Phylogeny and biogeography of hogfishes and allies (*Bodianus*, Labridae)

Francesco Santini^{a,*}, Laurie Sorenson^a, Michael E. Alfaro^a

^a University of California Los Angeles, Department of Ecology and Evolutionary Biology, 610 Young Drive South, CA 90095 Los Angeles, USA

* Corresponding author:

Department of Ecology and Evolutionary Biology,
University of California Los Angeles,
610 Young Drive South, CA 90095 Los Angeles, USA.
Phone: +1 310 794 5019;
E-mail: francesco.santini@alumni.utoronto.ca

Abstract

Bodianus wrasses comprise one of the most diverse genera of labrids. Also known as hogfishes due to the presence of a large pig-like snout, *Bodianus* species are found in warm waters across the Pacific, Atlantic and Indian Oceans. To this date no densely sampled molecular phylogeny is available for this group, and a single morphological study did not include two genera (*Clepticus* and *Semicossyphus*) that have been shown to belong within hogfishes. Our study produced the first multi-locus molecular phylogeny of *Bodianus* species, and corroborated the non monophyly of this group without the inclu-

sion of the Creole wrasse (*Clepticus*) and the sheepheads (*Semicossyphus*). We further showed that hogfishes and allies started to radiate during the Early Miocene, ~20 Ma, and that while this group originated in the Indo-western and South-western Pacific, it experienced multiple episodes during which it successfully invaded different geographic regions and/or ocean basins.

Keywords. *Bodianus*, *Clepticus*, *Semicossyphus*, phylogeny, biogeography.

1. Introduction

The wrasse genus *Bodianus* includes 43 currently recognized species distributed across all warm oceans. Most species occur in shallow, tropical waters less than 70 meters of depth or in coral reef habitats, but a number of species are known to occur at depths in excess of 150 meters or in temperate waters (Gomon, 2006; Froese and Pauly, 2014).

Commonly known as “hogfishes” due to an elongate snout, *Bodianus* wrasses are characterized by a laterally compressed body, a prominent frontal shelf on their neurocranium (absent in *B. cylindriatus* and *B. thoracotaeniatus*; Gomon 2006), and a sharp angle at the anteroventral edge of the dentary. Like most wrasses, a number of hogfishes are sequential hermaphrodites, changing sex during their life cycle, generally from female to male.

The greatest diversity of hogfishes is found in the Indo-western Pacific, but a number of species are also known from the South-western and North-western Pacific, the Eastern Pacific, the Western Indian Ocean, as well as both the Eastern and Western Atlantic, prompting questions regarding the age of this group, when and where the radiation of *Bodianus* began, and how did the various hogfish lineages disperse to

achieve their present day distribution. Unfortunately currently there is no molecular phylogeny available that includes more than five species of *Bodianus* (Westneat and Alfaro, 2005; Alfaro et al. 2009; Cowman et al 2009; Kazancıoğlu et al. 2009). This makes it impossible to determine whether there were one or multiple transitions between oceanic basins (e.g., Pacific to Atlantic, or *viceversa*), or if there were multiple events of colonization, for example from the Western Atlantic into the Eastern Pacific before the final closure of the Isthmus of Panama. In light of the recent suggestions that the closure of the isthmus may have occurred much earlier than commonly thought (Bacon et al. 2015), it would also be important to determine when the split between the closely related species that occur on the two sides of the Isthmus may have split from one another.

Furthermore, all large scale molecular studies of labrid relationships published to date (Westneat and Alfaro, 2005; Alfaro et al. 2009; Cowman et al 2009; Kazancıoğlu et al. 2009), point to the paraphyly of *Bodianus* without the inclusion of the genera *Clepticus* and *Semicossyphus*. Both genera are very small, with only three currently described species in each. While the creole wrasses of the genus *Clepticus* are found in the Western and Eastern Atlantic, the sheephead wrasses of the genus *Semicossyphus* are only present in the Pacific, with one species found in the North-eastern Pacific (the California sheephead), one in the Galapagos, and a third in the North-western Pacific. The only detailed phylogeny currently available for *Bodianus* is that published by Gomon (2006). Based on the parsimony analysis of a dataset of 43 morphological characters, which included 23 of the extant 43 *Bodianus* species, ten subgeneric lineages were

recognized. Unfortunately, neither *Clepticus* nor *Semicossyphus* were included in the sampling.

For this study we assembled a dataset that includes 22 species of *Bodianus*, as well as five other closely related labrid species, to test the monophyly of the genus, and produce the first time-calibrated phylogeny for hogfishes and allies. We used four new markers that have not been used in any of the major studies of labrid inter-relationships (Westneat and Alfaro, 2005; Alfaro et al. 2009; Cowman et al. 2009; Kazancioğlu et al. 2009), thus providing an independent test of the monophyly of hogfishes. We also used the program BioGeoBears to compare different biogeographic models in order to investigate the region of origin of hogfishes, and whether this group experienced multiple episodes of transitions between oceanic basins.

2. Materials and methods

2.1 DNA extraction and amplification

We secured tissue samples for 14 species of *Bodianus*, one species of *Clepticus*, two species of *Semicossyphus*, and two outgroups through loans from university or museum collections, or purchases through the pet trade (Table S1). We obtained sequence data from GenBank for eight additional *Bodianus* species, bringing our final sampling to 22 species of *Bodianus*, and 27 total species. We included *Pseudodax moluccanus* and *Choerodon zamboangae* as outgroups on the basis of recent studies of labrid higher level relationships (Westneat and Alfaro, 2005; Alfaro et al., 2009; Cowman et al., 2009; Kazancioğlu et al., 2009),

We extracted DNA from muscle tissue samples or fin clips stored in 70% ethanol using the Qiagen DNasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) following the protocol suggested by the manufacturer. Two mitochondrial genes, cytochrome oxidase subunit I (*coxI*) and cytochrome b (*Cytb*), and two nuclear genes, early growth response gene 3 (*EGR3*) and rhodopsin (*Rh*), were amplified using the polymerase chain reaction (PCR). Primers and PCR conditions were obtained from the literature: Ward et al. (2005) for *coxI*; Sevilla et al. (2007) for *Cytb*; Chen et al. (2013) for *EGR3*; and Chen et al. (2003) for *Rh*. We used ExoSap (Amersham Biosciences) to remove the excess dNTPs and unincorporated primers from the PCR products. Purified products were cycle-sequenced using the BigDye Terminator v.3.1 cycle sequencing kit (1/8th reaction) (Applied Biosystems) with each gene's original or additional internal primers used for amplification. The cycle sequencing protocol consisted of 25 cycles with a 10-s 94°C denaturation, 5-s of 50°C annealing, and a 4-min 60°C extension stage. Sequencing was conducted at the Yale University DNA Analysis Facility using an ABI 3730xl DNA Genetic Analyzer (Applied Biosystems). We used the barcode of life database (http://www.barcodinglife.com/index.php/IDS_OpenIdEngine) to verify the identification of our tissue samples, and retained only the samples that produced *cox I* sequences having 99% or higher similarity to corresponding sequences in the database.

2.2 Phylogenetic analyses

We used Geneious 5.4 (Drummond et al., 2011) to inspect the sequence chromatograms and assemble them into contigs, and used MUSCLE (Edgar, 2004) to align the consensus sequences for each individual gene. We then inspected the

alignments by eye for accuracy, and trimmed the sequences at the 3' and 5' ends to minimize missing characters. The final data matrix consisted of 651 bp for *cox1*, 1058 bp for *Cytb*, 767 bp for *EGR3*, and 829 bp for *Rh*, for a total of 3305 nucleotides used in the concatenated analyses. We deposited all the sequences that we generated for this study in GenBank (Table S1). We used jModelTest (Posada, 2008) to select the best fitting model of sequence evolution from the candidate pool of models that can be utilized in MrBayes 3.2 (Ronquist et al., 2012) using corrected Akaike information criterion (AICc; Akaike, 1973), but did not include the proportion of invariant sites parameter in the candidate pool, as this parameter is already taken into consideration by the gamma parameter (Yang, 2006). jModelTest selected HKY+G as the best model for all loci.

We concatenated the four individual gene datasets in Mesquite 2.75 (Maddison and Maddison, 2011), and ran maximum likelihood analyses using RAxML (Stamatakis, 2006), with each individual gene partition assigned a GTR+G model, the RAxML model closest to the jModelTest results. We ran 500 fast bootstrap replicates. We also used MrBayes 3.2 (Ronquist et al., 2012) to perform Bayesian analyses. We partitioned the concatenated dataset by locus and assigned the HKY + G model. We ran multiple replicates with two analyses of 10 million generations each, with four chains (one cold, three heated) sampling every 1000 generations. We used Tracer 1.6 (Drummond and Rambaut, 2007) to check the trace files and ensure that the chains had reached convergence, and discarded the first 25% of trees as burnin. We combined the post-burnin trees to obtain a 50% majority rule consensus tree and compared the topologies of the different replicates to each other to assess support for the results of the analyses.

To generate the timetree, we analyzed the concatenated alignment as four unlinked gene partitions, after having assigned HKY + G to each locus. We used uncorrelated lognormal priors in BEAST 1.8 (Drummond and Rambaut, 2007) and assigned a birth-death prior to the rates of cladogenesis. We ran two analyses of 10 million generations each, with sampling every 1000 generations. We used Tracer 1.6 (Drummond and Rambaut, 2007) to inspect the trace files, ensuring that the chains had reached convergence and the ESS values for all parameters were greater than 200. We removed the first 10% of the trees from each analysis as burnin, used LogCombiner to merge the files with the remaining trees, and TreeAnnotator (Drummond and Rambaut, 2007) to obtain a timetree. As no fossils can presently be assigned to either *Bodianus* or other closely related wrasse lineages (Carnevale, 2015), we employed two different strategies to date the tree. First we ran analyses using the Miocene fossil of *Trigondon jugleri* (Schultz and Bellwood, 2004) to date the split between *Pseudodax moluccanus* and the rest of this clade. This fossil has been used in several time-calibration studies of wrasse relationships (Alfaro et al., 2009; Cowman et al., 2009), and is the only fossil that can be placed with confidence within the crown Hypsigenyine. However, this fossil is from sediments that have been dated at about 14 my ago (Schultz and Bellwood, 2004), while that node appears to be much older in the molecular chronograms (i.e., 32 my in Alfaro et al., 2009; 33.7 my in Cowman et al., 2009). We also selected three key nodes in the Alfaro et al. (2009) timetree and used these as secondary molecular calibration points for additional analyses (with a single secondary calibration for each analysis): the split between *Pseudodax moluccanus* and the rest of this clade and the split between *Choerodon zamboangae* and the remaining taxa. For these secondary calibration points

we used the younger age of the 95% highest posterior density (HPD) as the offset, and the older age of the 95% HPD for the soft upper bound.

All phylogenetic analyses (using RAxML, MrBayes and BEAST) were run on the Cipres portal v. 3.3 (Miller et al., 2010) and all tree files have been archived in Dryad (accession number pending).

2.3 Historical biogeography

To investigate the biogeographic history of the *Bodianus* clade we performed biogeographic reconstruction with our time tree using the R package Bio-GeoBEARS (Matzke 2013). We used the dispersal–extinction–cladogenesis model (DEC; Ree, 2005) and the BayArea model (Landis et al., 2013) both with and without the founder-event speciation (indicated as +J). The fit of each of the different models was assessed using the Akaike information criterion (AIC) (Matzke, 2013). We did not constrain the directionality or timing of dispersal in our analyses and we set the maximum number of ancestral areas to three. Data on distribution of the species included in our study were obtained from Fishbase (Froese and Pauly, 2014). We identified seven different geographic areas inhabited by our species: the Western Atlantic (from here on referred to as WA), the Eastern Pacific (EP), the Indo-western Pacific (IWP), the Western Indian Ocean (WIO), the South-western Pacific (SWP), the North-western Pacific (NWP) and the Eastern Atlantic (EA), all of which correspond to well-established, or complexes of closely related, marine biogeographic provinces (Briggs and Bowen, 2012). Due to the widespread distribution

of several species across some of these regions, such as the IWP, and the already high numbers of areas, we chose not to further subdivide these areas.

3. Results

3.1 phylogeny of *Bodianus*

Both maximum likelihood and Bayesian analyses produced virtually identical topologies, with only one discordant node (Fig 1). Our results show that *Bodianus* is a paraphyletic genus, with two other genera (*Clepticus* and *Semicossyphus*), nested within it. *Clepticus* appears to be the sister taxon to *Bodianus anthoides*, while the two species of *Semicossyphus*, each other's sister taxa in our analyses, are the sister lineage to *Bodianus scrofa*. Our topologies show high support, both in Bayesian posterior probabilities (PP) over 0.95 and maximum likelihood bootstrap proportions (BSP) over 90% for a number of different groups of *Bodianus* species (all branches marked by a star in Fig. 1): *Bodianus flavifrons* + *B. frenchii*; *B. oxycephalus* + *B. unimaculatus*; *B. bimaculatus* + *B. opercularis*; *B. tanyokidus* + *B. trilineatus*; *B. axillaris* + *B. mesothorax* sister to *B. diana* + *B. dictynna*; *B. diplotaenia* sister to *B. pulchelus* + *B. rufus*, with this clade being the sister taxon to a clade that includes the following species, all sequential sister taxa to the others: *B. speciosus*, *B. eclancheri*, *B. perdition*, *B. bilunulatus*, and *B. macrorus*.

All BEAST analyses produced the same topology (Fig. 2), which recovers all the same subclades and the highly supported nodes found in the RAxML and MrBayes topologies, even though the relationships among some of the subclades are different. The clade of *Bodianus flavifrons* + *B. frenchii* sister to *B. oxycephalus* + *B. unimaculatus*, and

the *B. bimaculatus* + *B. opercularis* are still the sequential sister lineages to all the remaining *Bodianus* + *Clepticus* + *Semicossyphus*, as in the MrBayes and RAxML topologies. After these lineages, the clade formed by *B. speciosus*, *B. eclancheri*, *B. perdition*, *B. bilunulatus*, and *B. macrorus*, which in the RAxML and MrBayes topologies appears to be deeply nested within the *Bodianus* + *Clepticus* + *Semicossyphus* group, is the next lineage to branch off, followed by *B. diplotaenia* + (*B. pulchelus* + *B. rufus*). The relationships among the remaining species show *Clepticus* + *B. anthoides* sister to *B. tanyokidus* + *B. trilineatus*, while the *Semicossyphus* + *B. scrofa* group is the sister taxon to (*B. axillaris* + *B. mesothorax*) + (*B. diana* + *B. dictynna*).

3.2 Divergence times of *Bodianus* and historical biogeography

Regardless of the choice of secondary calibration, the BEAST analyses recover very similar results for all the nodes, with broadly overlapping 95% HPD (see table S2). We will discuss here the ages of the tree in which the calibration point had been applied to the split between *Pseudodax* and the remaining species. The split between *Pseudodax* and the remaining species in our sampling is dated at 28 Ma (HPD), while that of *Choerodon* and *Bodianus* + *Clepticus* + *Semicossyphus* is dated at 27 Ma (21-36 Ma 95% HPD). The crown *Bodianus* + *Clepticus* + *Semicossyphus* starts diversifying ~ 20 Ma (15-28 Ma 95% HPD), with all major *Bodianus* lineages originating during the Miocene between 17 and 9 Ma. The *Clepticus* + *B. anthoides* is ~ 10 Ma (6-16 Ma 95% HPD), while the two species of *Semicossyphus* diverged from one another 4 Ma (2-7 Ma 95% HPD), after having split from *B. scrofa* 11 Ma (7-17 Ma 95% HPD).

The DEC+J and BayAreaLike+J models obtain scores that are substantially better than these of the simple models (i.e., without the jump dispersal parameter) (Table S3), even though the difference between the score of the DEC+J model and the BayAreaLike+J model is not large (Table S3). In the text that follows we report and discuss the results of the DEC+J model, which obtained the better score of all models, but we report the results of the BayAreaLike +J model in the supplementary material (Fig. S2). The DEC+J model recovers an ancestral area formed by the IWP and the SWP with an immediate split into two lineages, one with predominantly SWP distribution, formed by the clade that includes *Bodianus flavifrons*, *frenchii*, *oxycephalus* and *unimaculatus*, and a second lineage that includes all remaining taxa in our study. Within the first lineage our analysis inferred two Pliocene transitions from a SWP ancestor to different areas: the first involves the *B. frenchii* lineage moving into the IWP, while the second involves the *B. oxycephalus* lineage moving into the NWP.

The biogeographic history within the second lineage, ancestrally distributed in the IWP shows multiple transitions in different geographic regions and oceanic basins. The *Bodianus opercularis* lineage appears to cross the Indian ocean to invade the WIO towards the very end of the Miocene, ~ 6 Ma. The next lineage to branch off from the main *Bodianus* clade is hypothesized to have invaded the EA between ~ 16 and ~ 11 Ma. The only species sampled in our study still in the EA is *Bodianus speciosus*; other taxa from this group established themselves in the EP, giving origin to the extant *B. eclancheri*, and reinvaded the IWP and WIO. The third lineage to split from the main *Bodianus* group includes the EP *B. diplotaenia*, as well as two WA species, *B. rufus* and *B. pulchellus*. The split between the *Bodianus diplotaenia* and its sister lineage appears to

have occurred ~ 7 Ma, while the two WA taxa separated at the very beginning of the Pliocene, ~ 5 Ma. An Atlantic/Pacific split is also seen in the next lineage to originate, with the WA creole wrasse *Clepticus parrae* having split from the IWP *Bodianus anthoides* ~ 10 Ma. Within the remaining members of the *Bodianus* clade we observe several additional transitions: at least two recent (Late Pliocene) transitions from IWP ancestors to WIO extant species are observed in *B. diana* and *B. trilineatus*; we further observe a second EA/EP clade that includes *Bodianus scrofa* (EA), as well as the two species of sheephead wrasses, the EP California sheephead (*S. pulcher*) as well as the Asian sheephead (*S. reticulatus*). While the split between the sheephead lineage and its sister taxon dates to the Late Miocene, ~ 11 Ma, the California and Asian sheepheads split at the beginning of the Pliocene, ~ 5 Ma.

4. Discussion and conclusion

Our analyses revealed a robustly supported molecular phylogenetic hypothesis for hogfishes that corroborates the paraphyly of *Bodianus* without the inclusion of the *Clepticus* creole wrasses and the *Semicossyphus* sheephead wrasses. We also recover a number of well supported groups that are also congruent with several of the subgeneric lineages identified by Gomon (2006), even though our sampling and Gomon's (2006) sampling only partially overlap. Our analyses recover a clade that includes *B. bimaculatus* and *opercularis*, corresponding to the subgenus *Trochocopus* of Gomon (2006), a group that is characterized by small size (~18 cm or less, Gomon, 2006), with some species, such as *B. bimaculatus* reaching sexual maturity at length of just ~ 8 cm. A second clade includes *B. frenchii* and *unimaculatus* corresponding to *Verreo*, a group that

Gomon (2006) defines on the basis of the reduction of procurrent caudal fin rays to seven. *Bodianus axillaris* and *mesothorax* corresponding to the subgenus *Lepidaplois*, which morphologically is characterized by the presence of a juvenile color pattern with contrasting pale spots in identical positions on a dark background (Gomon 2006). The clade including *B. perditio* and *B. speciosus* corresponds to the subgenus *Diastodon*, defined by the presence of a distinct row of small peripheral teeth, while the clade that includes *B. diplotaenia*, *B. rufus*, and *B. pulchellus* corresponds to the subgenus *Bodianus*, characterized by the presence in adult individuals of filamentous posterior extensions of the dorsal and anal fins (Gomon, 2006). The clade of *Bodianus scrofa* and *Semicossyphus* is characterized by a more temperate distribution and association with rocky bottoms, with *B. scrofa* inhabiting the Eastern Atlantic (Azores, Canary Island and Cape Verde) and the three species of *Semicossyphus* found in both the Eastern and Northwestern Pacific.

Our phylogenies, as well as all previous labrid molecular phylogenies (Westneat and Alfaro, 2005; Alfaro et al. 2009; Cowman et al 2009; Kazancıoğlu et al. 2009) suggest that the taxonomic status of *Bodianus* requires major revisions, and that the tree species of *Clepticus* creole wrasses and the three species of *Semicossyphus* sheepheads should be reclassified as *Bodianus*.

The time calibrated phylogeny (Fig. 2) shows that all the major lineages of hogfishes originated in the Miocene, between ~ 17 Ma and 9 Ma. This time frame matches that of diversification for many other groups of reef-associated fishes that have their greatest diversity in the Indo-West pacific, including other wrasse lineages such as parrotfishes (Alfaro et al. 2009; Cowman et al 2009; Kazancıoğlu et al. 2009);

surgeonfishes (Sorenson et al., 2013); pufferfishes, boxfishes, triggerfishes and filefishes (Santini et al., 2013a, 2013b, 2013c), several lineages of damselfishes (Cowman and Bellwood, 2011; Frederich et al., 2013) and butterflyfishes (Cowman and Bellwood, 2011).

Our timetree, together with the BioGeoBear analysis, suggests that hogfishes originated in the Indo-west Pacific and South-west Pacific, and that this group experienced several episodes of transition between biogeographic regions and Ocean basins. At least two episodes of invasion of both the Eastern and Western Atlantic occurred, as well as at least found events of invasions of the Western Indian Ocean and three episodes of invasions of the Eastern Pacific. All splits between Atlantic and Pacific sister lineages appear to consistently predate the “traditional” age of the closing of the Isthmus (3.1 Ma, Briggs and Bowen, 2012); however, this might be due to the fact that our sampling includes slightly less than the diversity of hogfishes and we are missing more recent lineages that might alter the age of the split between geminate species pairs.

A denser taxonomic sampling will be needed to determine with greater accuracy the routes of dispersal for some of these lineages and the timing of these events. For example, the current reconstruction suggests that the clade including *Bodianus speciosus*, *B. eclancheri*, *B. perditio*, *B. bilunulatus* and *B. macrourus* could have originated in the Eastern Atlantic, crossed the Atlantic to invade the Eastern Pacific and from there managed to recolonize the Indo-west Pacific and the Western Indian Ocean, but adding as yet unsampled species that belong to this group could suggest that the group was originally always distributed in the Indo-west Pacific and from that are a number of independent lineages manages to invade the Eastern Atlantic and the Eastern

Pacific. In spite of this it is clear that hogfishes and their allies experienced a highly dynamic biogeographic history with repeated transitions between geographic regions.

Acknowledgements

We thank Peter Wainwright (UC Davis) and Mark McGrouther (Australian Museum) for loan of tissues used for this study. Funding for this project was provided by NSF grant DEB 0842397 “Systematics and Influence of Coral Reefs on Diversification in Tetraodontiform Fishes.” to MEA as well as by XSEDE grants TG-DEB140025 to FS.

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Figure and table legends

Figure 1. Bayesian phylogenetic hypothesis of *Bodianus* relationships based on analysis of the concatenated dataset using Mrbayes 3.2. Nodes that have PP greater than 0.95 and BSP greater than 90% are indicated by a star symbol (*).

Figure 2. *Bodianus* timetree based on a Bayesian relaxed clock approach implemented in BEAST 1.8 Horizontal bars on each node indicate 95% HPD confidence intervals.

Timescale at bottom of figure is in million years before present. All fish images modified under Creative Commons license from original photographs by J.E. Randall (retrieved from <http://www.fishbase.org>) with the exception of: *Bodianus unimaculatus*, licensed under Public Domain via Wikimedia Commons; *Bodianus pulchellus* originally posted to Flickr by Cliff, Licensed under CC BY 2.0 via Wikimedia Commons; *Clepticus parrae*, pone.0010676.g111 by Williams et al. (2010), licensed under CC BY 2.5 via Wikimedia Commons; *Semicossyphus pulcher*, by Gerick Bergsma , Attribution-Non Commercial 3.0 Unported (CC BY-NC 3.0) via Wikimedia Commons.

Figure 3. Preferred model of biogeographic reconstruction (DEC + J) according to biogeographic analysis of *Bodianus* species distribution. Abbreviations of geographic areas as follows: A, Western Atlantic; B, Eastern Pacific; C, Indo-western Pacific; D, Western Indian Ocean; E, South-western Pacific; F, North-western Pacific; G, Eastern Atlantic.

Table 1. List of taxa included in this study with geographic distribution. Abbreviations of geographic areas as follows: W. Atl, Western Atlantic; E. Pac, Eastern Pacific; IW. Pac, Indo-western Pacific; W. Ind, Western Indian Ocean; SW. Pac, South-western Pacific; NW. Pac, North-western Pacific; E. Atl, Eastern Atlantic.

Figure 1

Figure 2

Figure 3

	W. Atl	E. Pac	IW. Pac	W. Ind	SW.	NW.	E. Atl
(areas in Fig 3)	A	B	C	D	E	F	G
<i>B. anthoides</i>	0	0	1	0	0	0	0
<i>B. axillaris</i>	0	0	1	0	0	0	0
<i>B. bilunulatus</i>	0	0	1	0	0	0	0
<i>B. bimaculatus</i>	0	0	1	0	0	0	0
<i>B. diana</i>	0	0	0	1	0	0	0
<i>B. dictynna</i>	0	0	1	0	0	0	0
<i>B. diplotaenia</i>	0	1	0	0	0	0	0
<i>B. eclancheri</i>	0	1	0	0	0	0	0
<i>B. flavifrons</i>	0	0	0	0	1	0	0
<i>B. frenchii</i>	0	0	1	0	0	0	0
<i>B. macrourus</i>	0	0	0	1	0	0	0
<i>B. mesothorax</i>	0	0	1	0	0	0	0
<i>B. opercularis</i>	0	0	0	1	0	0	0
<i>B. oxycephalus</i>	0	0	0	0	0	1	0
<i>B. perditio</i>	0	0	1	0	0	0	0
<i>B. pulchelus</i>	1	0	0	0	0	0	0
<i>B. rufus</i>	1	0	0	0	0	0	0
<i>B. scrofa</i>	0	0	0	0	0	0	1
<i>B. speciosus</i>	0	0	0	0	0	0	1
<i>B. tanyokidus</i>	0	0	1	0	0	0	0
<i>B. trilineatus</i>	0	0	0	1	0	0	0
<i>B. unimaculatus</i>	0	0	0	0	1	0	0
<i>C. parrae</i>	1	0	0	0	0	0	0
<i>S. pulcher</i>	0	1	0	0	0	0	0
<i>S. reticulatus</i>	0	0	0	0	0	1	0