dance versions and therefore has the bow phase expressed many more times (Fig. 2).

Likewise, the issue of where within the sequence a phase-module occurs is also an important part of comparative complexity among species. For example,

in *P. wahnesi* and *P. lawesii*, the horizontal perch sidle display has three phases: stand, hop, and sidle. In *P. sefilata* and *P. carolae*, the horizontal perch sidle module is comprised of one phase-module, the sidle. Yet, both *P. sefilata* and *P. carolae*, like *P. lawesii*, have the stand/hop or hop only in the form of the hops-across-court display. In this case, the sidle phase-module is autonomous and occurs independently of the hop and stand modules. The transition in all species is still largely the 'stand-hop-sidle' sequence, as represented in the horizontal perch sidle of *P. wahnesi* and *P. lawesii*, but it occurs at a different organizational level. This is best understood by comparing at the display phenotype of *P. sefilata* and *P. wahnesi*. In *P. sefilata*, the three phase-modules of the integrated horizontal perch sidle, as represented in *P. wahnesi*, have become separated and elaborated so that they are semiautonomous display entities, and not smaller parts of a single display.

Finally, although not illustrated in Figure 2, the relative differences in the total numbers of elements (not including recurrence) are nonetheless informative and deserving of mention. *Parotia wahnesi* has the fewest, with 46, and *P. carolae* has the most, with 58. *P. lawesii* and *P. sefilata* have 49 and 55 elements, respectively. With the exception of the elements used as characters in the phylogenetic analysis (see below), the names and descriptions of elements are described elsewhere (Scholes, 2006, 2008a, 2008b). The important result here is that the two species with the biggest difference in display phenotype complexity shown in Figure 2 (i.e. *P. wahnesi* and *P. carolae*) differ by only 12 elements.

PHYLOGENETIC ANALYSIS

Phylogenetic analysis of the 47 display-phenotype characters (Table 2, Appendix) produced a single most parsimonious tree of length 60 with a CI of 83% (81% excluding uninformative characters) and RI of 85% (Fig. 3). The resulting cladogram supports a topology with *P. wahnesi* as the basal lineage and sister to two clades. One clade has *P. lawesii* and *P. helenae* as sister taxa and the other has a monophyletic *P. carolae* complex as sister to *P. sefilata* (Fig. 3). High branch supports were found for the *Parotia* clade, the *P. lawesii* + *P. helenae* clade, and for the two *P. carolae* taxa. The remaining two branches are moderately supported with bootstrap and jackknife values in the 60s and Bremer support values of two.

Phylogenetic analysis at the level of display indicates that the horizontal perch pivot, horizontal perch sidle, and ballerina dance display modules were present in the common ancestor of the species included in the analysis (characters 6, 25, and 39; Fig. 3). Although the data show that the hop module was also

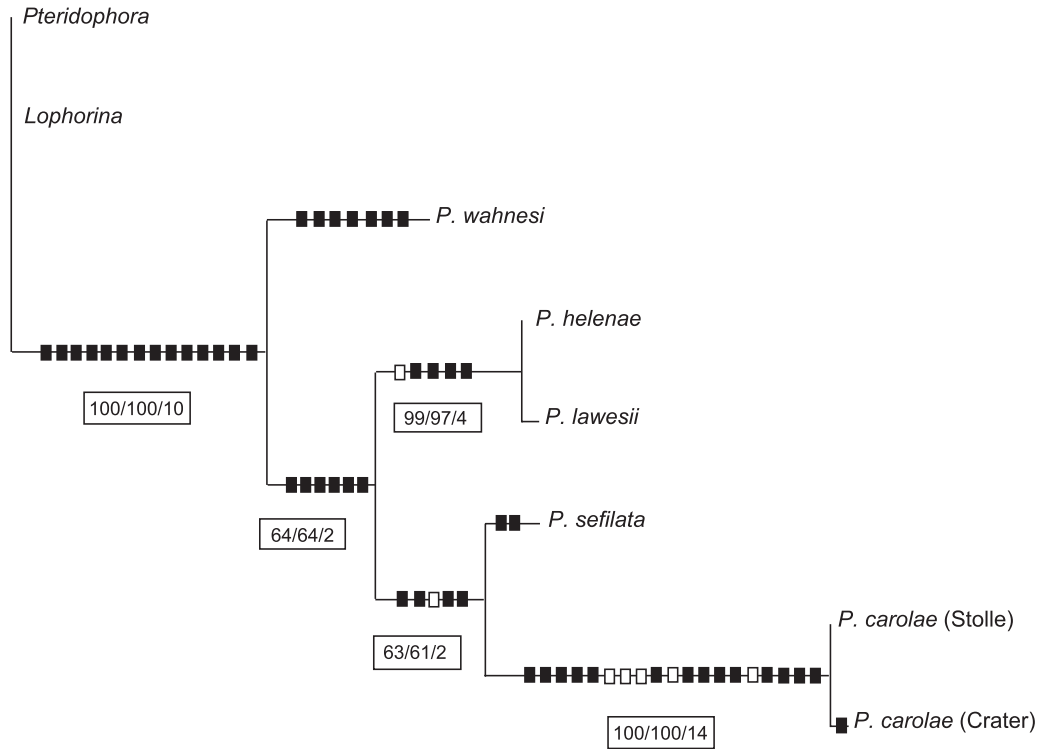


Figure 3. The single most parsimonious tree based on 47 display-phenotype characters (length = 60, CI = 0.83, RI = 0.85). Data matrix used for the analysis is presented in Table 2. Character descriptions are in the Appendix (online supplementary materials). Boxes beneath branches give bootstrap, jackknife, and Bremer support values, respectively. Black rectangles represent unambiguous apomorphic characters and white rectangles represent parallelisms and reversal based on ACCTRAN optimization.

present in the common ancestor (see below), the hops-across-court display-module is a shared derived character for the clade that includes all but *P. wahnesi* (characters 19 and 24; Fig. 3). The topology of the shortest tree supports the homology of the court clearing dance and swaying bounce display-modules of *P. sefilata* and *P. carolae* (character 35; Fig. 3). Even if characters 35–38 (all the court clearing dance/swaying bounce characters) are excluded from the analysis, the shortest tree retains the same topology. Only the two taxa from the *P. carolae* complex have a unique (autapomorphic) display-module, hop and shake, not found among the other species.

At the level of phases, analysis indicates that, as mentioned above, the plesiomorphic hop phase was part of the horizontal perch sidle display and was subsequently duplicated in the common ancestor (the *helenae/lawesii/sefilata/carolae* clade) to form a distinct display, the hops-across-court (characters 18, 19, and 21; Figs 2, 3; Appendix). Part of this transformation also included the origin of the ‘charge’ type of hop phase, which also appears to be a synapomorphy of that clade (character 24; Figs 2, 3; Appendix). Although not coded as a distinct character, the independent

sidle phase is nevertheless a synapomorphy of the *P. sefilata/carolae* clade, supporting the homology of the head tilting/horizontal perch sidle display modules. As coded, the origin of the independent sidle-only horizontal perch sidle is indicated by character 21 (Fig. 3), which shows the loss of the integrated stand/hop/sidle. The other important phase-level characters supporting the *P. carolae/sefilata* clade are stand phase modules with hops-in-place and without false court clearing (characters 14 and 15; Appendix) and the hop-waggle phase-module (character 47; Appendix) of the ballerina dance. The hop-waggle phase characterizes an entire ballerina dance version that coexists with the plesiomorphic stationary-waggle version (characters 39 and 47; Figs 2, 3; Appendix).

DISCUSSION

The present study examined the courtship display phenotypes of the genus *Parotia* through two comparative analyses (Figs 2, 3). The emphasis was on investigating variational modularity, or the state in which evolutionary lineages vary in a modular fashion (Eble, 2005). Two aspects of variational

modularity examined were homology and dissociability (West-Eberhard, 2003). Homology of courtship displays was tested via phylogenetic analysis of 47 male display-phenotype characters (Fig. 3; Table 2; Appendix) and dissociability was investigated through comparative study of the components comprising the display-phenotypes (Fig. 2). In the following sections, I review the evidence for homology of the courtship display components and then discuss the evidence for the dissociable properties of those units.

PHYLOGENY AND HOMOLOGY

Non-independence of phylogeny and character analysis?

Although this is the first phylogenetic reconstruction for the genus *Parotia*, the primary purpose was not to recover phylogeny. The analysis was performed to examine the components of courtship display in a phylogenetic context. Although some might consider it circular to examine evolutionary patterns for characters related to those used to build a phylogenetic hypothesis, I did so here for three reasons. First, there are no other options; the phylogeny presented here is currently the only available for these taxa. Second, in some cases, it has been shown that direct study of the characters of interest is preferable to character mapping on an independently derived phylogeny (Wenzel, 1997; Noll, 2002). This logic is bolstered by the high degree of congruence between phylogenies derived from behavioural, morphological, and molecular data (de Queiroz & Wimberger, 1993; Wimberger & de Queiroz, 1996). Third, due to details of character distribution for characters of interest (i.e. display-modules), major conclusions will not change if tree topology changes in view of more or better supported data (i.e. most display-modules are either stacked at the base of the clade (plesiomorphic) or clustered at terminal tips (apomorphic)). Furthermore, there are relatively few taxa, monophyly is not questioned, and it is easy to examine alternative scenarios.

Nevertheless, due to the possibility of non-independent covariation among characters used in the present study, the hypothesis of phylogeny presented should be considered provisional until a fully independent data matrix (whether DNA or morphology based) is available. Fortunately, a comprehensive molecular phylogeny for the Paradisaeidae is underway and includes the taxa used here as well as many more. Preliminary analyses recover the same phylogenetic network as recovered here, but differ in where the clade is rooted (J. Cracraft, pers. comm.).

INTERPRETATION OF PHYLOGENETIC ANALYSIS

A phylogenetic analysis of 47 display-phenotype characters coded for six ingroup and two outgroup taxa

was used to test homology of the male display components of the *Parotia* courtship (Table 2; Fig. 3; Appendix). The analysis shows that these characters evolve fairly cleanly with little homoplasy. A CI of 0.83 is higher than expected for a study of this many taxa (Sanderson & Donoghue, 1989). This finding is consistent with previous studies that have found behavioural characters to perform as well as, or better than, morphological characters across a wide range of taxa and taxonomic levels (Prum, 1990; Wenzel, 1992; de Queiroz & Wimberger, 1993; Kennedy, Spencer & Gray, 1996; Wimberger & de Queiroz, 1996; Slikas, 1998; Bostwick, 2000; McLennan & Mattern, 2001; Noll, 2002).

The phylogeny produced here supports a novel topology for the genus *Parotia* (Fig. 3). Previously, several studies have suggested nonphylogenetic hypotheses of interspecific relationships based on limited character analysis, which can be considered preliminary at best (Gilliard, 1969; Schodde & McKean, 1973). Gilliard (1969) treated *P. wahnesi* as the basal member of the genus due to its unusually long tail, which he believed was a plesiomorphic character linking the *Parotia* to the genus *Astrapia*. Likewise, Schodde & McKean (1973) produced a hypothesis that treated *P. wahnesi* and *P. sefilata* as the least derived members but with no real resolution for the remaining species other than to comment that they believed *P. carolae* to be the most derived with characters shared with both *P. sefilata* and *P. lawesii*.

The present analysis used a comprehensive suite of characters not used in previous studies (Appendix) and supports the basal placement of *P. wahnesi* (Fig. 3). However, unlike earlier efforts, the tree presented was constructed using modern phylogenetic methods and is fully resolved and fairly well supported. The biggest difference between the results of this analysis and the previous nonphylogenetic hypotheses is the sister-group relationship between *P. sefilata* and the *P. carolae* complex (Fig. 3). Most studies have treated *P. helenae* as a subspecies of *P. lawesii*, so finding them to be sister taxa is not surprising, and is consistent with biogeographical evidence (Schodde & McKean, 1973; Frith & Beehler, 1998).

HOMOLOGY OF ETHOLOGICAL CHARACTERS AND DISPLAY-MODULES

Two behaviours at the level of displays, the horizontal perch pivot and ballerina dance, are unambiguously homologous among all taxa as well as present in the common ancestor (plesiomorphic) (Figs 2, 3). The ballerina dance is the most complex *Parotia* display with five phases, all of which are present in each taxa examined and most likely were present in the common ancestor as well (Figs 2, 3). Four distinct

versions (i.e. alternative forms) of the ballerina dance have been described in previous studies (Scholes, 2006, 2008a, 2008b; Fig. 2). Although all four versions are comprised of the same set of homologous components, and represent instances of iterative homology within lineages, only two exemplify supraspecific, or taxic, homology. The stationary waggle version, for example, is shared among all taxa and is probably the closest in form to the ancestral version of the ballerina dance. The hop waggle version is a shared derived character of the *P. carolae/sefilata* clade, and thus represents another instance of taxic homology.

A third display, the horizontal perch sidle, is also homologous in all taxa, but its substructure has been modified making interpretation more challenging. For example, in two taxa, the horizontal perch sidle is comprised of three distinct phases (stand/hop/sidle) and, in the other two taxa, it is comprised of just one phase (sidle) (Fig. 2). Because the three phases of horizontal perch sidle are plesiomorphic, and using the character transformation scenario implied by the phylogeny employed in the present study, it appears that the combined three-phase horizontal perch sidle was the ancestral condition. Furthermore, the single-phase horizontal perch sidle is a shared derived feature of the *P. carolae/sefilata* clade. Hence, the 'original' horizontal perch sidle was probably similar in form to that of *P. wahnesi* and was subsequently transformed into the more complex *P. lawesii/helenae* type and also the simplified single-phase type of *P. carolae/sefilata* (Figs 2, 3).

Two other displays exemplify taxic homologies at different nodes in the recovered phylogeny. The hops-across-court display, for example, is a synapomorphy of the clade that includes all but *P. wahnesi* (Fig. 3). Likewise, the topology recovered here supports the homology of the *P. sefilata* court clearing dance with the swaying bounce of *P. carolae* (Figs 2, 3). Of all the behaviours hypothesized to be homologs in the present study, these two are the most dissimilar. Yet, these units share a unique set of special similarities that are support them as homologs (Fig. 3; character 35 Appendix).

DISSOCIABILITY

Dissociability is the property of being able to be separated and yet maintaining integrity as an independent unit. Dissociation appears to have been a common evolutionary feature within the evolution of the *Parotia* courtship phenotype. A particularly good example is the horizontal perch sidle display (Fig. 2). As the name implies, the most significant part of this display is the 'sidle' component, or sidle phase-module. Phylogenetic analysis indicates that the common ancestor to the extant *Parotia* had a horizontal perch

sidle display very similar to that of *P. wahnesi* and *P. lawesii* (Fig. 2). In both these species, the horizontal perch sidle is comprised of three fairly tightly integrated phase-modules: stand, hop, and sidle. In *P. sefilata* and *P. carolae*, the horizontal perch sidle display consists of just one phase-module, the sidle.

One interpretation of this pattern is that the horizontal perch sidle display of *P. sefilata* and *P. carolae* has been refined in such a way that the preliminary phase modules have been lost from the display phenotype altogether. However, a closer look at Figure 2 reveals that the stand and hop modules have not been deleted entirely, but have been duplicated in the *lawesii/helenae/sefilata/carolae* clade so that they exist outside of the horizontal perch sidle display. Duplication is most clearly evident in *P. lawesii*, which has both the plesiomorphic three-phase horizontal perch sidle, but also has the stand and hop modules as part of the hops-across-court display (Fig. 2). In other words, the relatively simple-hop of the plesiomorphic form of the horizontal perch sidle display has been duplicated and elaborated into a distinct stereotyped behaviour in which the displaying male repeatedly hops back and forth across the court in a highly ritualized way (a behaviour present in all taxa but *P. wahnesi*). The stand module is also duplicated but shows little or no elaboration.

Under the above scenario, duplication of the hop module represents a dissociation event in which the hop became separable from the horizontal perch sidle and achieved a more complete level of autonomy when it diverged in a path independent from the hop of the horizontal perch sidle; the condition represented by *P. lawesii* (Fig. 2). Yet even more convincing evidence comes from looking at what has happened in the lineage leading to *P. carolae* and *P. sefilata* (Fig. 3). Examination of the *P. sefilata* phenotype (Fig. 2) reveals that dissociation of the horizontal perch sidle did not end with the duplication of the hop module and the emergence of the hops-across-court display. Instead, the process of dissociation continued to the extent that the entire sequence that was once the horizontal perch sidle (stand, hop, sidle) has been separated and elaborated into a series of three distinct autonomous displays: court clearing dance, hops-across-court, and horizontal perch sidle (Fig. 2). In both *P. sefilata* and *P. carolae*, the horizontal perch sidle display is comprised of the sidle module only and the other two modules (i.e. stand and hop) are featured in two separate displays. In other words, the sidle module has become entirely dissociated from the stand and hop of the plesiomorphic condition and, in doing so, has become elaborated into distinct display module (i.e. moved up a level in the organizational hierarchy).

In addition to the example above, there are other instances of dissociability among display-phenotypes.

For example, the hop and shake display of the *P. carolae* taxa represents the outcome of dissociation. The hop and shake display is a highly ritualized and elaborated rendition of the more widespread and stand phase-module (Fig. 2). Although the stand phase is recurrent throughout the phenotypes of all species examined (Fig. 2), and perhaps represents a dramatic example of behavioural iterative homology, the hop and shake is exceptional in the degree to which it has become unlinked from other phase-modules to become a uniquely derived unit within the *P. carolae* display phenotype. With respect to form, the hop and shake is the most similar to the synapomorphic stand phase-modules of the *P. sefilata* and *P. carolae* ballerina dance (Fig. 2). In the ballerina dance of these taxa, the stand phase involves an elaboration of the plesiomorphic 'steps-in-place' element into a ritualized 'hops-in-place' (character 14, Appendix; Fig. 3) as well as a lack of false court clearing (character 15, Appendix; Fig. 3). Similarly, the hop and shake display of *P. carolae* involves repeated, pronounced hopping in place, while fluttering the 'whiskers' and repeatedly expanding and shaking the flank plumes in a modified rendition of the more widespread plumage ruffling displacement behaviour (Scholes, 2006; characters 16 and 17, Appendix). Although not reflected in this analysis, the hop and shake display has become so distinct (i.e. so extensively dissociated from the other stand modules) that it has begun to diversify independently with substructure of its own (i.e. phases of its own, the puff phase and skirt phase; Scholes, 2006). Further evidence of dissociation comes from the observation that the hop and shake display has begun to function as a variational module in its own right. Previous studies found that two populations of the *P. carolae* complex (those represented here) differ substantially in the tempo of hops during the hop and shake display (Scholes, 2006). All evidence points to the conclusion that the hop and shake is a derived homolog (i.e. iterative homolog) of the stand phase-module that has become dissociated from its roles in other contexts and has become a distinct display module. Like the side module of the horizontal perch side display, this dissociation seems to have involved an elaboration of display related function and a shift upwards in the organizational hierarchy (i.e. from phase module to display module).

NON-MODULAR DIVERSIFICATION

Not all diversification within *Parotia* display phenotypes is modular. Many differences among taxa are attributable to divergence in the elements that comprise phase modules. For example, although the ballerina dance display is the most complex, and most modular, of all the *Parotia* displays, the greatest

differences in form of this display among species are in the details of elements that comprise the same set of shared phases. Specifically, although different versions (i.e. the columns in the ballerina dance-box of most species shown in Fig. 2) are examples of modular differentiation (different combinations of phase-modules making unique ballerina dance versions; Fig. 2), some of the most striking differences among species are due to divergence of component elements. The ballerina dance of *P. wahnesi* has the same suite of phase-modules shared by all *Parotia* species and that were also present in the common ancestor, yet the bow phase-module has undergone a series of unique transformations. The bow of *P. wahnesi* has been elaborated (character 40, Appendix) so that the bowing posture is held for an extended period with tail cocked to highlight the species' unusually long tail. Although bowing with tail cocked, the body is lifted up and down by flexing the toes and the bird often leans to the side and then returns upright, all the while maintaining the bowing posture. The bow phases of all the other species are essentially the same as one another: shorter in duration, no lifting up on the toes, no leaning to the side, and no focus on the tail. This kind of within-module elaboration and divergence has been a common feature of *Parotia* display-phenotype evolution.

OTHER DIVERSIFICATION

Many of the biggest differences between the *P. carolae* group taxa and the other species are also attributable to divergence of elemental components throughout the entire courtship phenotype. For example, the 'whisker' fluttering element has been repeatedly incorporated to phase-modules throughout the entire display phenotype (e.g. head tilting, hop and shake, and all 'stand' phase modules). Likewise, the loss of some elemental features contributes to divergence in *P. carolae* taxa relative to the other species. For example, the horizontal perch pivot does not include any flicking of the wings open/shut to the sides. The wing-flicking element is shared by all other taxa and was likely present in the common ancestor to the *Parotia* clade (Fig. 3). However, in the *P. carolae* group, the role of the wing-flicking element appears to have been transferred to the flank plumes. In this case, the unique white portions are conspicuously flared, in a somewhat wing-like fashion, out from the sides of the body during display. This type of evolution has been common in the history of the *P. carolae* complex.

CONCLUSIONS

Modularity is the property of discreteness among parts and integration within parts and is a fundamental aspect of phenotypic complexity (Raff, 1996;

Wagner, 1996; West-Eberhard, 2003; Schlosser & Wagner, 2005). It is hypothesized to facilitate the evolution of phenotypic disparity among evolutionary lineages by increasing evolvability and promoting mosaic evolution where components are reorganized independently of each other through development and evolution (Raff, 1996; West-Eberhard, 2003).

The present study examined modularity as a component of the pronounced phenotypic disparity that characterizes the extraordinary bird of paradise radiation by examining patterns of evolutionary diversification within the courtship phenotype of the genus *Parotia*. Previous studies have shown that the *Parotia* courtship phenotype is organizationally modular (Scholes, 2006, 2008a, 2008b), and thus, over evolutionary time, the units of modular organization are expected to become the units of evolutionary change (i.e. variational modules) within and among species. Two fundamental aspects of variational modularity were investigated here: homology and dissociability. The units comprising *Parotia* display-phenotypes exhibit a relatively high degree of homology. Over the course of *Parotia* evolutionary history, complexity of *Parotia* display-phenotypes has increased as ancestral displays have been duplicated and separated into distinct display components that are diverging independently of other such units. Taken together, these data support the hypothesis that the *Parotia* courtship phenotype is an inherently modular component of phenotype with modularity evident both within and among species.

Assuming the *Parotia* to be typical of the paradisaeid radiation, the virtually inexplicable degree of disparity in courtship-related form among lineages may be attributable modular evolution. Intense intersexual sexual selection has long been associated with rapid phenotypic change, but this change is typically conceived as a largely quantitative selective force (i.e. shorter/longer tails, brighter/darker plumage, etc.) that contributes to large-scale (i.e. macroevolutionary) changes insofar as different populations diverge in different quantitative directions over relatively long spans of time. By contrast, the conclusions presented here support a novel scenario in which sexual selection may be the primary force in large-scale patterns of phenotypic transformation by promoting the duplication, divergence, and reorganization of etho-phenotypic modules. Coupled with the more standard quantitative elaboration of most evolutionary models dealing with behaviour and signal evolution, sexual selection should be more thoroughly investigated as a major force of macro-evolutionary change. For the birds of paradise at least, sexually selected modular phenotypic evolution appears to be an important contributor to the pronounced disparity in form for which the family is renowned.

ACKNOWLEDGEMENTS

R. O. Prum, A. T. Peterson, and K. S. Bostwick provided valuable comments on the manuscript. I am grateful to the Papua New Guinea (PNG) Department of Environment and Conservation and the National Research Institute for facilitating research in PNG. I thank the many landowners in New Guinea who permitted me to work on their land and assisted with data collection. I thank T. Laman for granting permission to use his outstanding photographs for Figure 1. The Macaulay Library at the Cornell Laboratory of Ornithology made the use of video vouchers possible. Fieldwork was funded with support from the National Geographic Society, the Pacific Biological Foundation, the Wildlife Conservation Society, and the University of Kansas Natural History Museum.

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SUPPLEMENTARY MATERIAL

The following material is available for this article online:

Appendix. Character coding.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1095-8312.01012.x>

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