



Molecular and morphological systematics of *Doto* Oken, 1851 (Gastropoda: Heterobranchia), with descriptions of five new species and a new genus

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Abstract

The nudibranch family Dotidae has been an extremely challenging group to study taxonomically due to their small body size, lack of distinct internal morphological differences and similar color patterns. This integrative systematic study of the Dotidae encompasses 29 individuals from the north Atlantic and Mediterranean, and 11 from the Indo-Pacific. Two mitochondrial genes, 16S, COI, and a nuclear gene, H3, were sequenced for 31 specimens and Bayesian and RAxML concatenated analyses were run. Dotidae is monophyletic and possesses strong geographic structure. Co-evolution between some of the north Atlantic taxa and their hydroid prey is apparent, thus supporting the hypothesis that speciation may be correlated with prey diversification. This study also supports the notion that the hydroid prey is a reliable indicator for distinguishing between cryptic species. *Doto coronata* Gmelin, the type species for the genus *Doto*, is re-described and a neotype, collected near Goes, Netherlands, is designated. From the molecular data, *D. millbayana*, *D. dunnei*, *D. koeneckeri*, *D. maculata* Lemche within the *Doto coronata* species complex, are confirmed to be distinct from *D. coronata*. Based on molecular data, specimens previously identified as *D. coronata* from South Africa are determined to represent a new species. It is described here and named *Doto africoronata* n. sp. *Kabeiro* n. gen. is introduced for the clade of elongate individuals from the Indo-Pacific, which diverges by 11.6% or greater in 16S from short-bodied *Doto* species. These elongate species are sister to all the short-bodied species and possess an enlarged pericardium, elongate cerata, a reproductive system with a pocketed prostate (penial gland), and an external tube-like digestive gland, which are absent in

short-bodied *Doto*. Species of *Kabeiro* described here are: *Kabeiro christiana* n. sp., *Kabeiro rubroreticulata* n. sp., and *Kabeiro phasmida* n. sp. from the Philippines. The Indo-Pacific short-bodied species, *Doto greenamyeri* n. sp. from Papua New Guinea is also described.

Key words: cryptic species, co-evolution, Indo-Pacific, north Atlantic, South Africa, phylogenetics

Introduction

Nudibranchia is the most diverse traditional order of opisthobranch mollusks. Nudibranchs have been classified with the suborders Doridina, Aeolidina, Dendronotina, and Arminina (Odhner 1939). Two major clades of Nudibranchia were identified by Wägele and Willan (2000), the Anthobranchia, which contains Bathydoridoidea plus Doridoidea and the other clade Cladobranchia, composed of Dendronotoidea, Aeolidoidea, and the paraphyletic group Arminoidea. Based on morphological and molecular data, the Dendronotina is paraphyletic within the Cladobranchia, (Wollscheid & Wägele 1999; Wägele & Willan 2000), but there is poor resolution of relationships among the well-supported taxa traditionally considered as families (Pola & Gosliner 2010).

The nudibranch family Dotidae traditionally has been placed within the Dendronotina, but systematically, it is considered an unassigned taxon group outside the other Dendronotacea (Bouchet & Rocroi 2005; Wägele & Willan 2000; Pola & Gosliner 2010) within the Cladobranchia (Pola & Gosliner 2010). Unlike the remaining Dendronotoidea, Dotidae lacks the processes of the oral veil, tentacular grooves, and the cuticular lining the stomach (Wägele & Willan 2000).

Overall, Dotidae requires substantial taxonomic and systematic work, since it contains a number of cryptic species complexes (Morrow *et al.* 1992), many undescribed species (Gosliner *et al.* 2008), and is unassigned to a higher clade (Pola & Gosliner, 2010). The Dotidae has been an extremely challenging group to study taxonomically due to their small body size, similar color patterns and lack of reliable morphological characters, such as the radula (Thompson *et al.* 1990), to distinguish relationships. This group has received little revisory attention since Lemche (1976) and Morrow *et al.* (1992), but several additional species were described (Yonow 2000; Ortea 2001; Ortea & Caballer 2007; Ortea *et al.* 2010; Ortea 2010; Ortea 2013; Ortea *et al.* 2014). The studies of Lemche and Morrow *et al.* were focused exclusively on northeastern Atlantic taxa and did not employ contemporary molecular phylogenetic techniques. Pola and Gosliner (2010) included ten species of *Doto* in their analysis, but comprehensive taxon sampling of Dotidae was not the focus of their study.

This is the largest molecular and morphological systematic study of the Dotidae to date, although it does not represent a comprehensive review of global taxa. This study focuses on the members of the *Doto coronata* complex and species of *Doto* from the tropical Indo-Pacific. It includes broad taxon sampling and geographical coverage, which will attempt to increase our understanding of the diversity and relationships within this family. Many previous studies have illustrated the importance of incorporating morphology alongside molecular analysis to assist in understanding the evolutionary relationships within molluscan taxa of interest (Wollscheid-Lengeling *et al.* 2001; Pola *et al.* 2006; Moore & Gosliner 2011) and we also adopt this approach. In this study, reproductive system characters are mapped onto the molecular tree.

Taxonomic and morphological history—Dotidae

The family Dotidae and the generic name *Doto* were both made official by the International Commission of Zoological Nomenclature (China 1964). Prior to this study, *Doto* Oken, and the monotypic *Miese* Marcus, are the only valid genera within the Dotidae. *Caecinella* Bergh and *Doto* are still considered synonyms, with *Doto* taking precedence (McDonald 2006). However, the taxonomic placement of *Miese* and *Caecinella*, still requires greater in depth investigation.

The general morphology of the *Doto* includes a small limaciform body, dorso-lateral appendages with tubercles, which can be irregularly arranged or organized in whorls, lack of cnidosacs in appendages, and pseudobranchs (gills), which are located on the interior faces of the appendages of most species. Their smooth, finger-like rhinophores are surrounded at the base by a cup-like sheath. Their gonopore is situated on the right side of the body below the first dorsal appendage with an anal papilla, which lies latero-dorsally, between the 1st and 2nd