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Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes

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ABSTRACT

Freshwater mussels of the order Unionida are key elements of freshwater habitats and are responsible for important ecological functions and services. Unfortunately, these bivalves are among the most threatened freshwater taxa in the world. However, conservation planning and management are hindered by taxonomic problems and a lack of detailed ecological data. This highlights the urgent need for advances in the areas of systematics and evolutionary relationships within the Unionida. This study presents the most comprehensive phylogeny to date of the larger Unionida family, i.e., the Unionidae. The phylogeny is based on a combined dataset of 1032 bp (COI + 28S) of 70 species in 46 genera, with 7 of this genera being sequenced for the first time. The resulting phylogeny divided the Unionidae into 6 supported subfamilies and 18 tribes, three of which are here named for the first time (i.e., Chamberlainiini *nomen novum*, Cristariini *nomen novum* and Lanceolariini *nomen novum*). Molecular analyses were complemented by investigations of selected morphological, anatomical and behavioral characters used in traditional phylogenetic studies. No single morphological, anatomical or behavioral character was diagnostic at the subfamily level and few were useful at the tribe level. However, within subfamilies, many tribes can be recognized based on a subset of these characters. The geographical distribution of each of the subfamilies and tribes is also presented. The present study provides important advances in the systematics of these extraordinary taxa with implications for future ecological and conservation studies.

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1. Introduction

Understanding phylogenetic diversity is crucial for conservation prioritization of freshwater mussels (Bivalvia: Unionida), which are among the most threatened freshwater taxa in the world (IUCN, 2015; Lydeard et al., 2004). Due to their ecological and economic importance, interesting biological traits (e.g., a parasitic life with the reproductive dependence on a host fish and a particular form of mitochondrial inheritance called double uniparental inheritance; Barnhart et al., 2008; Breton et al., 2007; Hoeh et al., 1996, 2002a), scientific research on Unionida has grown in recent years (Haag, 2012; Lopes-Lima et al., 2014). However, taxon-based conservation efforts focused on the Unionidae are hindered by various phylogenetic and taxonomic uncertainties (e.g., Inoue et al., 2014; Pfeiffer et al., 2015), and many species, especially those outside of North America and Western Europe, have been assigned a Data Deficient status by the IUCN (Bogan and Roe, 2008; IUCN, 2015; Kohler et al., 2012).

The Unionidae is by far the most species rich family within the order Unionida, with 620 species in 142 genera (Bogan and Roe, 2008) widely distributed across the freshwater ecosystems of Europe, Asia, North America and Africa. The first classification of the global Unionidae fauna was attempted by Lea (1836, 1838, 1852, 1870), and later updated by Simpson (1900, 1914). These works, in which the marsupium (i.e., the gill structure where the eggs and larvae are brooded), anatomy, larvae type and umbo sculpture were used as key classification characters, divided the Unionidae into two subfamilies, Unioninae and Hyriinae (Table 1). Subsequently, A.E. Ortmann performed a series of studies on North American taxa including additional anatomical classification characters and divided the Unionidae into three subfamilies: Unioninae, Anodontinae and Lampsilinae (Table 1: Ortmann, 1910, 1911, 1912, 1919, 1921; Ortmann and Walker, 1922). In discussing his classification, Ortmann (1912) noted the inadequacy of shell characters to define families and subfamilies due to widespread convergences in shell morphology; a problem that was further discussed by Prashad (1931). Apart from regional works (e.g., Frierson, 1927; Haas, 1940; Iredale, 1934), little progress was made on Unionidae classification until the middle of the twentieth century, when Modell and Haas published their comprehensive classification systems (Table 1: Haas, 1969a,b; Modell, 1942, 1949, 1964). Both Haas and Modell classification systems used a set of morphological and anatomical characters, but relied heavily on shell morphology. Haas (1969a,b) classified the Unionidae into six subfamilies. One of these, i.e., the Hyriinae, combined species from South America and Australasia and would later be recognized as a distinct family. Modell (1942, 1949, 1964) developed a more complex and inflated classification system, which organized the Unionidae genera in distinct families and multiple subfamilies. Both authors' use of highly variable conchological characters for classification above the genus level led to incoherent associations. Nevertheless, the work by Haas has been widely recognized as the more reliable in terms of representing generic and subgeneric distinctiveness and is considered as fundamental in establishing the main genera of the Unionida and in particular, the Unionidae (Roe and Hoeh, 2003). Concurrent with the work of Haas (1969a,b) and Modell (1942, 1949, 1964), an even more inflated classification scheme was proposed by Starobogatov (1970) and Zatravkin and Bogatov (1987), who relied on conchological differences and focused on the curvature of the frontal section of the valves. This system is merely typological and was disregarded by most of the western school of malacologists (see Graf, 2007) and emergent Russian studies (Bolotov et al., 2015; Klishko et al., 2014).

A comprehensive molecular phylogenetic study of the Unionidae has not been attempted to date, primarily due to the difficulties in developing a dataset of sufficient geographical and species coverage. The first classification system using a phylogenetic framework was published by Heard and Guckert (1970; Table 1) for the North American Unionida fauna. Disregarding shell characters, these authors used a broad anatomical and reproductive behavior character set within a phylogenetic context. Their analyses resulted in the division of the North American Unionidae into two families and several subfamilies. The subsequent development of powerful molecular and statistical tools, providing a basis for more objective approaches, has led to the publication of several studies on unionid phylogeny (e.g., Campbell and Lydeard, 2012a, b; Campbell et al., 2005; Davis, 1983, 1984; Davis and Fuller, 1981; Davis et al., 1977, 1981; Graf and Cummings, 2006; Hoeh et al., 1998, 2001, 2002b, 2009; Pfeiffer and Graf, 2013, 2015; Roe and Hoeh, 2003; Whelan et al., 2011; Zanatta and Murphy, 2006). In many of these studies, unionid genera or species that had been identified by morphological characters were not consistent with those revealed through molecular phylogenetic analyses (e.g., Campbell and Lydeard, 2012a,b; Nagel and Badino, 2001; Roe and Hoeh, 2003). Although the vast majority of these molecular studies have focused almost exclusively on North American and European taxa, geographic and taxonomic sampling has recently increased, particularly in Africa (Elderkin et al., 2016; Graf, 2013; Whelan et al., 2011) and Asia (Huang et al., 2002; Pfeiffer and Graf, 2013, 2015; Zhou et al., 2007; Zieritz et al., 2016).

Recent molecular phylogenetic studies have achieved considerable progress in describing the main divisions within the Unionidae (Campbell and Lydeard, 2012a, 2012b; Graf and Cummings, 2006; Pfeiffer and Graf, 2013, 2015; Whelan et al., 2011). The status of the North American Ambleminae with four recognized tribes has been recently confirmed (Table 1: Campbell and Lydeard, 2012a,b; Campbell et al., 2005). Studies including species from Africa and the Indotropics examined the subfamily Parreysiinae in detail and recognized several subfamilies (Table 1: Pfeiffer and Graf, 2015; Whelan et al., 2011). Despite the considerable recent progress (Huang et al., 2002; Pfeiffer and Graf, 2013, 2015; Zhou et al., 2007), the vast majority of unionid genera from the Eastern Palearctic and the Indotropics have never been analyzed in a modern phylogenetic framework.

Based on bibliographical research, the classification of the Unionidae was recently reviewed, establishing the currently accepted subdivisions of the Unionidae (Carter et al., 2011; Table 1). This classification divided the family into six subfamilies: the Ambleminae with a North and Central American distribution; the Parreysiinae with a disjunct distribution primarily in Sub-Saharan Africa and the Indian subcontinent; the Modellnaiinae with a single species from Thailand; the Rectidentinae with a South East Asian distribution; and two subfamilies, the Unioninae and Gonideinae, distributed through most of Asia, Europe, North Africa and west coast of North America.

In order to increase the success of ongoing and future management efforts and to inform conservation priorities more effectively, a better understanding of the evolutionary history of freshwater mussels is necessary. Our objective herein is to improve the understanding of unionid phylogeny through analysis of a combination of nuclear and mitochondrial molecular markers from a wide coverage of genera. In detail, this study aims to: (i) resolve the main phylogenetic relationships within the Unionidae; (ii) discuss the systematics, taxonomy and distribution of the recovered unionid subdivisions (subfamilies and tribes); and (iii) compare the obtained classification with those based on morphological characters.

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