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## CHAPTER 1

# SUBSPECIES REPRESENT GEOGRAPHICALLY PARTITIONED VARIATION, A GOLD MINE OF EVOLUTIONARY BIOLOGY, AND A CHALLENGE FOR CONSERVATION

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**ABSTRACT.**—In this review I summarize the history of the subspecies concept and the major debates and issues surrounding its use, with an emphasis on ornithology, in which the concept originated. The study of subspecific variation in birds has been an important driving force in the development of evolutionary biology. Subspecific study has also been essential in the description and preservation of biodiversity. Although controversy has surrounded the concept of subspecies since its inception, it continues to play an important role in both basic and applied science. I cover 10 relevant issues that have been largely resolved during this 150-year controversy, although not all are widely appreciated or universally accepted. These include nomenclature, sampling theory, evolutionary biology, and the heterogeneity of named subspecies. I also address three big unresolved questions and some of the philosophy of science related to them: What are subspecies, how do we diagnose them, and what does subspecific variation mean? Discordance between genotypic and phenotypic data at these shallow evolutionary levels should be expected. The process of diagnosing states that exist along a continuum of differentiation can be difficult and contentious and necessarily has some arbitrariness; professional standards can be developed so that such diagnoses are objective. Taxonomies will change as standards do and as more data accrue. Given present evidence, our null hypothesis should be that subspecific variation probably reflects local adaptation. In looking forward, it seems assured that geographically partitioned variation—and the convenient label “subspecies”—will continue to play an integral role in zoology.

Key words: adaptation, birds, diagnoses, evolution, history, philosophy of science, sampling error, speciation, taxonomy.

## Las Subespecies Representan Variación Estructurada Geográficamente, una Mina de Oro de la Biología Evolutiva y un Desafío para la Conservación

**RESUMEN.**—En esta revisión hago un resumen sobre la historia del concepto de subespecie y los principales debates y asuntos que rodean su uso con énfasis en la ornitología, en donde el concepto se originó. El estudio de la variación subespecífica en las aves ha sido una fuerza importante que ha impulsado el desarrollo de la biología evolutiva. El estudio de las subespecies también ha sido esencial en la descripción y la preservación de la biodiversidad. Aunque la controversia ha rodeado el concepto de subespecie desde que fue acuñado, éste continúa jugando un papel importante tanto en la ciencia básica como en la aplicada. Abordo 10 asuntos relevantes que han sido resueltos en buena parte a lo largo de esta controversia de 150 años, aunque no todos son apreciados ampliamente ni aceptados de manera universal. Entre éstos se incluye la nomenclatura, la teoría sobre muestreos, la biología evolutiva y la heterogeneidad de las subespecies nombradas. También abordo tres preguntas grandes no resueltas y parte de la filosofía de la ciencia relacionada con ellas: ¿qué son las subespecies, cómo establecemos su diagnosis y qué significa la variación

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