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A Taxonomic Revision and Cladistic Analysis of the Oxudercine Gobies (Gobiidae: Oxudercinae)

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ABSTRACT. The gobiid subfamily Oxudercinae was revised to assess the monophyletic nature of the subfamily; the intergeneric relationships within the subfamily; the relationships of oxudercines to other gobiid genera; the recognisable species and their distinguishing characters; and the distribution patterns of the subfamily and component taxa. The following results were obtained: (1) The Oxudercinae can be defined on the basis of derived states of certain neurocranial bones and muscles, eye position, nasal flap morphology, the palatine-ectopterygoid arrangement, reduction in size of the premaxillae ascending processes, and in having a single anal fin pterygiophore anterior to the first hemal spine. (2) Within the subfamily, one undefined and nine monophyletic terminal assemblages are recognised, with relationships amongst them based on derived states of various morphological features. These assemblages are recognised at the generic level and one new genus *(Zappa)* is described; a key to the genera is provided. Thirty four species are recognised of which one *(Boleophthalmus birdsongi)* is described for the first time. Each species is described in detail and a key is provided for each genus. (3) Two monophyletic assemblages (one comprising three genera, the other seven) are recognised at the tribal level. Defining characters for each tribe are provided and illustrated. (4) Biogeographic analysis indicated that nine of the ten genera are distributed in an area bounded by the Arabian Gulf to the west, southern Japan to the north, northern Australia to the south, and Papua New Guinea to the east. The remaining genus, *Periophthalmus,* overlaps and exceeds the above limits, ranging from west Africa eastward to Samoa. Species-specific correlations linking *Periophthalmus* with mangrove distributions are discussed.

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The Oxudercinae, a subfamily of gobiid fishes, are found in soft bottom intertidal areas and mangrove swamps of the Indo-west Pacific (*sensu* Springer, 1982), with one representative in tropical west Africa. All oxudercines are at least occasional burrow dwellers and several genera can be referred to the vernacular name of mudskippers which describes their habits on exposed littoral surfaces.

Historically, the taxon has been treated as a monotypic family (Oxudercidae) of uncertain affinity. Springer (1978) exposed the gobiid nature of the type genus *(Oxuderces)* and species *(O. dentatus)* and stated that although the Oxudercidae is a junior synonym of the Gobiidae, the name has priority over the closely related Apocrypteinae, Boleophthalminae and Periophthalminae. Hoese (1984) defined the characters that unite the included genera of the Oxudercinae.

Oxudercine gobies, especially *Boleophthalmus* and *Periophthalmus,* have been the subject of numerous morphological, physiological and natural history studies. Petit (1922) described burrow construction by *Periophthalmus koelreuteri* (=*argentilineatus* or *kalolo*). Harms (1929) described differences in associations among several species of *Periophthalmus* and Eggert (1929 a,b; 1935) recognised morphological differences among these and other species. Schöttle (1931) described aspects of morphology and physiology in ten mudskipper species and compared them to other gobioids. Hora (1935) studied the physiology of air-breathing fishes including several oxudercines. Lele & Kulkarni (1938, 1939) described the skeleton of *Periophthalmus barbarus* (= *kalolo*). Harris (1960) studied locomotion in *Periophthalmus koelreuteri* (= *barbarus*). Stebbins & Kalk (1961) reported on nesting, locomotion and thermal tolerance in the east African *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*). Gordon *et al.* (1965, 1968, 1978) studied physiological aspects of terrestriality in *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*) and *Periophthalmus cantonensis* (= *modestus*). Teal & Carey (1967) examined respiratory adaptations in *Periophthalmus sobrinus* (= *argentilineatus* or *kalolo*) from Madagascar. Macnae (1968) provided information on the natural history of several mudskippers. Graham (1971) reported on aerial visual modifications in *Periophthalmus* and respiratory adaptations (1976) in several oxudercines. Nursall (1974, 1981) analysed inter- and intraspecific aggression in four sympatric species of *Periophthalmus.* Sponder & Lauder (1981) examined feeding mechanics of *Periophthalmus koelreuteri* (= *barbarus*) by cineradiographic analysis. The thermal ecology of *Periophthalmus koelreuteri* (= *waltoni*) and *Boleophthalmus boddarti* (= *dussumieri*) was studied by Tytler & Vaughan (1983). Unfortunately, in most of the above studies, the inexactness of the group's taxonomy caused invalid specific names to be used. Consequently, it is difficult to associate the data and experimental results with a particular species. This is especially true for *Periophthalmus,* the species of which have been notoriously difficult to identify (Macnae, 1968; Nursall, 1974). In fact, Smith (1959:219) stated "...the precise diagnosis of species in this almost circumtropical genus is difficult, for it involves either the recognition of a multitude of intergrading forms, or the lumping of most in one highly polymorphous form." *Periophthalmus,* the most amphibious and best known oxudercine, has long fascinated ichthyologists. The first published account of *Periophthalmus* I can confirm is Vlaming (1701) and the first published figure appeared in Ruysch (1718). Valentijn (1726) and Prevost (1747) were also pre-Linnaean works that figured *Periophthalmus.* Linnaeus described the first species of *Periophthalmus (Gobius barbarus)* in 1766 and the first oxudercine in 1758. Subsequent authors have described more than 100 nominal oxudercine species and subspecies.

The most important post-Linnaean works pertaining to the taxonomy and systematics of oxudercines are the following: Pallas (1770) described and figured two oxudercines; Bloch & Schneider (1801) coined *Periophthalmus* and described three new oxudercines; Hamilton (1822) described five new oxudercines and figured three of them; Valenciennes (1837) erected two