MONOPHYLY OF THE PICIFORMES:
A REPLY TO OLSON

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Abstract.—Olson (1983) questioned the hypothesis that the order Piciformes is mono-
phyletic and suggested instead that each piciform suborder is allied with a nonpiciform
group. His attempt to discredit the synapomorphies joining the Galbulae and Pici is refuted
by corrections of his interpretations of previous work. The Piciformes share a complex
derived hindlimb morphology involving zygodactyly, a tripartite flexor hallucis longus, and
Type VI flexor tendons. Olson's argument for polyphyly combines inadequate data with the
inappropriate technique of equating general overall similarity with affinity. His hypothesis
is therefore rejected. Problems concerning fossil taxa are also discussed. Based on current
information, we believe that a monophyletic origin of the Piciformes remains the hypothesis
of choice. Received 18 August 1982, accepted 18 October 1982.

Swierczewski and Raikow (1981) and Simp-
son and Cracraft (1981) studied the phyloge-
netic relationships of the Piciformes. Both con-
cluded that the order is monophyletic and that
it contains two monophyletic suborders, the
Galbulae (Bucconidae and Galbulidae) and Pici
(Capitonidae, Ramphastidae, Indicatoridae,
and Picidae). Olson (1983) criticizes the hy-
pothesis of monophyly. First, he questions the
arguments supporting this view. He then pre-
sents an alternative hypothesis that the Gal-
bulae are most closely related to the Coracii
and the Pici to the Passeriformes. Finally, he
criticizes Simpson and Cracraft's discussion of
certain fossil birds. After carefully examining
Olson's critique, we believe that monophyly
remains the more strongly supported hypoth-
esis. The possible value of these discussions
goes beyond the question of a single branching
point in a phylogeny, as it provides an oppor-
tunity to compare and contrast two profoundly
different approaches to systematic analysis.

PICIFORM MONOPHYLY

Zygodactyly.—Olson suggests that zygodac-
tyly arose independently in the Pici and Gal-
bulae because Steinbacher (1935) found differ-
ences in their tarsometatarsi. He does not
consider the possibility that the differences
arose after the two groups diverged from a zy-
godactylous common ancestor. Olson consid-
ers that the tarsometatarsus of the Galbulae is
more primitive than that of the Pici, which is
more "specialized," and therefore that mono-
phyly requires the condition in the Pici to have
evolved from that in the Galbulae. Here, he
confuses sister-group relationship with ances-
tor-descendent relationship. We did not pro-
pose that the Pici evolved from the Galbulae
(higher taxa cannot be ancestors). Olson asks
". . . why would such a transformation take
place? Once a group of birds has become per-
manently zygodactyl, is it possible to become
more zygodactyl?" This question manifests a
confusion. One group is not "more zygodac-
tyl" than the other; both are described by this
term. It may be expected, however, that dif-
ferences will accumulate in separately evolving
lineages after they have split; it is this process
of evolutionary divergence or character trans-
formation that gives rise to the hierarchical
structure of organic diversity. We suggest that
the zygodactyl conditions of the Galbulae and
Pici are homologous because other characters
(see below) corroborate the unity of the Pici-
formes.

M. flexor hallucis longus.—Swierczewski and
Raikow (1981) reported that the flexor hallucis
longus muscle (FHL) shows a derived condi-
tion in its origin by a certain pattern of three
heads. In most birds there are one or some-
times two femoral heads, but the Piciformes
have as well an extensive origin from the fib-
ula. Olson dissected one capitonid (*Trachy-
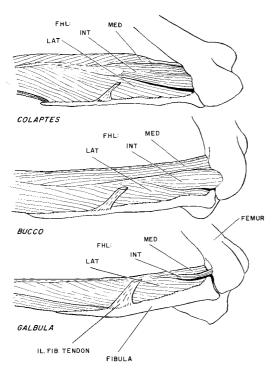phonus*; Pici) and one bucconid (*Hypnelus*; Gal-

Fig. 1. Lateral views of the region of the knee and upper crus in three species of piciform birds to show the mode of origin of M. flexor hallucis longus (FHL). In all Piciformes the muscle arises by three separate heads, medial (MED), intermediate (INT), and lateral (LAT), all of which lie medial to the tendon of M. iliofibularis (IL. FIB.). The representative forms illustrated are *Colaptes auratus* (Picidae; Pici), *Bucco tamiata* (Bucconidae; Galbulae), and *Galbula dea* (Galbulidae; Galbulae). The drawings were made with a camera lucida and dissecting microscope and are not to scale.

bulae). In *Trachyphonus* he confirmed the report of Swierczewski and Raikow (1981), but in *Hypnelus* he did not. Olson quotes Swierczewski (1977: 57) as saying that in the Galbulae the heads are "somewhat difficult to separate from each other." Swierczewski's *full* statement, however, conveys a different meaning: "In the Galbulidae and Bucconidae, the medial head arises semitendinous from the intercondyloid region of the femur, and the intermediate head arises fleshy from the proximocaudal surface of the external femoral condyle; the heads being somewhat difficult to separate from each other." This statement refers to only two of the three heads; it does not refer to the fibular head, which is the significant structure. Olson dissected one specimen

each of two species. In contrast, Swierczewski dissected between one and four specimens each of 45 species, and concluded unequivocally (1977: 58) that "Three heads of origin were found in all species studied herein."

Nevertheless, one of us (R.J.R.) has, in response to Olson's comments, dissected the limb of *Colaptes auratus* (Picidae), *Bucco tamiata* (Bucconidae), and *Galbula dea* (Galbulidae). Like Olson, Raikow confirmed in *Colaptes* the three heads previously described (Fig. 1). In *Hypnelus,* Olson ". . . could not detect any separate heads of origin . . ." and questioned whether ". . . the nature of the origin of this muscle is homologous between the Galbulae and the Pici or even that it can really be said to have three heads in the Galbulae." The dissection of *Galbula* and *Bucco* has fully confirmed our previous report that the three heads, including the large fibular head, are present in the pattern described (Fig. 1). This corroborates the hypothesis of piciform monophyly and refutes Olson's claim that the condition is not found in both piciform suborders.

Type VI flexor tendons.—Did this condition arise once in the Piciformes or separately in the Galbulae and Pici? Olson states that it is "probably a convergent similarity," but offers no evidence. He suggests that the Galbulae would be difficult to identify with their feet cut off, but fortunately all of our specimens possessed feet. (Actually, the relevant structures are legs, not feet, as the FHL belly lies in the crus.) Olson feels that such characters do not justify *ordinal* rank, but we do not agree that taxonomic rank is related to the corporeal location of the relevant characters. Here, Olson confuses phylogeny with taxonomy; the question at issue is whether the group is monophyletic, not what rank it should have in a classification. Perhaps the FHL should rank the group at the generic level, because its origin lies at the knee joint (*Junctura genus*).

ANALYSIS OF OLSON'S HYPOTHESIS

Inadequate data.—Olson compares characters in only some of the relevant groups, so that comprehensive comparisons cannot be made. For example, he notes that "in plumage pattern, the ground roller *Brachypteracias leptosomus* is quite similar to certain of the Bucconidae such as *Malacoptila.*" But what are the patterns in the other Coracii, the other Buc-

conidae, and the Galbulidae? Why are they not discussed? Convergence in plumage patterns is common, which is why comprehensive comparisons are needed to distinguish between synapomorphies and spurious resemblances.

Again, in discussing the skull Olson argues for similarities between the Galbulae and Coracii, but restricts his comparison almost entirely to the Bucconidae and *Coracias* when listing several features. "In all of these characters," he notes, "the Bucconidae are consistently different from the Pici." But what about the Galbulidae and other Coracii?

This pattern of selective, almost casual choice of data characterizes Olson's entire presentation. It is also difficult to assess his data, because they are presented in a narrative form within the text but are not tabulated in a way that would allow one to determine the state of each character in all the relevant taxa. A tabulation of this sort would have revealed that broad conclusions are often based on little data; e.g. Olson dissected only one barbet to determine the form of the postorbital ligament in the large and diverse suborder Pici.

Incorrect determination of polarity.—Although generally eschewing cladistic methods, Olson does make one attempt to show the derived nature of a condition, the complex of the postorbital process, postorbital ligament, and adductor mandibulae. He considers this derived because it ". . . does not occur in *Archaeopteryx*, in presumably primitive land birds such as *Opisthocomus* and the Cuculiformes, or elsewhere in the higher groups of land birds." Several problems invalidate this conclusion. First, there is no reason to assume that a character is primitive because it occurs in "primitive" taxa. All taxa, including fossil forms, are mosaics of primitive and derived characters. Second, while we concede the general primitiveness of *Archaeopteryx*, we question the extent to which the ligament and muscle can be reconstructed in it. Furthermore, on what basis are the Cuculiformes and *Opisthocomus* "presumably primitive"? What are "higher groups" of land birds? Why is the comparison limited to the nonmonophyletic nontaxon of *land* birds? Olson's analysis fails to show that the condition is derived, or even that it is generally characteristic of the groups involved.

Use of phenetic similarity.—The basic problem with Olson's study is that he tries to determine phylogenetic relationships by phenetic similarity. He claims that we accept the idea that ". . . differences between taxa [are] evidence of nonrelationship . . . ," but this is incorrect. We mean only that the absence of similarities fails to corroborate a hypothesis of monophyly, not that the presence of differences refutes such a hypothesis. "Nonrelationship" has no intrinsic meaning; we are searching for patterns of common ancestry identified by synapomorphy.

The problem with phenetic comparisons is that characters are not analyzed so as to identify the level within the phylogenetic hierarchy at which they define taxa. To illustrate this point, we will consider one example from a recent study of the relationships of *Pedionomus torquatus.* This species is placed in the monotypic family Pedionomidae, and the problem is to find its closest relatives. Olson and Steadman (1981) rejected the previous hypotheses that it is related to the Turnicidae (Gruiformes) or the Galliformes and concluded that it belongs in the Charadriiformes. Olson and Steadman (1981: 3) note that a hallux is present in *Pedionomus* and most Charadriiformes but is absent in the Turnicidae. They consider (p. 21) that this supports the removal of *Pedionomus* "from the vicinity of the Turnicidae and its placement in the Charadriiformes." Actually, it does nothing of the kind. The hallux evolved in vertebrates as part of the transformation of the pelvic fin into a limb. As such, it is a derived character at the level of the Tetrapoda. Inasmuch as birds form a tetrapod subgroup, the presence of a hallux is a primitive state and reveals nothing about the relationships of any avian species to any other. It tells us *one thing only* about *Pedionomus*, namely that it is a member of the Tetrapoda. It definitely refutes any hypothesis that *Pedionomus* is a fish, but that is all it does.

This example illustrates the principle that character comparisons convey maximum information about phylogenetic relationships only when one determines the specific points at which they are relevant within the nested system of clades forming a phylogeny. Simplistic phenetic comparisons fail to provide this information. Olson's assessments of "similarity" cannot be interpreted, because we do not know which of them represent shared primitive characters and which derived for any group of species. The necessity for such analysis may be emphasized by pointing out the distinction

between similarity and phylogenetic relationship, namely that they do not necessarily coincide. When an evolving lineage splits, one daughter lineage may evolve faster than the other, so that a form may be less similar to a genealogically closer relative than to a more distant one. Lungfishes are more similar to goldfishes than they are to goldfinches, but they are more closely related to goldfinches than to goldfishes. Crocodiles are more similar to turtles than to turtle doves, but they are more closely related to turtle doves than to turtles. Such statements are based on the idea that relationship is defined by recency of common ancestry and are correct within the context of specific phylogenetic hypotheses, in this case those of Wiley (1979). Genealogical relationships are postulated by the recognition of patterns of monophyly, which are defined by synapomorphy. For extended discussions of this principle, see Eldredge and Cracraft (1980), Wiley (1981), and Raikow (1982).

DISCUSSION OF FOSSIL TAXA

The section of Olson's critique "Comments on Fossil Taxa" adds nothing new about the systematics of the taxa placed in the Primobucconidae and Zygodactylidae but does illustrate the limitations of his systematic methodology. Simpson and Cracraft (1981) pointed out that no evidence exists to support the monophyly of the Primobucconidae; Olson in contrast, believes that this observation is "irrelevant." But inasmuch as the "primobucconids" have played a pivotal role in the speculations of Olson and his colleagues about the history of the North American bird fauna, it does not seem "irrelevant" to us to ask whether the Primobucconidae have any objective reality as a natural group. Indeed, if the primobucconids are not monophyletic, then Olson and his colleagues are constructing evolutionary scenarios based upon an imaginary taxon. As a consequence, one might expect that Olson would want to demonstrate that monophyly. His critique, however, is a weak attempt to defend the conclusions of Feduccia and Martin (1976) and lacks any relevant empirical evidence.

Olson's attempt to shift the burden of proof onto Simpson and Cracraft is altogether spurious. We suggest that the burden of proof lies with workers who erect a taxon without positive evidence for its existence as a genealogical unit. Present morphological evidence suggests that the Primobucconidae are a grade, not a clade. If so, then the family has no ontological status, and Olson should instead be defending the usefulness of discussing the evolution of a fictitious taxon.

Simpson and Cracraft (1981: 491) were very specific in their criticism; none of the taxa of the Primobucconidae is known to have an enlarged sehnenhalter. For that reason, they concluded that there is no justification for saying that the primobucconids are piciforms as currently accepted, let alone closely related to the Bucconidae. That conclusion, if true, also falsifies Olson's unsupported speculations about the independent origin of zygodactyly in the Galbulae. From our standpoint, the latter group was already zygodactylous when it arose, because the origin of zygodactyly took place at a higher hierarchical level. This is why Simpson and Cracraft (1981: 491) suggested that one or more taxa currently included in the Primobucconidae might be the sister group of the Piciformes.

Olson's comments about the Zygodactylidae contain further inaccuracies. Simpson and Cracraft (1981: 492) *did* provide evidence for including this fossil taxon in the Pici, namely an advanced form of the sehnenhalter, but they also stressed the very tentative nature of this placement. Furthermore, Simpson and Cracraft did not voice any major disagreement with Ballman's (1969a, b) interpretations, as implied by Olson. Their disagreement was with the placement of the Zygodactylidae in the Galbulae (Brodkorb 1971). Simpson and Cracraft specifically stated that Ballman may be correct in believing that *Zygodactylus* is not a piciform.

CONCLUSIONS

Rather than reply to every individual point raised by Olson, we have instead addressed the basic differences in systematic philosophy that exemplify current controversy in biology. Olson's attempt to question the synapomorphies linking the Galbulae and Pici stands refuted; the Piciformes are characterized by a complex derived morphology of the hind limb involving zygodactyly, tripartite flexor hallucis longus, and Type VI tendons. Olson supports his hypothesis with a potpourri of casual phenetic similarities analyzed by inappropriate

methods, and his argument is little more than an opinion. On the basis of present understanding, we conclude that piciform monophyly remains the preferred hypothesis.

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