LITTLE EVIDENCE FOR SYMPATRIC SPECIATION
IN ISLAND BIRDS

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Abstract.—It has been suggested that the presence of sister species in small circumscribed areas, such as isolated lakes or islands, might imply that these species originated sympatrically. To investigate this possibility in birds, we searched for endemic, congeneric species on isolated islands in the ocean. Among 46 islands and small archipelagos chosen because they contain at least one species of endemic land bird, we identified seven pairs of endemic congeners (excluding flightless rails). Of these seven, only four pairs are potentially sister species and thus possible candidates for sympatric speciation. However, three of these four pairs have always been considered the results of double invasion from a mainland source (in two of these cases, molecular-phylogenetic work has either confirmed a double invasion or is ambiguous). The one remaining pair may have speciated allopatrically on a small archipelago. Additional phylogenetic studies are required to understand these cases, and our results should also be considered in light of the large number of island-bird extinctions in historic time. We conclude that, at present, there is little evidence for sympatric speciation in island birds.

Key words.—Biogeography, birds, oceanic islands, sympatric speciation.

One of the most persistent controversies in evolutionary biology is whether the formation of new species requires a period of geographical isolation between populations (allopatric speciation) or whether reproductive isolation can evolve without any such isolation (sympatric speciation). Nearly all evolutionists agree that most species arise in allopatry, but there is no present consensus about whether sympatric speciation is common or rare.

For much of the past 50 years, most biologists believed that sympatric speciation was extremely rare. This view derived largely from the arguments of Mayr (1942, 1963), from analyses of claimed cases of sympatric speciation (Futuyma and Mayer 1980), and from theoretical studies suggesting that sympatric speciation might occur only under relatively stringent genetic and environmental conditions (e.g., Felsenstein 1981).

Recently, however, sympatric speciation has again become popular. New theoretical models have shown that the process is plausible under some conditions, especially the absence of competitors or predators (Dieckmann and Doebeli 1999; Higashi et al. 1999; Kondrashov and Kondrashov 1999). At least one laboratory experiment (Rice and Salt 1990) demonstrated the sympatric origin of habitat isolation via disruptive artificial selection. Finally, many biologists (e.g., Rice and Hostert 1993; Skúlason and Smith 1996; Feder 1998; Seehausen and van Alphen 1999) now feel that at least the initial stages of sympatric speciation can be seen in nature. Although the strength of the evidence varies among cases, the most convincing examples are the miniradiations of tiliapine cichlid fish in two tiny volcanic crater lakes in Cameroon, 4 km^2 and 0.6 km^2 in area (Schliewen et al. 1994). Molecular evidence shows that each caldera lake harbors a recently evolved monophyletic group (11 and nine fish species, respectively). If, as seems likely, this is a true case of

sympatric speciation, it implies that the process has also occurred elsewhere, but is much harder to detect in geographically complex habitats. Allopatric speciation, in contrast, is much easier to infer because many closely related species, such as those formed on islands after invasion from the mainland or on land masses that have drifted apart, are unlikely to have ever been sympatric.

There are at least two types of evidence for which sympatric speciation seems a more parsimonious explanation than does allopatric speciation. The first involves comparative data. In a large group with a well-understood phylogeny, one may find a correlation between the age of divergence of pairs of sister taxa and the degree of geographic overlap between them. Sympatric speciation would be indicated if the youngest pairs had the highest range overlap (Barraclough and Vogler 2000). The second method involves assaying isolated patches of habitat for the presence of endemic sister species whose individuals are quite mobile. White (1978) was among the first to use this method and considered sympatric speciation responsible for several adaptive radiations of insects on isolated oceanic islands, including the proliferation of weevils on Rapa and St. Helena. White's evidence, however, is problematic because there have been no thorough phylogenetic studies showing that the insect groups cited are monophyletic. More important, the candidate taxa have individuals of rather low mobility. The weevils of St. Helena and Rapa, for example, are tiny wingless insects having limited ranges upon the islands (Paulay 1985). These groups may thus have undergone microallopatric speciation, that is, true allopatric speciation occurring in a small geographic area.

Because most birds are highly mobile, and thus unlikely to speciate allopatrically on islands of moderate size, they are especially useful for the island test of sympatric speciation. Although some consider sympatric speciation in birds

as a priori unlikely or impossible, several workers have posited that it may occur rarely (e.g., Grant and Grant 1989) or even with moderate frequency (e.g., Skúlason and Smith 1996; Payne and Krakauer 1997; Dieckmann and Doebeli 1999). Here we examine the possibility of sympatric speciation in birds by searching for pairs of endemic sister species on remote and relatively small oceanic islands. The opportunities for allopatric speciation on such islands are greatly reduced because of their size and the mobility of birds. At the same time, the difficulty of dispersal results in relatively few competitors and predators, a situation that, according to recent theory (e.g., Dieckmann and Doebeli 1999; Higashi et al. 1999), is favorable for sympatric speciation.

Diamond (1977) suggested that only very large islands or archipelagoes—roughly the size of New Guinea or the Hawaiian Islands—have endemic sister species of birds, in agreement with the common view that birds speciate allopatrically. However, he did not present a systematic survey of the birds on smaller oceanic islands. Recently, Stattersfield et al. (1998) published a comprehensive survey of geographically restricted bird species. We used this catalogue to search for pairs of endemic, congeneric species on 46 oceanic islands or small archipelagos and on one continental island.

Our goal is not to make a definitive statement about the frequency of sympatric speciation in birds, but to determine whether the process seems rare or frequent. Moreover, we wanted to bring to the attention of evolutionists any *potential* cases of sympatric speciation that deserve further study. As we shall see, nearly all of the few potential cases have been reasonably interpreted as allopatric speciation following double invasions from another land mass (e.g., Mayr 1942; Lack 1944; Grant 1968; Diamond 1977). We therefore find no strong evidence for sympatric speciation in birds.

METHODS

Our criterion for a *possible* case of sympatric speciation was the discovery on an isolated island of two or more species of endemic bird in the same genus. If evidence from other sources indicated that these were likely to be sister species (i.e., each other's closest relative), we would regard this as a *potential* case of sympatric speciation. We did not include congeners in which one species was not endemic, but discuss below the results of this omission.

Using Stattersfield et al. (1998) and other sources, we located islands throughout the world that were fairly isolated from the nearest mainland (see Table 1 for all data). Each chosen island had to harbor at least one endemic species of land bird (we excluded all seabirds from the analysis). We used only islands smaller than 10,000 km², an area chosen arbitrarily on the assumption that bird speciation on larger islands could be allopatric. In 10 cases, we used data from very small archipelagoes, which we defined as an isolated group of at least two islands, each no more than 50 km from one other island in the group and not including small islets (Table 1).

RESULTS

The sizes of our 46 islands or archipelagos ranged from 0.8 km² (Nihoa) to 3500 km² (Socotra) with a median size

of 78.5 km². The only continental island we included was Socotra (190 km from the nearest mainland) because it has a pair of endemic congeners. Seven of our 46 islands and archipelagos were in the Atlantic Ocean, seven in the Indian Ocean, and the remaining 32 in the Pacific. Most of the islands are tropical. The median distance of the islands from the nearest mainland or subcontinent was 2250 km, and the median distance from the nearest island (including islands in small archipelagos) was 200 km.

Besides listing the islands studied, Table 1 gives their areas and the number of endemic land bird species, including recent extinctions (roughly within the past 200–300 years). The number of endemic species per island ranged from one to 16, with a median of two. We also give the number of indigenous land bird species, including those known from fossils, as an indication of the availability of ecological niches for birds on these islands. Because extinction on islands has been widespread (Steadman 1995) and because not all islands have been surveyed for fossils, these lists provide minimum estimates of the number of species inhabiting each island during human history. The number of resident species of land birds on each island or small archipelago ranged from one to 36, with a median of nine.

We identified seven pairs of endemic congeneric species inhabiting an oceanic island and one pair inhabiting a continental island. Yap, Norfolk, and Lord Howe each have a pair of endemic white-eyes (*Zosterops*). Sao Tome has a pair of congeneric weavers (*Ploceus*) and a pair of congeneric sunbirds (*Nectarinia*). The small archipelago of Tristan da Cunha has a pair of congeneric endemic buntings (*Neosospiza*). The small Chatham archipelago has a pair of extinct flightless rails, *Gallirallus*. Such rails were formerly widespread in the Pacific, so there may have been other islands containing pairs of endemic rails in which one or both members have gone extinct (Steadman 1995). Finally, the continental island of Socotra has two endemic species of *Cisticola*.

Of these eight pairs of congeners, three—the Yap white-eyes (*Z. olagineus* and *Z. hypolais*), the Sao Tome buntings (*P. grandis* and *P. sanctithomae*), and the Socotra cisticolas (*C. haesitatus* and *C. inanus*)—are clearly not each other's closest relatives because each of the two species is a member of a different superspecies group that is widely distributed (see, respectively, Slikas et al. 2000; Moreau 1966; Ripley and Bond 1966). Recent phylogenetic analysis of the congeneric Yap white-eyes based on mitochondrial DNA sequences confirms that they are not sister species (Slikas et al. 2000). These three pairs are thus very unlikely to be products of sympatric speciation.

Of the five remaining pairs, three—the Lord Howe white-eyes (*Z. tephlopleurus* and *Z. strenuus*), the Norfolk white-eyes (*Z. tenuirostris* and *Z. albogularis*), and the Sao Tome sunbirds (*N. newtoni* and *N. thomensis*) have always been considered cases of double invasion, in which the same mainland lineage invaded an island twice in succession, with each invader becoming a new species allopatrically (Mayr 1963, pp. 504–506; Moreau 1966, pp. 323–324). The double-invasion hypothesis rests on the observation that, in each case, one of the two endemic island species closely resembles a mainland species (and thus is supposedly derived from a more

TABLE 1. Islands in the ocean and their bird inhabitants. Endangered bird area (EBA) numbers are taken from Stattersfield et al. (1998) and refer to the section of that book for that island. Endemic land bird species are from Stattersfield et al. (1998) and include species that went extinct after 1700. Total species are taken from various sources in the literature (list of references available at www.biology.ucsd.edu/~tprice/Islandbirds), and includes, where known, species that have become extinct since human colonization (in parentheses).

Island name	EBA number	Area (km²)	Endemic land bird species	Total species (extinct)
Aldabra	99	160	2	23 (10)
Alejandro Selkirk	59	85	1	5
Annobon	81	17	2	6
Antipodes*	s133	21	1	4
Atiu	210	28	1	6
Auckland Islands	208	610	2	12
Chatham Islands*	209	970	8	36 (19)
Christmas Island	188	140	2	9
Clarion	s008	28.4	1	4
Cocos	22	47	3	4
Easter (Rapa Nui)[1]	—	163	—	6 (6)
Enggano	159	450	2	9
Fernando de Noronha*	69	18	2	4 (1)
Gough	80	65	2	2
Guadalupe	3	280	2	10
Henderson	215	31	4	9 (5)
Kosrae	192	110	2	10 (30)
Laysan	216	3.7	3	5
Lord Howe	204	17	5	21 (8)
Mangaia	210	65	1	16 (13)
Mauritius	102	1900	9	28
Nauru	s124	21	1	3
Nihoa	s138	0.8	2	4
Niuafo'ou	s129	55	1	11
Norfolk*	205	35	5	20 (5)
Northern Line Islands (Kiritimati)*	s134	364	1	3 (1)
Pemba	110	980	4	72
Pitcairn	s137	4.6	1	2
Pohnpei	192	30	5	18
Principe	83	140	6	19
Rapa	s136	40	1	3
Rarotonga	210	67	2	6
Rennell and Bellona*	199	825	5	36
Réunion	101	2500	6	27
Rimatara	211	8	1	2
Robinson Crusoe	59	93	1	7
Rodrigues	103	110	6	13 (10)
Rotuma	s127	47	1	10
Sao Tome	81	860	16	28
Socorro	4	150	4	9
Socotra	117	3500	6	28
St. Helena	s038	122	5	5 (4)
Tristan da Cunha*	79	110	5	5 (1)
Truk (Chuuk)*	192	72	3	16
Wake	s122	7	1	1
Yap Islands*	191	120	3	14 (4)

* These islands are actually small archipelagos.
[1] Easter Island is not in Stattersfield et al. (1998); data are from Steadman (1995).

recent invasion), whereas the other is more divergent (thus derived from an earlier invasion). Indeed, one of the two Lord Howe white-eyes, *Z. tephlopleurus,* is usually considered conspecific with the mainland species *Z. lateralis* (Sibley and Monroe 1990).

Populations of *Z. lateralis* inhabit other offshore islands around Australia. For example, the species became established on Norfolk Island in the early part of this century. Species of *Zosterops* are generally good dispersers and inhabit islands throughout the Pacific. These observations make multiple colonization events the most plausible explanation for the presence of pairs of endemic *Zosterops* on islands.

However, there is an alternative explanation to double colonization: A single colonization from the mainland could result in the sympatric production of two island species, one remaining morphologically similar to the mainland form and the other becoming more divergent. This possibility can be tested with phylogenetic analysis, as was recently done for the white-eyes of Lord Howe and Norfolk by S. Degnan, L. Kelleman, and C. Moritz (pers. comm.). Mitochondrial DNA evidence clearly shows that the Lord Howe white-eyes represent a double invasion. The Norfolk Island species, *Z. tenuirostris* and *Z. albogularis,* are genetically only slightly less distinct from each other than they are from the mainland form.

For now the sequence of colonization and speciation in this pair remains equivocal.

Phylogenetic analysis of mitochondrial DNA from rails on the Chatham Island archipelago (*Gallirallus dieffenbachii* and *G. modestus*) suggests that they may be sister species (Trewick 1997a). This, in turn, implies intra-island, or at least intra-archipelago, speciation. Nevertheless, Trewick (1997b) considers the double-invasion scenario to be plausible, apparently because the phylogeny is not sufficiently resolved. Flightless rails are unusual because their limited mobility causes a high degree of endemicity (Trewick 1997b). Some islands of the Pacific may have harbored up to four species of such rails, but most are now extinct (Steadman 1995). Although the widely accepted scenario for island speciation in rails involves multiple invasions from a flying ancestral form, we need more genetic analyses of fossil material along the lines of Trewick's study.

The final example of congeneric endemics includes the two species of bunting (*N. acunhae* and *N. wilkinsi*) endemic to the small archipelago of Tristan da Cunha. Even here we cannot rule out allopatric speciation because both buntings inhabit more than one island. Lack (1976) and others favored the allopatric scenario for Tristan buntings by noting that the isolated island of Gough, which is 350 km from Tristan, contains only a single endemic species. But this is at best weak support for allopatric speciation on Tristan.

DISCUSSION

We find no conclusive evidence for sympatric speciation of birds on oceanic islands and (excluding rails) only three cases (Sao Tome sunbirds, Norfolk island white-eyes, and Tristan buntings) for which the double-invasion hypothesis remains equivocal and in need of further study. It is common to find double invasions across smaller water gaps, such as within Hawaii and Galapagos, as well as between continents and continental islands (Lack 1944; Grant 1968; Diamond 1977), so we might expect to see a few examples of this phenomenon occurring over greater distances. Only phylogenetic analysis can resolve this problem by determining whether each island's endemic congeners are sister species. Such analysis may not be definitive, however, because of the problems of resolving phylogenetic trees if there is hybridization, persistent polymorphisms inherited from recent ancestors, or unequal rates of molecular evolution. Moreover, the phylogenetic test is less useful for congeners on small archipelagos than on isolated islands, because sister species on archipelagos may have originated allopatrically and re-invaded other islands. The buntings of Tristan da Cunha and rails of the Chatham Islands may thus be unresolvable cases.

There are at least three reasons why our method may not detect some cases of sympatric speciation. First, we arbitrarily set the upper limit on island size at 10,000 km^2, and sympatric speciation may occur on larger islands. The slightly larger oceanic island of Jamaica (11,400 km^2), for example, contains an endemic genus of hummingbird (*Trochilus*) with two species. However, their abutting distributions, with one species on each side of the John Crow Mountains, imply that this pair has speciated allopatrically (Schuchmann 1978; del Hoyo et al. 1999, p. 572). These species are also very similar in morphology and have often been considered conspecific (e.g., Lack 1976). We know of no other examples of intra-island bird speciation occurring on islands smaller than Madagascar (600,000 km^2; see Diamond 1977).

Second, there have been many historical extinctions, especially on Pacific islands. Steadman (1995), for example, estimates that these islands harbored at least 2000 species of birds that became extinct after human colonization. Many of these were flightless rails, usually assumed to be descendants of flying colonists (Trewick 1997b). There were also many species of doves and parrots that were probably widely distributed (Steadman 1995, 1997) and thus are unlikely to meet our criteria for sympatric speciation. There is nothing we can do to recover these missing species, a fact that should be borne in mind when considering our results.

Finally, our test involves observing two or more endemic congeners on an island. Thus, we may have missed examples of speciation in which one endemic is produced sympatrically from a widespread ancestral form with which it continues to co-occur. For example, if Stattersfield et al. (1998) had agreed with Sibley and Monroe (1990) in considering the Lord Howe white-eye (*Z. tephlopleurus*) conspecific with the Australian mainland species (*Z. lateralis*), we would not have considered the pair of *Z. tephlopleurus/Z. strenuus* as a possible case of sympatric speciation. We found a few examples of this possible form of sympatric speciation. The widespread Micronesian starling *Aplonis opaca,* shares one endemic congener (*A. pelzelni*) on Pohnpei and another (*A. corvina*) on Kosrae. The Antipodes have two parrots—one endemic and the other nonendemic—in the genus *Cyanorhamphus*. The nonendemic species inhabits the Antipodes and in the Macquarrie Islands, but is found nowhere else (Waite 1909). Phylogenetic analysis might be used to determine the likelihood of sympatric speciation in these cases. For example, if the population of *A. opaca* on an island was genetically more similar to the endemic congener than to other island populations of *A. opaca,* this would suggest that the endemic congener had arisen sympatrically. However, such a finding might only indicate some gene flow between two species that are currently sympatric but originated allopatrically. Alternatively, true sympatric speciation might be missed because ongoing gene flow between island populations of the widespread *A. opaca* would genetically homogenize the species and reduce the phylogenetic signal of sympatric speciation.

We studied oceanic islands because they offer the best opportunity to detect sympatric speciation. However, oceanic islands may have features that reduce the likelihood of sympatric speciation; thus, our failure to find evidence for the process may not hold in other habitats (but see the discussion of Barraclough and Vogler's work below). Nevertheless, sympatric speciation driven by sexual selection or by competition for resources proceeds most effectively in the absence of competitors and predators (Dieckmann and Doebeli 1999; Higashi et al. 1999), conditions perhaps more frequent on islands than on continents. Although we know little about the distribution of resources on oceanic islands, in many cases islands are able to support multiple *allopatrically* formed species of birds (Table 1). For example, the 150-km^2 island of Socorro contains nine unrelated species of land birds, four

of which are endemic (Brattstorm and Howell 1956; Stattersfield et al. 1998).

Additional evidence for appreciable resource diversity on islands comes from habitat-related morphological differences *within* species on oceanic islands. Réunion, for example, contains three morphologically differentiated populations of the gray white-eye, *Zosterops borbonicus* (Gill 1973). On Inaccessible, part of the small Tristan da Cunha archipelago, the Tristan bunting (*N. acunhae*) shows an altitudinal cline in color (Ryan et al. 1994). There are other examples of such differentiation within oceanic and nonoceanic islands (e.g., Wunderle 1981) as well as evidence for extraordinarily broad resource use by some species (e.g., Werner and Sherry 1987).

The best interpretation for the absence of endemic congeners on isolated islands is that sympatric speciation is uncommon in birds. This conclusion supports the general impression of earlier writers (e.g., Mayr 1947), who often cited the observation that whereas small islands in the Galapagos archipelago harbor multiple species of Darwin's finch, the isolated island of Cocos has only one species. More recent analysis also supports a general rarity of sympatric speciation in birds. Using comparative methods, Barraclough and Vogler (2000) examined various animal groups, correlating the divergence time between sister taxa with their amount of range overlap. Sympatric speciation would be indicated if the most recently diverged groups had very high range overlap and allopatric speciation if there were very low range overlap for recently diverged taxa followed by increasing overlap of older taxa due to range expansion. In fact, Barraclough and Vogler (2000) observed the latter pattern in all four groups of birds examined: warblers (*Sylvia*), fairy wrens (*Malurus*), cranes (Gruidae), and auks (Alcidae).

The paucity of endemic sister taxa of birds on oceanic islands contrasts with data on less mobile species. As noted above, St. Helena and Rapa were sites of dramatic radiations of some insects, which almost certainly included the production of endemic sister taxa. The disparity between birds and these insects probably derives from two factors: host-specificity and mobility. Many groups of insects are more host specific than birds and often tend to mate on the host plant, factors that considerably ease the difficulty of sympatric speciation (Johnson and Gullberg 1998). The lesser mobility of insects could also facilitate allopatric speciation on islands or small archipelagoes (for distributional data supporting microallopatric speciation in Rapa weevils, see Paulay 1985). Flightless rails, such as the extinct pair on Chatham, likewise have limited mobility, and it is possible that phylogenetic analysis of extinct rails will turn up cases of intra-island speciation in this group.

Finally, of course, our results say nothing about whether sympatric speciation may be more likely in other groups (Bush 1994). Indeed, Barraclough and Vogler (2000) show several possible cases in tephritid flies (*Rhagoletis*) and tiger beetles (*Ellipsoptera*), although not in swordtail fish (*Xiphophorus*) or leafhoppers (*Flexamia*). As the controversy about sympatric speciation eventually moves beyond demonstrations of its occurrence to questions about its relative frequency, we encourage others to search for related, endemic species occupying small and isolated patches of habitat.

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SPECIES RECOGNITION AS A POSSIBLE FUNCTION FOR VARIATIONS IN POSITION AND SHAPE OF THE SEXUALLY DIMORPHIC TUSKS OF *MESOPLODON* WHALES

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Abstract.—Beaked whales of the genus *Mesoplodon* are characterized by the presence of a single pair of sexually dimorphic tusks. Variation in the position and shape of these tusks was examined in four sympatric species and was found to be consistent with the hypothesis that these differences may have evolved to aid species recognition between sympatric and otherwise morphologically similar species of this genus.

Key words.—Beaked whales, dentition, *Mesoplodon,* species isolating mechanism, species recognition.

Beaked whales of the genus *Mesoplodon* are characterized by the presence of a single pair of teeth located in the lower mandible which only erupt in adult males where they form tusks (Mead 1989). These tusks, which are used in intrasexual combat, vary greatly in position and shape between the fourteen *Mesoplodon* species. Position varies from the tip of the jaw (*M. mirus*) to close to the middle of the lower jaw in the dense beaked whale, *M. densirostris* and shape varies from small conical tusks in True's beaked whale, *Mesoplodon mirus,* to 30 cm long strap-like tusks in *M. layardii* (Heyning 1984; Mead 1989).

Here I propose that the variation in position and shape of the tusks observed in *Mesoplodon* species may function as a precopulatory species isolating mechanism by acting as a species recognition character. However, testing such a hypothesis for the genus *Mesoplodon* is fraught with problems.

The beaked whales are one of the least known families of mammals and, due to their preference for oceanic habitats and generally boat-shy behavior, it is likely to remain this way in the near future. Several species of beaked whale, mostly of the genus *Mesoplodon* have yet to be seen alive and it is unclear whether all species are as yet known to science. However, some circumstantial evidence does suggest that this hypothesis may be correct.

Mesoplodon is the only genus of the six genera of beaked whales which contain similar sympatric species and also is the only genus where the sexually dimorphic tusks common to all beaked whales have changed from the primitive apical position and conical shape. In addition, sympatric species of *Mesoplodon* differ greatly in the position and/or shape of their tusks. For example in the North Atlantic, Sowerby's beaked whale, *Mesoplodon bidens*; True's beaked whale; the Antil-
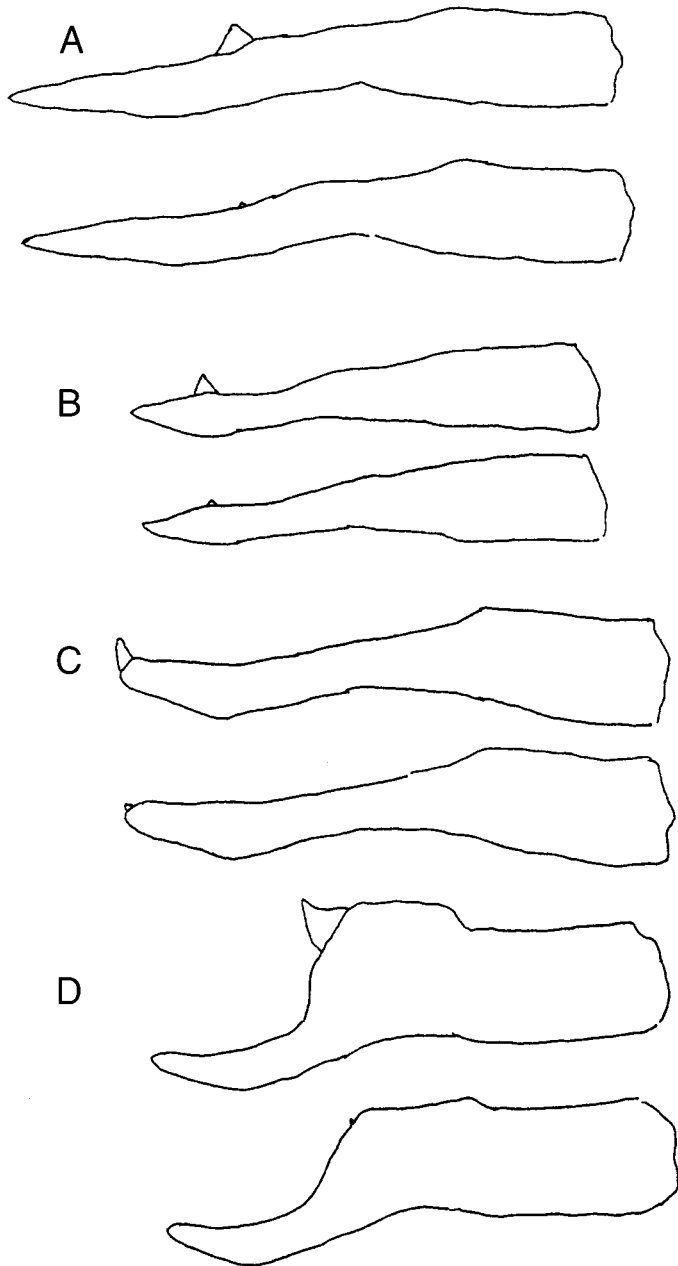
FIG. 1. Mandible morphology in the four species of *Mesoplodon* which occur sympatrically in the North Atlantic. (a) *M. bidens,* (tusks 38% of mandible length from tip, mandible flat), (b) *M. europaeus* (tusks 17% of mandible length from tip, mandible flat), (c) *M. mirus* (tusks at the tip of the mandible, mandible flat), and (d) *M. densirostris* (tusks 41% of mandible length and raised on stepped mandible). Males are upper drawing and females lower in all cases.

lean beaked whale, *Mesoplodon europaeus*; and the dense beaked whale are sympatric in warm temperate waters (MacLeod, in press). These four species differ considerably in position, and to a lesser extent, shape of their tusks (see Fig. 1). Adult males with their erupted tusks are easily identifiable to species level. In comparison females of the first three species, lacking erupted tusks, are virtually indistin-

guishable when external morphology is examined, whereas females of *M. densirostris* only differ due to the presence of a slight step in the mandible which is presumably related to its greater development in males rather than being functional in females (see Fig. 1).

Whether beaked whales of the genus *Mesoplodon* require a specific species recognition character is a somewhat speculative area. Mead (1989) noted that the only morphometric measurements which differed significantly between *Mesoplodon* species occurred in the mandibles and rostrum. These differences may relate to tooth position as species with relatively longer rostrums generally have teeth in a more posterior position. In addition, in the order Cetacea, there appears to be few, if any, postcopulatory species isolating mechanisms as successful hybridization between many species, genera, and even sub-families have been recorded, (e.g., Fraser 1940; Nishiwaki and Tobayama 1982; Reyes 1996). This suggests that there is a need for precopulatory species isolating mechanism in Cetaceans to ensure that similar sympatric species do not interbreed.

Based on the present limited data, species recognition provides a feasible explanation for the variation in position and shape of the sexually dimorphic tusks found in this genus. However, the possibility of whether any other functions can also explain such variation must be considered. The function of the tusks in male-male combat cannot readily explain the variation in dental morphology. Analysis of scarring indicates all *Mesoplodon* species, and possibly all beaked whales, fight in a similar manner (a series of passes where the animals swim towards each other and make contact using the tusks; forward movement is then used to create long linear wounds; MacLeod and Claridge 1998). It would, therefore, be expected that, if fighting was the main selective pressure on tusk position and shape, all beaked whales would have tusks in a similar position due to similar selective pressures imposed by fighting (i.e., all at the tip of the jaw or all set more posteriorly). In addition in one species, *M. layardii,* the tusks have changed in such a way that the cutting points have been greatly reduced in comparison to other species, consisting of small points on the top of otherwise elaborate tusks which cross over the upper jaw.

It is possible that ecological differences between species which are apparently sympatric could be responsible for any differences in morphology and indeed could negate the need for a specific species recognition character. The most likely ecological differences to affect dentition is diet. However, there is no evidence that the tusks are required for feeding as both juveniles and adult females are functionally toothless and still manage to feed, and where it has been examined no difference has been found between the diet of adult males and other age/sex classes (Sekiguchi et al. 1996). In addition, all *Mesoplodon* species apparently fill a very similar ecological niche as they all eat similar, and in many cases the same, prey species (such as deep water squid of the genera *Gonatus, Histioteuthis,* and *Taonius*; Mead et al. 1982; Debrot and Barros 1992; Herman et al. 1994; Sekiguchi et al. 1996; Gannon et al. 1998). In addition, sympatric *Mesoplodon* species are often recorded occurring in the same areas (see MacLeod, in press). This suggests there is little or no eco-

logical separation which could account for variations in tusk position and shape.

The hypothesis outlined above, if it is correct, has two important implications for the study of the genus *Mesoplodon.* Firstly, it may help to explain the current distribution of *Mesoplodon* species. Most are limited to one or two oceans, whereas *M. densirostris* is found in all tropical and subtropical waters of the world (Mead 1989). Species may be prevented from entering other oceans, despite the presence of suitable habitats, by the existence of species which already occupy their species recognition ''niche'' (i.e., their tooth position and to a lesser extent tooth shape) and other neighbouring ones. However, *M. densirostris,* in addition to altering the shape and position of the teeth, has altered the shape of the lower jaw itself. As a result, *M. densirostris* has filled a novel and previously unoccupied species recognition ''niche'' not seen in any other *Mesoplodon* species. This may have permitted *M. densirostris* to colonize all possible zoogeographic areas without clashing with species recognition characteristics of existing species.

Secondly, it may help to clarify the evolution of this genus, which is currently shrouded in uncertainty due to the lack of an adequate fossil record (Mead 1989). Allopatric species may have evolved similar dental morphologies as a result of similar unoccupied species recognition niches being available in different area, rather than it reflecting a close evolutionary relationship. This may help to explain why otherwise morphologically very similar species, such as *M. carlhubbsi* and *M. bowdoini* and the northern and southern Pacific *M. hectori,* do not group together when their molecular relatedness is examined (see Dalebout et al. 1998).

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