THE SYSTEMATIC POSITION OF THE PLANTCUTTERS, *PHYTOTOMA*

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ABSTRACT.—We used electrophoretic, syringeal, and osteological characters to establish affinities of the plantcutter genus *Phytotoma*. Both biochemical and morphological characters support placement of the plantcutters within the cotinga genus *Ampelion*. We retain the genus *Phytotoma* to recognize the distinctiveness of the plantcutters and we split *Ampelion* into the previously recognized genera *Ampelion, Doliornis,* and *Zaratornis*. We recommend placement of these taxa (seven species) within the family Phytotomidae. *Received 26 August 1988, accepted 9 March 1989.*

THE PLANTCUTTERS, three species endemic to southwestern South America, have been placed traditionally in the family Phytotomidae within the nontyrannid complex (cotingas, manakins, sharpbills, and plantcutters) of the New World Tyrannoidea (see literature reviews by Kuchler 1936, and Sibley 1970). The evolutionary relationships of the plantcutters to the other members of this complex remain unclear. Kuchler's recommendation that *Phytotoma* be placed within the Cotingidae, based on a general anatomical study, has not been followed (Meyer de Schauensee 1966; Snow 1973, 1982). Ames (1971) on the basis of syringeal morphology stated that "The evident similarity of the syrinx of *Phytotoma* to that of some cotingas (particularly *Heliochera* [now *Ampelion*]) may indicate merely that both groups have retained primitive syringeal structure." Ames maintained plantcutters as a distinct family. Sibley and Ahlquist (1985) also argued that *Phytotoma* should be placed with cotingas in their Cotinginae. Their argument was as follows: "Although we do not yet have DNA hybridization data for the plantcutters, it seems clear that they are members of the cotingine radiation. Morphologically *Phytotoma* is even more like typical cotingas than is *Oxyruncus*, which is clearly a cotinga. We therefore include *Phytotoma* in the Cotinginae." Warter (1965) examined the cranial evidence and commented that "*Phytotoma* skulls are every bit as distinct as the phytophagous habits of the birds would lead one to anticipate. Even if a common ancestry is assumed for the two families (Phytotomidae and Cotingidae), there is evident an evolutionary gap great enough to justify family-level separation."

Such evolutionary "gaps," though of great interest as they pertain to questions concerning adaptive zones and rates of evolution, may be problematical for phylogenetic systematists. There is no guarantee that the clusters are monophyletic unless the characters that define the gap are all both shared and derived. The ability to detect correct transformation series, however, is frequently limited. Through inappropriate selection or unavailability of outgroups, it is possible to devise incorrect transformation series. Because such errors are not generated by any underlying pattern, they should not be repeated in the analysis of additional character sets. Therefore, to improve our ability to reconstruct phylogenetic patterns, we may employ multiple character sets and look for points of congruence.

Observations of behavior and vocalizations, made by Theodore A. Parker III (pers. comm.), suggested a close relationship between *Phytotoma* (Traylor 1979) and those cotingids presently assigned to the genus *Ampelion* (Snow 1979). Allelic frequencies in the Tyrannoidea (S. Lanyon 1985a) provided further support for a close relationship between these taxa. Our goal was to examine the phylogenetic affinities of *Phytotoma* as indicated by three distinct types of characters. The electrophoretic study was expanded to include less conservative enzymes in an effort to further resolve the biochemical phy-

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logeny for these taxa. W. Lanyon constructed phylogenies on the basis of shared derived cranial and syringeal morphology (1984, 1985, 1986, 1988a, b) to examine Parker's suggestion.

Methods

Fieldwork.—The 24 tissue samples we analyzed (voucher specimen information is available from the authors upon request) were collected from 1980 through 1983 in Bolivia, Panama, and Peru. All specimens were accessioned and cataloged in the Museum of Zoology at Louisiana State University. Samples of heart, liver, and pectoral muscle were placed in aluminum foil packets and immersed in liquid nitrogen generally within 2 h of the time birds were collected.

Electrophoresis.—For each individual, separate homogenates were prepared for the three tissue types; 0.5–1.0 g of tissue homogenized in an equal volume of Cleland's Reagent. Homogenates were centrifuged at 12,000 rpm for 60 min, the precipitate was discarded, and the supernatant was stored at −70°C. Electrophoresis, as described in S. Lanyon (1985a), was carried out for 36 enzymes (Table 1). Each enzyme was investigated on a minimum of two electrophoretic buffer systems to reduce the probability of chance comigration of distinct character states (Aquadro and Avise 1982).

We calculated Rogers' modified distance measure (Wright 1978) for each pairwise comparison of taxa. This distance measure was selected because it satisfies the triangle inequality which must be met for a distance measure to be biologically interpretable (Farris 1981). These distance measures were then analyzed with the Fitch-Margoliash algorithm contained in Felsenstein's PHYLIP package (Felsenstein 1985). The resultant networks were rooted using *Querula* as the outgroup (S. Lanyon 1985a). To arrive at a conservative estimate of phylogenetic relationships, a jackknife manipulation of taxa was added to the Fitch-Margoliash analysis and a jackknife strict consensus Fitch-Margoliash tree (S. Lanyon 1985b) was produced. A consensus tree of this type contains only those nodes consistently supported despite manipulation of the taxa included in the analysis. Nei's *D* values (Nei 1978) were calculated for the electrophoretic data and were not used in the distance analyses, but are presented to facilitate comparisons with previous studies.

A character analysis of electrophoretic data was performed to determine whether the Fitch-Margoliash tree reliably summarized the phylogenetic information in the data set. There remains considerable uncertainty about the proper means of conducting a character analysis of electrophoretic data for phylogeny reconstruction. The fundamental difficulty in character analyses of electrophoretic data is that taxa are often polymorphic, a condition character analyses are not designed to handle. Swofford and Berlocher (1987) suggest treating the locus as the character and using allele frequency information to infer evolutionary trees. An alternative is to consider each allele as a binary character (Buth 1979), the "independent alleles model." Unfortunately, as character analyses, neither approach is without flaws. The locus-as-character approach depends heavily on frequency information when, from a cladistic viewpoint, only presence or absence is relevant. In contrast, the allele-as-character approach ignores the fact that alleles at a single locus are not independent. To maximize the probability of producing a different topology in this second analysis, we selected the allele-as-character approach. It ignores frequency information and employs a data matrix dramatically different than that in the distance analysis. This is not the case for the locus-as-character approach. Each allele was treated as a unique binary character (either present or absent) and the distribution of alleles was analyzed using PAUP (Swofford 1985). As for the distance analysis, a jackknife manipulation was performed for the PAUP analysis to identify strongly supported clades.

Anatomical methods.—W. Lanyon examined the skulls of 517 species (representing 143 of the 151 genera) and the syringes of 517 species (146 genera) of the New World Tyrannoidea. All syringes were stained with alcian blue and alizarin red for cartilage and bone (after Dingerkus and Uhler 1977). We follow Ames (1971) in the method of dissection and in terminology. Shared and derived character states of the cranium and the syrinx are identified and assigned numbers in the text that correspond to the numbers in Figure 6 and Table 3.

In addition to the anatomical collections at the American Museum of Natural History (AMNH) and Field Museum of Natural History (FMNH), we borrowed specimens from the British Museum (Natural History), Tring; the Carnegie Museum of Natural History, Pittsburgh; the Delaware Museum of Natural History, Greenville; the Museu Parense Emilio Goeldi, Belém, Brazil; the Museum of Natural History at the University of Kansas, Lawrence; the Museum of Zoology at Louisiana State University (LSU), Baton Rouge; the Museum of Zoology at the University of Michigan, Ann Arbor; the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the Peabody Museum of Natural History at Yale University, New Haven; and the collections of Peter L. Ames and Pierce Brodkorb. Specimens cited in the text and in figure captions are identified to collection by the abbreviations given above.

Results

Electrophoresis.—An earlier electrophoretic study (S. Lanyon 1985a) demonstrated that among a representative sample of 14 cotingid

TABLE 1. Allelic frequency distributions for 30 polymorphic presumptive loci. Six loci were monomorphic: ICD-2 (EC 1.1.1.42), SOD-2 (EC 1.15.1.1), CK-2 (EC 2.7.3.2), LAP (EC 3.4.11.1), GDA (EC 3.5.1.2), and FH (EC 4.2.1.2). The 7 species identified by numeric column headings correspond to the taxa in Table 2; sample sizes are in parentheses.

	Querula	*Ampelion*				*Phytotoma*	
Locus	1 (6)	2 (3)	3 (2)	4 (3)	5 (2)	6 (4)	7 (4)
1 ADH (EC 1.1.1.1)	a	b	b	b	c	b	b
2 G3PDH (EC 1.1.1.8)	b	a	a	a	b	a (0.13) b (0.87)	a
3 SDH (EC 1.1.1.14)	b	a	a	c	c	c	c
4 LDH (EC 1.1.1.27)-1	a	c	c	c	b	c	c
5 (EC 1.1.1.27)-2	b	c	c	c	a (0.50) c (0.50)	c	c
6 MDH (EC 1.1.1.37)-1	a	a	b	a	a	a	a
7 (EC 1.1.1.37)-2	a	a	a	a	b	a	a
8 ME (EC 1.1.1.40)	a	d	d	d	c	b	b
9 IDH (EC 1.1.1.42)-2	d	b (0.17) e (0.83)	e	e	f	a (0.13) c (0.83)	c
10 6-PGD (EC 1.1.1.44)	d	b	b	b	b	a (0.37) c (0.63)	c
11 SOD (EC 1.15.1.1)-1	a (0.90) b (0.10)	d	d	d	c	d	d
12 NP (EC 2.4.2.1)	e	b	b	a	c	d	b
13 AAT (EC 2.6.1.1)	b	d	d	c	a	a	a
14 PK (EC 2.7.1.40)	a	c	c	b	c	b	b
15 CK (EC 2.7.3.2)-1	a (0.10) c (0.90)	c	b	c	c	c	c
16 PGM (EC 2.7.5.1)-1	b	a (0.33) b (0.67)	b	b	b	b	b
17 (EC 2.7.5.1)-2	b	c	d	c	c	a (0.13) c (0.87)	a
18 EST (EC 3.1.1.1)-D	b	b	b	b	b	b	a
19 (EC 3.1.1.1)-visual	a	d	c	e	b	f	f
20 EAP (EC 3.1.3.2)	b	a	a	b	b	b	b
21 PEP (EC 3.4.11)-A	c	b	f	d	e	b	a
22 (EC 3.4.11)-B	b (0.10) d (0.50) e (0.40)	a	c	c	f	e	g
23 (EC 3.4.11)-C	d	a (0.13) b (0.13) c (0.74)	d	d	e	c	b
24 (EC 3.4.11)-D	c	a	a	b	c	d	d
25 ADA (EC 3.5.4.4)	c (0.20) d (0.70) f (0.10)	a	d	f (0.83) g (0.17)	d	b (0.50) e (0.50)	d
26 ALD (EC 4.1.2.13)	b	b	b	b	b	b	a
27 ACON (EC 4.2.1.3)-1	a (0.20) e (0.80)	d	d	d	c	b	b
28 (EC 4.2.1.3)-2	a	c	c	b	b	c	c
29 MPI (EC 5.3.1.8)	a (0.30) b (0.70)	a (0.33) b (0.67)	b	a	b	a (0.37) b (0.63)	b
30 GPI (EC 5.3.1.9)	a	b	a	a	a	a	a

genera (Cotingidae), 12 manakin genera (Pipridae), 1 sharpbill genus (Oxyruncidae), and 1 flycatcher genus (Tyrannidae), the plantcutters were most closely related to a set of 3 cotinga taxa currently placed in the genus *Ampelion*. This study used a set of 20 conservative enzyme loci.

To examine more fully the affinities of *Phytotoma*, we analyzed an additional 16 variable loci. Also, the remaining species of *Ampelion* and a second species of *Phytotoma* were examined. Of the 36 presumptive loci surveyed, 6 (17%) were monomorphic across the 7 analyzed taxa (Table 1).

TABLE 2. Matrix of genetic distance coefficients.[a]

	1	2	3	4	5	6	7
1 *Querula purpurata*	—	1.0342	0.9576	0.8222	0.7547	0.7675	0.9651
2 *Ampelion rufaxilla*	0.7818	—	0.2966	0.4740	0.8569	0.5372	0.7010
3 *A. rubrocristata*	0.7733	0.5012	—	0.4885	0.9024	0.7348	0.6931
4 *A. sclateri*	0.7361	0.6065	0.6205	—	0.7104	0.4876	0.6351
5 *A. stresemanni*	0.7145	0.7477	0.7683	0.7092	—	0.6628	0.8357
6 *Phytotoma rutila*	0.7101	0.6281	0.7110	0.6110	0.6836	—	0.2809
7 *P. raimondii*	0.7751	0.7022	0.7071	0.6843	0.7500	0.4880	—

[a] Above diagonal, Nei's distance (Nei 1978); below diagonal, Rogers' modified distance (Wright 1978).

Roger's modified distances between the in-group taxa ranged from 0.4880 between the two *Phytotoma* species to 0.7818 between the out-group, *Querula purpurata*, and *Ampelion rufaxilla* (Table 2). In the Fitch-Margoliash tree generated from these distance values (Fig. 1; %SD = 1.80308), the two species of *Phytotoma* were identified as sister taxa, as were the two species of *Ampelion* sensu strictu. *A. sclateri* is identified as the sister taxon of *Ampelion* sensu strictu, with *Phytotoma* as the sister taxon to this clade. The electrophoretic data fail to link *A. stresemanni* closely with the in-group taxa. A jackknife manipulation of the Fitch-Margoliash analysis revealed no taxon-dependent instability in topology.

We analyzed the 110 alleles observed for the 30 polymorphic loci for phylogenetic information with a cladistic analysis. The resultant cladogram was entirely concordant with that produced by the Fitch-Margoliash analysis. A jackknife manipulation of taxa revealed no instability in the shortest tree obtained by PAUP (Fig. 1). This branching structure requires 132 evolutionary steps for the 110 allelic characters (Consistency index = 0.826). All branches are supported by multiple characters (6–17 steps/branch). Similarly, a jackknife manipulation of characters had limited effect on the results. For 28 (93%) of the pseudoreplicate data sets, the resultant topology is identical to Figure 1. When either *Me* or *Acon*-1 alleles are eliminated, the relationships between *Ampelion* sensu strictu, *A. sclateri*, and *Phytotoma* remain unresolved. That is, when either of these sets of alleles is deleted, PAUP identified three equally shortest trees (the three possible arrangements of these three lineages). Both enzymes contain one allele that identifies *A. sclateri* as the sister taxon of *Ampelion* sensu strictu.

Of the 110 alleles observed for the 30 polymorphic loci, 31 were synapomorphies and, as such, are potentially informative about relationships within the in-group. Sixty-nine alleles were present (or absent) in only one of the in-group taxa (autapomorphies) which, though of importance for the estimation of evolution on terminal branch segments, are uninformative about relationships. Finally, one allele (allele c of LDH-m) was shared by all members of the postulated in-group but absent in *Querula*. The remaining alleles were identified as symplesiomorphies.

Although the philosophically distinct Fitch-Margoliash and cladistic approaches produced identical topologies, the lengths of the component branches were quite different. The cladistic analysis distributed evolutionary change more evenly over all branches than did the Fitch-Margoliash analysis which concentrated much evolutionary change on terminal branch segments. In the cladogram, terminal branches ($\bar{x}$ = 11.67; range 9–17) averaged almost 1.5 times more steps than internal branches ($\bar{x}$ = 8.0; range 6–9). In the Fitch-Margoliash tree, terminal branches ($\bar{x}$ = 0.27; range 0.216–0.345) were over 4.5 times longer than internal branches ($\bar{x}$ = 0.06; range 0.034–0.081). This suggests that a great deal of allelic *frequency* evolution has taken place since these various species diverged and that this aspect of evolution is undetected by the character analysis.

Syringeal morphology.—Shared derived syringeal characters of *Phytotoma* involve the position of the first two A elements and the first two B elements (the rings that lend support to the tracheobronchial junction) relative to one another and the nature of the pessulus (the structure that supports the juncture of the bronchi). In all three species the A1 and B1 closely parallel one another, while the B1 is at approximately a 45° angle to the B2 and the A1 at approximately a 45° angle to the A2 (Character 1; as labeled in Fig. 2: A–C). The pessulus is

very narrow, completely ossified, and continuous with the A2 elements (as labeled in Fig. 2: A). The tracheobronchial junction is extremely simple, for there are no complete A rings caudal to the pessulus. Though the B1 elements are normally not ossified, there is partial ossification (with alizarin red stain) in one specimen of *rutila* (AMNH 4313).

Only the four species of *Ampelion* within the Tyrannoidea share these derived syringeal characters (1 and 2) with *Phytotoma* (Fig. 2: D–F). Of these, *Ampelion rubrocristatus* and *A. rufaxilla* (similar to *rubrocristatus* and not illustrated here) have syringes that are closest to those of *Phytotoma*. Our specimens of syringes of *Ampelion* would not be separable from our series of *Phytotoma* except for the greater enlargement of the bronchi (in the area of the B2 elements) in *Ampelion*. Even the tendency toward ossification of the B1 elements noted in one of the *Phytotoma* specimens was found in one specimen of *Ampelion rubrocristatus* (LSU 86219). Ames (1971) reported a similarity between his four syringes of *Phytotoma* and his single specimen of *Heliochera* (=*Ampelion*) *rubrocristatus*. Ames was reluctant to make any taxonomic recommendation for fear that this might "indicate merely that both groups have retained the primitive syringeal structure." The uniqueness among the Tyrannoidea of this suite of syringeal characters argues against this position. Ames did not have access to syringes of either *A. sclateri* or *A. stresemanni*.

The single specimen of *A. stresemanni* (LSU 79584) has the B1 elements completely ossified, and the ventral ends of these elements are expanded broadly (Character 4). The pessulus is continuous with the A1 instead of with the A2 elements (Character 5). At the point of insertion of the *M. tracheolateralis*, within the connective tissue massed just caudal to the medial segments of the B1 elements, there are small oval-shaped areas of ossification not seen in the other genera (Character 6).

Both specimens of *A. sclateri* (LSU 81150 and LSU 75016) differ from those of *Phytotoma*, *A. rufaxilla* and *A. rubrocristatus*, and have cartilaginous connections between the ends of the A1 elements and the pessulus, and have the latter connected to both the complete A3 ring and the A2 elements. For purposes of comparison we have included photographs of the syringes of a variety of cotingid genera (Fig. 3), none of which share the derived characters that characterize the syringes of *Phytotoma* and the four *Ampelion* species.

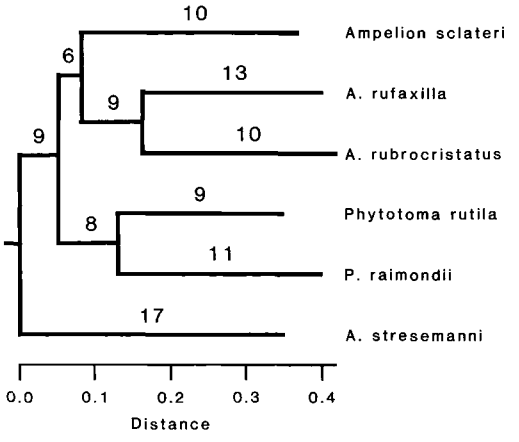

Fig. 1. Fitch-Margoliash tree (mean % SD = 1.803; sum of squares = 0.013) generated from the Rogers' modified genetic distances (Table 2). *Querula* was used to root the tree. The MULPARS option of PAUP produced a single cladogram (length = 132 steps; consistency index = 0.826) with this same topology. Numbers above each branch refer to the number of evolutionary steps for the electrophoretic data.

Cranial morphology.—The primitive condition of the nasal capsule within the Tyrannoidea is one of little or no ossification. The nasal septum is represented generally by a thin, shallow projection from the roof of the nasal cavity (Warter 1965; W. Lanyon 1984, 1985, 1986, 1988a, b). Most cotingid genera (as defined by Snow 1979) have this unossified condition, as in the ventral view of the skull of *Pipreola intermedia* (Fig. 4: A). In the three species of *Phytotoma*, the nasal capsule, the alinasal walls and turbinals are ossified fully (Character 8; Fig. 4: B–D). Ossified nasal capsules also occur in the cotingid genera *Phoenicircus, Lipaugus, Haematoderus, Rupicola*, and *Ampelion* (Fig. 4: E–F, Fig. 5: A–B). To distinguish between convergent development of this derived condition and evolutionary relatedness will require that additional character complexes be analyzed. *A. sclateri* and *A. stresemanni* do *not* have fully ossified nasal capsules (Fig. 5: C–F).

The distinctive features of the skull of *Phytotoma* are the strongly decurved finchlike bill and the rows of tubercles on the palatal surface of the premaxillae (Character 9; "t" in Fig. 4). These are not found elsewhere within the Ty-

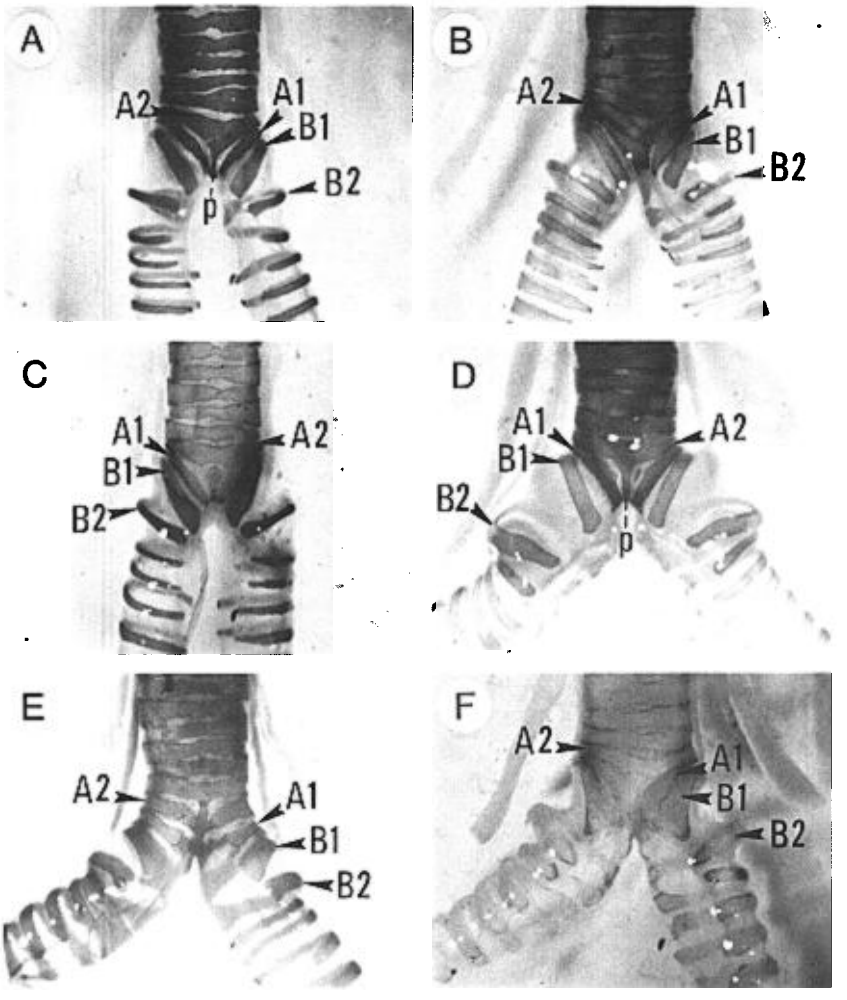

Fig. 2. Syringes of *Phytotoma* and *Ampelion* (dorsal aspect; magnification = 10×: (A) *Phytotoma raimondii*, LSU 81156; (B) *P. rara*, AMNH 4314; (C) *P. rutila*, LSU 102788; (D) *Ampelion rubrocristatus*, LSU 79583; (E) *A. sclateri*, LSU 75016; (F) *A. stresemanni*, LSU 79584. A and B elements as labeled; p = pessulus.

rannoidea, and are presumably associated in some manner with the equally unique derived phytophagous habits of this genus.

Phytotoma appears to be in the process of developing a small transverse trabecular plate on the nasal septum. There are well developed but small heart-shaped plates in *rara* (Character 10; AMNH 6738 and 6708; arrow in Fig. 4: D) and a poorly developed plate in one specimen of *rutila* (AMNH 5302). There were no plates in two specimens of *raimondii* (AMNH 9030, Fig. 4: C; LSU 50811) and two specimens of *rutila* (AMNH 5356 and 6734). Transverse trabecular plates are not characteristic of cotingid skulls and, where they occur, are of a different shape or in a different location on the septum.

Ampelion rubrocristatus (AMNH 6141 and 6142; LSU 74880, 75617, 95399, and 114282) has a broad and long plate at the ventral edge of the nasal septum (Character 11; Fig. 4: F), while *A. rufaxilla* (LSU 78600 and 84017) has an equally long but much narrower plate in the same location (Fig. 5: B). Both *A. sclateri* (LSU 75618 and 81262) and *A. stresemanni* (LSU 42898 and 106939) also have well-developed trabecular plates, but these are narrow and long and located within the septum, well dorsal to its ventral edge (Character 3; Fig. 5: C–F). The nasal septum in *A.*

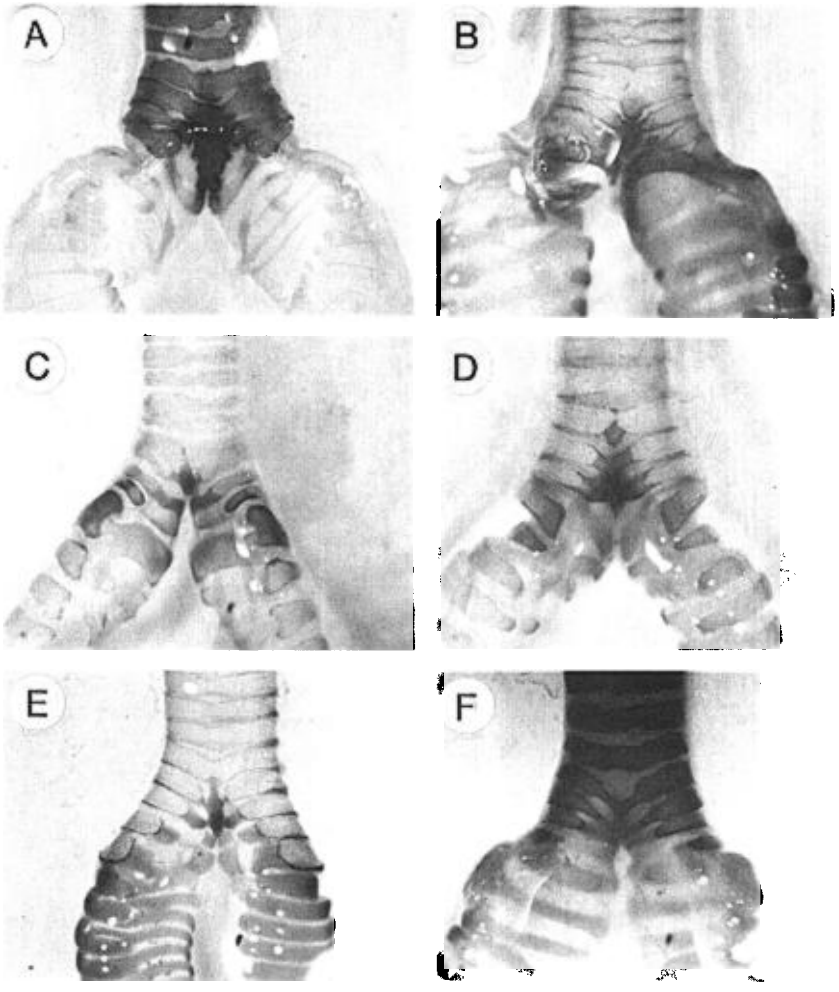

Fig. 3. Syringes of 6 genera of cotingas (dorsal aspect; magnification = 10×: (A) *Phoenicircus nigricollis*, AMNH 9348; (B) *Carpornis cucullatus*, AMNH 2551; (C) *Ampelioides tschudii*, LSU 90759; (D) *Lipaugus subalaris*, FMNH 290407; (E) *Xipholena punicea*, AMNH 6653; (F) *Conioptilon mcilhennyi*, LSU 42866.

sclateri and *A. stresemanni* is largely unossified except for that region bearing the transverse trabecular plate (Fig. 5: C, 5: E).

Figure 6 illustrates the phylogenetic relationships of *Phytotoma* and *Ampelion* suggested by the syringeal and cranial characters (Table 3). The uniqueness (among the Tyrannoidea) of the well-developed syringeal characters 1 and 2 makes it highly probable that the assemblage is monophyletic. Likewise, the sharing of derived cranial morphology leaves little doubt that the three species of *Phytotoma* are monophyletic and that *Ampelion rufaxilla* and *A. rubrocristatus* are sister taxa. The syringes of *Ampelion stresemanni* and *A. sclateri* are markedly different from each other and from those of *rufaxilla* and *rubrocristatus*. This indicates considerable divergence which deserves generic rank. The argument for clustering *stresemanni* and *sclateri* is less robust, as based on the sharing of one character state of the nasal septum that may well be due to convergence. These two species share the largely unossified and presumed primitive state of the nasal capsule which tells us nothing about their relatedness. Additional character sets are needed to clarify this point.

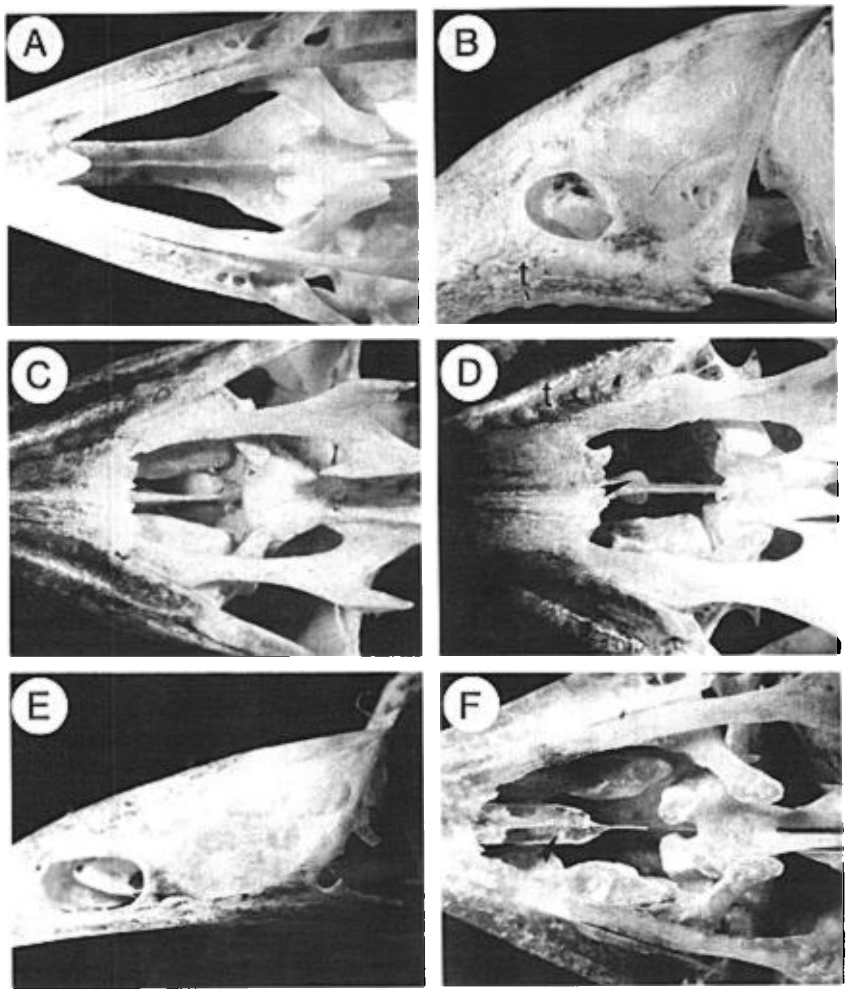

Fig. 4. The nasal capsule in *Phytotoma* and *Ampelion* compared with that in a typical cotinga, *Pipreola intermedia* (anterior end of skull to left; skulls viewed ventrally except laterally in B and E; magnification = 7× except 10× in B and D): (A) *Pipreola intermedia*, AMNH 8166; (B) *Phytotoma rutila*, AMNH 6734; (C) *Phytotoma raimondii*, AMNH 9030; (D) *Phytotoma rara*, AMNH 6738; (E) and (F) *Ampelion rubrocristatus*, LSU 75617. Arrows point to trabecular plates on the nasal septum; t = tubercles on the palatal surface of the premaxillae in *Phytotoma*.

Discussion

Monophyly of the cotingid genus *Ampelion* and the plantcutter genus *Phytotoma* is supported by electrophoretic and syringeal characters. We found no cranial characters that link *Phytotoma* unequivocally with any particular group of tyrannoids. Unlike the situation within the Tyrannidae, where clusters of genera share the same derived cranial characters (W. Lanyon 1984, 1985, 1986, 1988a, b), cotingid skulls are frequently distinct at the generic level (Warter 1965, Lanyon pers. obs.). Consequently, cranial characters are useful at relatively lower levels in the development of phylogenies among the cotingids than among tyrant flycatchers. However, syringeal characters 1 and 2 are unique within the Tyrannoidea, and, together with electrophoretic results, provide strong support for the monophyly of this assemblage.

Because *Phytotoma* and *Ampelion* form a monophyletic assemblage, it is desirable to

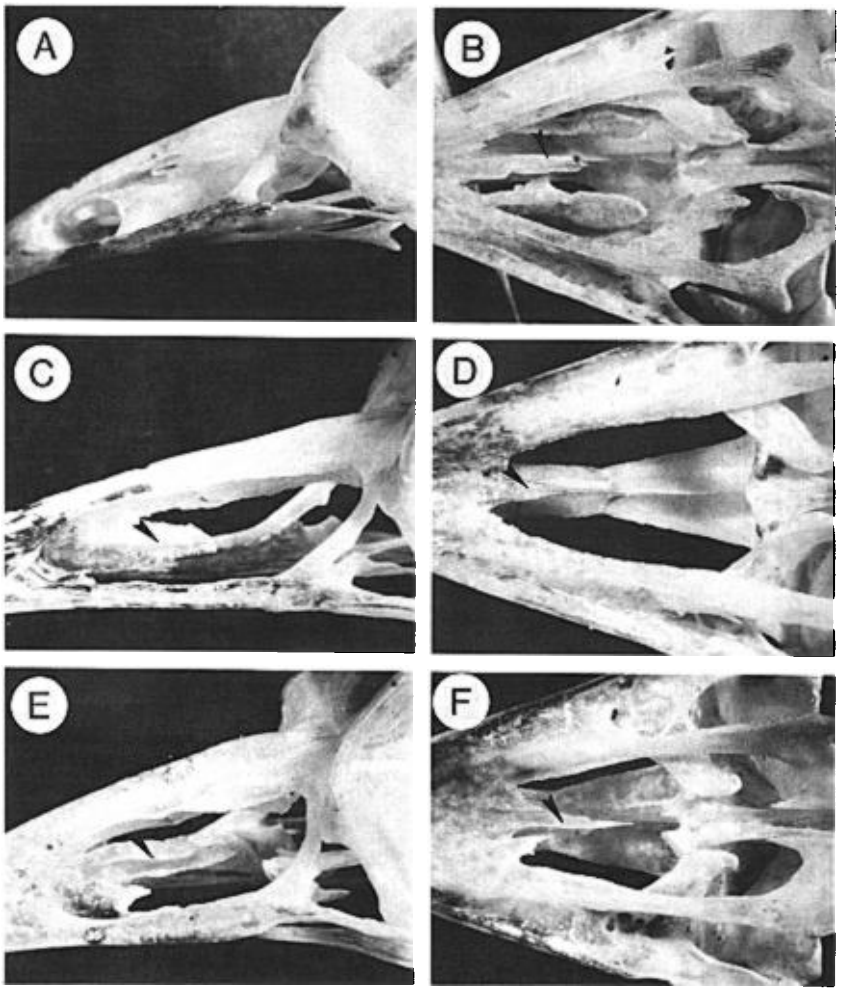

Fig. 5. The nasal capsule in other *Ampelion* (anterior end of skull to left); skulls viewed laterally in A, C, E, and ventrally in B, D, F; magnification = 7×. Arrows indicate trabecular plates located along the ventral edge of the nasal septum in *rufaxilla*, and within the septum, dorsal to the ventral edge, in *sclateri* and *stresemanni*.

modify the existing classification. Although analyses of biochemical characters and anatomical characters result in conflicting hypotheses concerning the placement of *A. sclateri*, both analyses agree in the placement of *Phytotoma* **within** the currently constituted genus *Ampelion*. We are faced with either maintaining the genus *Phytotoma* distinct from the other four species—in which case it is necessary to resurrect the genera *Doliornis* (containing *sclateri*) and *Zaratornis* (containing *stresemanni*)—or submerging *Ampelion* into the older genus *Phytotoma*.

We have elected to maintain four monophyletic genera to emphasize the behavioral and morphological divergence of these clades. Snow (1973, 1982) discussed the arguments for placing *sclateri* and *stresemanni* in *Ampelion*, and favored the merger of the former but was less certain of the wisdom of merging the latter. Marten and Johnson (1986) reported a mean Nei's genetic distance between avian congeners of 0.174 (0.028–0.527). The distances between *sclateri* and *Ampelion* sensu strictu fall in the upper end of this range and could conceivably be joined as a single genus. The distance be-

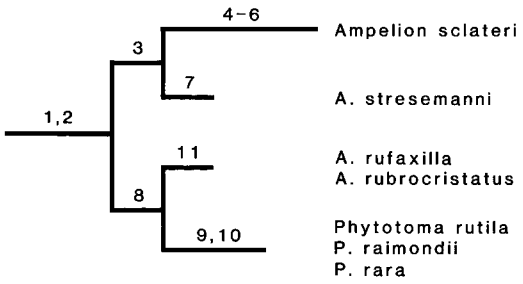

Fig. 6. Phylogenetic relationships of *Phytotoma* and *Ampelion* as indicated by syringeal and cranial characters. Numbers identify diagnostic character states described in text and in Table 3.

tween *stresemanni* and *Ampelion* sensu strictu fall well outside this range (Table 2). From the standpoint of the nasal capsule, *stresemanni* and *sclateri* are closer to each other than either is to *Ampelion* sensu strictu. But there are substantial differences in their syringeal morphology (characters 4–6) which suggest that they are generically distinct.

Finally, we emphasize that these seven species represent a monophyletic clade. Ideally, such a clade should be recognized by assigning to it some higher taxonomic category. Unfortunately, there remains considerable doubt that the "cotingas" represent a monophyletic group (Snow 1979, S. Lanyon 1985a). One option is to transfer *Ampelion, Doliornis,* and *Zaratornis* to the family Phytotomidae. This approach requires no changes in nomenclature. The four generic names as well as both Cotingidae and Phytotomidae would be retained. The alternative is to eliminate the family Phytotomidae, transfer *Phytotoma* to the Cotingidae, and erect a subfamily (the Ampelinae or Phytotominae) that contains these four genera. Recognizing the uncertainty regarding the monophyly of the "cotingas," we recommend the former approach.

Our results provide an excellent example of why "gaps" in morphological or behavioral space cannot always be used to identify monophyletic assemblages of taxa. The "gap" between *Ampelion* and *Phytotoma* is a consequence of the highly derived nature of the bill in *Phytotoma.* These derived characters, while important for identifying the three species of *Phytotoma* as sister taxa, are uninformative about the relationships of *Phytotoma* to other avian lineages. The plumage, behavioral, and vocal similarities of *rubrocristatus; rufaxilla, sclateri,* and *stresemanni* (Parker pers. comm.) are presumably primitive character states within the in-group. Through an analysis of additional character sets, we identified synapomorphies that support the monophyly of these seven species that have for so many years been placed in separate families.

TABLE 3. Morphological characters used to develop phylogenetic relationships of *Phytotoma* and *Ampelion.*

Character 1—A1 and B1 elements closely parallel one another, while the B1 is at approximately a 45° angle to the B2 and the A1 at approximately 45° angle to the A2.
Character 2—the pessulus is very narrow, completely ossified, and continuous with the A1 and/or A2 elements, making for a very simple tracheobronchial junction, with no complete A rings caudal to the pessulus.
Character 3—well-developed narrow and long transverse trabecular plate, located within the nasal septum, well dorsal to the ventral edge of the septum.
Character 4—B1 elements completely ossified, with ventral ends expanded broadly.
Character 5—pessulus continuous with the A1 elements.
Character 6—small oval-shaped areas of ossification at point of insertion of *M. tracheolateralis.*
Character 7—cartilaginous connections between the ends of the A1 elements and the pessulus, the latter connected to the complete A3 ring as well as to the A2 elements.
Character 8—nasal capsule fully ossified, including alinasal walls and turbinals.
Character 9—strongly decurved finchlike bill and rows of tubercles on the palatal surface of the premaxillae, presumably associated with phytophagous habits.
Character 10—some specimens with small heart-shaped transverse trabecular plate located well dorsal to ventral edge of nasal septum.
Character 11—long transverse trabecular plate located at ventral edge of the nasal septum.

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