Phylogeny of the Wormfishes (Teleostei: Gobioidae: Microdesmidae)

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Microdesmidae (sensu stricto) includes 30 species of elongate, cryptic, benthic gobioid fishes. The phylogenetic relationships among microdesmid species have been unknown, and the sister taxon to Microdesmidae has been a matter of debate. In this study, the relationships of microdesmid species are hypothesized based on morphological characters, analyzed with cladistic parsimony methods. Characters previously used as evidence for a sister-taxon relationship between Microdesmidae, s.s., and five genera classified as a subfamily (Ptereleotrinae) in an expanded Microdesmidae are reexamined and found to be invalid. Microdesmidae s.s. is restored, including only Cerdale, Clarkichthys, Microdesmus, Gunnellichthys, and Paragunnellichthys. Monophyly of the microdesmid genera is confirmed, and characters diagnosing each genus, and other clades revealed in this analysis, are discussed. The five genera formerly placed in Ptereleotrinae are referred to Ptereleotridae (incertae sedis within Gobioidae), bringing the total number of gobioid families to nine. Microdesmidae is also placed incertae sedis in Gobioidae; some sister-taxon candidates could be excluded based on the characters surveyed in this analysis, but among other gobies, no clear sister taxon to Microdesmidae could be identified.

MICRODESMIDAE (as used here: sensu stricto, of Dawson, 1974) includes five genera (Cerdale, Microdesmus, Clarkichthys, Gunnellichthys, and Paragunnellichthys) of small, elongate, benthic, and often burrowing gobioid fishes found nearshore throughout tropical oceans and estuaries. Microdesmids possess the derived gobioid features of five rather than six branched rays and a single rather than a pair of epurals in the caudal skeleton (Hoese, 1984). Additionally, microdesmids are unusual among gobies in having a single, elongate dorsal fin rather than one with separate spined and rayed portions. Microdesmids vary in size; Microdesmus longipinnis is the largest microdesmid, reaching lengths of up to 300 mm (Dawson, 1962, 1974). The species of Gunnellichthys are also generally large (up to 125 mm standard length; Smith, 1958; Dawson, 1968a, 1973a), and those of Paragunnellichthys are the smallest (22–34 mm standard length; Dawson, 1967, 1969, 1970). Most Cerdale, Clarkichthys, and Microdesmus are of intermediate size relative to the other genera.

Microdesmid species occur worldwide; three of the genera are distributed in the eastern Pacific, Caribbean, and Atlantic (near the Americas), and the other two are found in the Indo-Pacific. Cerdale and Clarkichthys are mostly restricted to the Caribbean and eastern Pacific near Central America; exceptions are Cerdale fasciata, which is found off the southern coast of Brazil, and Clarkichthys bilineatus, which occurs in the eastern Pacific, from the Panamanian isthmus north to Baja California (Dawson, 1974). The speciose Microdesmus occurs in the same regions but is more widely distributed, inhabiting waters of the tropical eastern Atlantic as well as the western Atlantic, Caribbean, and eastern tropical Pacific (Robins and Manning, 1958; Dawson, 1979). Gunnellichthys and Paragunnellichthys are found in the Indo-Pacific, and their ranges do not overlap with those of the other genera. The American genera are found nearshore in sandy, muddy, and swampy habitats; the Indo-Pacific Gunnellichthys and Paragunnellichthys occur near coral reefs, on rocky, silty, or sandy substrate. Microdesmids are usually found at depths of less than 5 m, buried in or closely associated with the substrate, and are egg predators. They are uncommon in museum collections, with many species represented by only one or a few specimens. This scarcity is because of their habitat and ecology; because they are burrowers, they are not sampled effectively except with ichthyocides. Microdesmids also appear to be sparsely distributed; typically only a few specimens are taken at a site, and sustained high doses of ichthyocide are required to cause them to emerge.

Microdesmids have rarely been studied, and no infrageneric phylogenetic hypotheses have been advanced. The purpose of this study is to propose a hypothesis of the phylogenetic relationships of microdesmid species using cladistic parsimony methods and morphological characters. The analysis evaluates the monophyly of Microdesmidae and each included genus and provides insight into the character evolution in the group. A previous hypothesis of a sister-group relationship between the five microdes-
mid genera and five genera assigned to the subfamily Ptereleotrinae (Hoese, 1984) is also investigated.

**MATERIALS AND METHODS**

Adults of all 30 described microdesmid species, as well as representatives of several other gobioïd groups, were obtained from museum collections. Various gobioïd outgroup taxa were examined; *Ptereleotris evides* and *Nemateleotris magnifica* are classified in Hoese’s (1984) Ptereleotrinae and are representative of both primitive and derived ptereleotrine as indicated by the phylogeny of Rennis and Hoese (1987). Gobiognellinae of Birdsong et al. (1988) and Pezold (1993) was represented by *Gnatholepis thompsoni*, *Oligolepis acutipinnis*, and *Tridentiger bifasciatus* and Sicydiinae by *Sicydiwm multipunctatum*. There is no single clear choice for the appropriate microdesmid outgroup; evidence supporting various postulated microdesmid outgroups is not strong, and some suggestions are based on a putative sister-taxon relationship with Hoese’s ptereleotrine genera, which is itself questionable. Therefore, a variety of gobioïd taxa were examined and included in the phylogenetic analysis as a single composite outgroup taxon. Several members of Gobiinae were examined; these taxa have not been phylogenetically investigated, but Birdsong et al. (1988) have established several groups based on vertebral and median fin characters. *Asterophrys semifasciatus*, Coryphopterus personatus, *Gobiodon citrinus*, *Eviota prasina* and *Lophogobius cypriodides* are representatives of the speciose Old World Priolepis group; *Barbulifer caudatus*, *Chirodela minutilis*, *Edaphichthys jessii*, and *Gobulus crescentalis* are New World species, representing the Gobiomuraena group. *Microgobius gulosus* (New World), *Nemateleotris maculosa* (Old World), *Pomatoschistus microps* (Old World), and *Bathygobius lineatus* (worldwide) are each placed in their own eponymous groups.

Specimens were cleared and double stained for bone (alizarin red) and cartilage (alcian blue) by the method of Pothoff (1984) and dissected by a modification of the method for small teleosts outlined in Weitzman (1974). Six species (*Cerdale prolata*, *Pavagunnellichthys springeri*, *Gunnellichthys virdus*, *Microdesmus hildebrandtii*, *M. intermedius*, and *M. lanceolatus*) were too rare to be cleared and stained; radiographs of these and *M. africana*, *M. athiopicus*, *M. luscus*, *M. affinis*, *M. knappi*, *C. paludicola*, and *P. fehlmanni* were made using a Hewlett-Packard Faxitron cabinet X-ray system with Kodak Ortho M film. The holotype of *Cerdale fasciata* was unavailable; the only other existing specimen is a cleared-and-stained paratype. For this species, some characters were coded from the description of Dawson (1969). Additional characters were taken from Dawson’s descriptions and revisions; except where noted, the characters were reexamined and verified. For the outgroup gobioïds, each taxon was examined and coded for each character. A composite outgroup taxon was then created; when all the taxa shared the same state for a character, that state was assigned to the composite outgroup. When the surveyed taxa differed, the state was coded in the composite outgroup as ambiguous.

A data matrix of 59 characters for 31 taxa (30 ingroup and one composite outgroup) was analyzed with PAUP (vers. 3.1.1, D. L. Swofford, unpubl.) using 1000 replications of a heuristic search, with TBR branch swapping and the composite outgroup taxon designated as the outgroup and used to polarize characters and root the tree. Five of the 59 characters were multistate (characters 40, 42, 46, 47, and 57). To avoid imposing unjustified models of evolution on these characters, they were treated as unordered. The remainder were binary characters; a '?' in the matrix is used to indicate missing data. Missing data indicate that the character could not be observed, because the structure was internal, cleared-and-stained specimens were unavailable, or the character could not be resolved by radiography. The consistency index (CI) and retention index (RI) were generated for the phylogeny as a whole and for each character by PAUP (Farris, 1989). MacClade 3.0 (W. P. Maddison and D. R. Maddison, 1992, unpubl.) was used to assemble the data matrix and to visualize character change on the cladograms. Bremer support indices (Bremer, 1988, 1994) were calculated using TreeRot (M. D. Sorenson, unpubl.).

**RESULTS**

Characters listed below are grouped into anatomical units from anterior to posterior and numbered (in parenthesis following the character name) in correspondence with the numbering in the data matrix (Appendix). For each character, the primitive and derived states are described, followed by the consistency and retention indices for each character in the format (CI, RI); when equivalent, only one number is shown.

**Ossification of frontal bones (1).—(0) Frontal bones fully ossified, contacting median ethmoid; (1) frontals unossified anteriorly, not con-
tacting median ethmoid. A gap between the ethmoid and frontals is seen in all microdesmids except *Gunnellichthys* (Figs. 1–2). In state one, the narrow anterior portion of the frontals does not ossify, resulting in the frontals terminating anteriorly in slender points between the orbits. Dawson presented examples of radiographs of state zero in *Gunnellichthys curiosus* and *G. viridescens* (Dawson, 1968a: fig. 4), and state one in *Cerdale* and *Clarkichthys* (Dawson, 1974: fig. 10) and *Paragunnellichthys seychellensis* (Dawson, 1967: fig. 5). All outgroup taxa exhibit state zero: fully ossified frontals. (1.00)

*Sphenotic elongation* (2).—(0) Sphenotics not elongate; (1) sphenotics elongate dorsally, extending onto cranium. All microdesmids have elongate sphenotics, reaching near (*Gunnellichthys* and *Paragunnellichthys*) or contacting (*Clarkichthys, Cerdale, and Microdesmus*) the supraoccipital. Gobies lack parietal bones, and this portion of the neurocranium is occupied by a posterior extension of the frontals (the most common condition) or a dorsal extension of the sphenotics. Hoese (1984) reported that members of his *Ptereleotrinae* possess elongate sphenotics, but this observation was not confirmed. Instead, as described by Gosline (1955), small sphenotics were observed in *Ptereleotris*, and elongate sphenotics were seen in *Microdesmus, Gobiodon, and Eviota* (Figs. 1–2). Other outgroup taxa have small, nearly square sphenotics. This character was coded as ambiguous (0&1) in the composite outgroup. (1.00, 0.0)

*Epioccipital/frontal placement* (3).—(0) Frontals extended posteriad, epioccipitals extended anteriorly, in contact with frontals; (1) frontals, epioccipitals not extended, not in contact. State one occurs in *Microdesmus* (Fig. 1), *Cerdale* (Fig. 2), and *Clarkichthys*, in which the sphenotic alone or the sphenotic and pterotic both contact the supraoccipital, between the frontals and the epioccipitals. In *Gunnellichthys, Paragunnellichthys*, and most outgroups (with the exception of *Eviota*), the frontals extend posteriad to contact the epioccipitals. This character was coded as ambiguous (0&1) in the composite outgroup. (1.00)

*Dorsal extension of pterotic* (4).—(0) Pterotic not extended, not contacting supraoccipital; (1) pterotic extends dorsally, contacts supraoccipi-
tal. State one is present in Microdesmus (Fig. 1), except for M. bahianus and M. retropinna. In these two species and the other microdesmids and outgroups, the pterotic is excluded from contact with the supraoccipital by the sphenotics and epioccipitals, or by the frontals. (0.50, 0.92)

**Supraoccipital shape (5).**—(0) Supraoccipital with posterior expansion and expanded anterior edge; (1) supraoccipital without or with only small posterior process. The supraoccipital commonly has a pointed, rounded, or rectangular process that extends posteriorly, overlapping or intruding between the paired epioccipitals, and some degree of expansion on the anterior edge; this condition (state zero) is seen in most Microdesmus species, other microdesmids, and outgroups. State one is shared by M. multiradiatus (Fig. 1), M. intermedius, M. hildebrandi, and M. luscus. This character was coded from radiographs of a dorsal view of the head for M. intermedius and M. hildebrandi; in these species, the condition of the supraoccipital was clear. In the absence of cleared-and-stained material and ambiguous radiographs for M. lanceolatus, this species was coded as ?. (1.00)

**Rostral cartilage ossification (6).**—(0) Rostral cartilage not ossified; (1) rostral cartilage ossified. The rostral cartilage between the anterior premaxillary processes and the ethmoid region is ossified in Paragunnellichthys, unossified in other microdesmids and outgroups examined. (1.00)

**Anterior maxillary projection (7).**—(0) Maxilla without anterior projection; (1) maxilla with elongate projection extending anteriad, overlapping dorsal process(es) of premaxilla. Microdesmids all possess state one. The projection is most extended and slender in Gunnellichthys (Fig. 3) and is illustrated for Cerda and Clarkichthys in Dawson (1974:figs. 5, 13, 18, 23). In outgroup taxa, the maxilla is anteriorly blunt and lacks the process. (1.00, 0.0)

**Extended dentary processes (8).**—(0) Processes absent or short, pointed, fully ossified; (1) processes elongate, much wider, thinner. All microdesmids and many gobies possess processes that extend ventrad from the most anterior portion of the dentaries at the dentary symphysis. State one, in which thin processes, often so thin that they do not stain with alizarin red, project ventrad and caudad from the dentary symphysis, is present in Cerda floridana, C. ionthas, and C. fasciata (Fig. 5). In C. paludicola (single cleared-and-stained specimen damaged), and C. prolata (no cleared-and-stained specimen available), the character is coded as ? because the bone is so thin that it cannot be reliably coded from a radiograph. Other microdesmids and outgroup taxa lack these thin, elongate dentary processes; when dentary processes are present they are robust and short. (1.00)

**Recurved teeth (9).**—(0) Teeth recurved; (1) teeth straight. Teeth are recurved in Gunnellichthys and Paragunnellichthys. The derived condition of smaller, straight teeth is found in Cerda, Clarkichthys, and Microdesmus (Fig. 4). Teeth of M. dorsipunctatus and M. dipus were figured in Dawson (1968b:figs. 3–4), and of M. knappi in Dawson (1972:fig. 3). Outgroups exhibit state zero, with the exception of Sicydium multipunctatum and Gobiodon citrinus. In these species, arrays of many slender minute teeth are present. This condition is coded as state 2. The character was coded as 0&2 in the composite outgroup. (1.00)

**Spatulate teeth (10).**—(0) Teeth pointed, not spatulate; (1) some teeth blunt, spatulate. Clarkichthys and Cerda share state one, with an outer
row of conical teeth and inner row of spatulate teeth (Fig. 4). Other microdesmids and outgroups do not have any spatulate teeth in the jaw. Dentition in *Cerdale ionthas* was figured in Dawson (1974:figs. 5, 13, 18). (1.00)

**Large pointed outer teeth (11).**—(0) Several large, laterally compressed, pointed teeth present, distributed along outer anterior border of jaws; (1) large pointed teeth absent. In most outgroups and *Gunnellichthys*, several large, laterally compressed teeth are present as the outermost tooth row in both the upper and lower jaws (Fig. 4). In some outgroup taxa (*Sicydium multipunctatum*, *Gobiodon citrinus*), these teeth are not present; the teeth are numerous and slender, as discussed in character 9. For this reason, this state was coded as 2, and the character was coded as 0&2 in the composite outgroup. The microdesmid genera *Paragunnellichthys*, *Clarkichthys*, *Cerdale*, and *Microdesmus* share state one, in which these teeth are absent. (1.00)

**Large conical outer teeth (12).**—(0) Absent; (1) present. In *Microdesmus hildebrandi*, *M. intermedius*, *M. luscus*, and *M. multiradiatus*, several large blunt teeth are present in the upper and lower jaws, outside the inner tooth row (Fig. 4). Other microdesmids and outgroup taxa lack these teeth. (1.00)

**Dentary shape and articulation (13).**—(0) Slightly bowed laterally; (1) thin, straight, meeting in sharp “V.” *Microdesmus aethiopicus*, *M. africanaus*, *M. bahianus*, *C. carri*, *M. suttkusi*, and *M. retrofissi* all have sharp dentary symphyses, manifested externally as very acute jaws. Other microdesmids and outgroups have the more typical goby condition, in which the dentaries bow laterally anteriad, resulting in a rounded jaw in ventral view. (1.00)

**Lacrimal (14).**—(0) Present; (1) absent. The lacrimal bone, a slender, elongate element that articulates dorsally with the lateral ethmoid, is primitively present in gobies but is commonly absent. Among microdesmids, species of *Gunnellichthys* possess a lacrimal; it is absent in the other genera (Fig. 3). Outgroup taxa examined all possess a lacrimal. (1.00)

**Palatine size and length (15).**—(0) Long (width less than one-quarter of length), broadly opposed to ectopterygoid; (1) short (width more than one-quarter of length), with small area opposed to ectopterygoid. *Gunnellichthys* and *Paragunnellichthys* exhibit state one; other microdesmids and outgroups exhibit state zero.

Harrison (1989), in his extensive survey of the palatopterygoquadrate (PPQ) complex of gobiods, described the primitive PPQ condition as including a palatine that extends halfway along the ectopterygoid. The two derived variations on this are “long palatine extending towards, or meeting the quadrate, or a very short, stubby palatine.” Harrison coded *Microdesmus longipinnis* and all the outgroup genera of this study (except *Barbulifer* and *Gobulus*, which he did not examine) as having the condition of a palatine reaching halfway along the ectopterygoid or a long palatine extending toward the quadrate. *Cerdale ionthas* was scored as having a short palatine, with the shaft “related to only the dorsal third” of the ectopterygoid. The character is here coded differently than in Harrison (1989), but this is simply a matter of con-
text; Harrison did not examine *Gunnellichthys* or *Paragunnellichthys*. When these taxa are considered, and more *Cerdale* and *Microdesmus* species are included, the conditions in *Gunnellichthys* and *Paragunnellichthys* (palatine stubby and with small area of articulation with ectopterygoid) are distinct from those in *Cerdale*, *Microdesmus*, and *Clarkichthys* (elongate palatine with long articulation with ectopterygoid). Thus, the palatine is coded as short in *Gunnellichthys* and *Paragunnellichthys*, and long in *Clarkichthys*, *Cerdale*, *Microdesmus*, and outgroups. (0.50, 0.86)

**Palatine medial process (16).**—(0) Present, articulating with lateral ethmoid; (1) absent, apposing lateral ethmoid on anterodorsal surface. In microdesmids, the palatine is slender and does not bear a medial process articulating with the lateral ethmoid. Instead, a slight raised portion on the anterodorsal surface may be present where the palatine contacts the lateral ethmoid. In specimens that were cleared, stained, and dissected, these portions of the palatine and lateral ethmoid appear pebbled or rugose. Outgroup taxa examined have a distinct inner process on the palatine contacts the lateral ethmoid. In one outgroup taxon (*Gobiodon citrinus*), the ectopterygoid flange is present, and so this character is coded as ambiguous (0&1) in the composite outgroup. (0.50, 0.90)

**Rounded dorsal ectopterygoid flange (18).**—(0) Absent; (1) present. In *Microdesmus dorsipunctatus*, *M. dipus*, *M. affinis*, *M. longipinnis*, *M. carri*, *M. suttikus*, *M. retropinnis*, *M. bahianus*, *M. africanaus*, and *M. aethiopicus*, the posterodorsal surface of the ectopterygoid bears a moderate to large rounded expansion, anterior to the point at which the ectopterygoid contacts the quadrate (Fig. 3). Other microdesmids and most outgroup taxa examined have no such expansion; instead, the dorsal surface of the ectopterygoid is flat. In one outgroup taxon (*Gobiodon citrinus*), the ectopterygoid flange is present, and so this character is coded as ambiguous (0&1) in the composite outgroup. (1.00, 0.0)

**Deeply forked quadrate (20).**—(0) Quadrate not forked, with square dorsal expansion; (1) quadrate forked, without square dorsal expansion. The quadrate is deeply forked in microdesmids, lacks a square dorsal expansion, and only the anteroventral corner of the quadrate articulates with the ectopterygoid (Fig. 3). Most outgroup taxa do not have a deeply forked quadrate; instead, the quadrate bears a square anterodorsal portion that articulates broadly with the ectopterygoid. Some outgroup taxa (*Sicydium multipectinatum*, *Gobiodon citrinus*, and *Oligolepis acutipinnis*) exhibit the derived condition of a forked quadrate, and so this character is coded as ambiguous (0&1) in the composite outgroup. This character was discussed in more detail and illustrated in Harrison (1989). (1.00, 0.0)

**Anteroventral anguloarticular projection (21).**—(0) Present; (1) absent. An anteroventral projection on the posterior end of the anguloarticular is absent in *Paragunnellichthys*. Other microdesmids and outgroup taxa possess state zero; the
Thin-walled chin pouch (24).—(0) Absent; (1) present. This pouch was described in Dawson (1967) for Paragunnellichthys seychellensis as “lower lip fleshy, poorly defined, forming pouchlike lateral expansions which receive upper lips and snout when mouth is closed, discontinuous across symphysis where it is interrupted by a subtriangular, fleshy dorsal continuation of the chin.” State one is present in all species of Paragunnellichthys, Microdesmus carri, M. suttkusi, M. bahianus, and M. africanus. Other microdesmids and outgroups do not have expansions from the lower lip. (0.33, 0.67)

Extended tissue flaps at mouth corners (25).—(0) Absent; (1) present. State one is present in Microdesmus hildebrandi, M. intermedius, M. knappi, M. luscus, and M. multiradiatus (Fig. 5). The most pronounced example is found in M. knappi (Dawson, 1972:fig. 2). These species possess greatly expanded folds, with flat extensions of the tissue reaching beyond the posterior extent of the gape. Other microdesmids and outgroups lack these expansions at the mouth corners. (1.00)

Bilobed palp between nares (26).—(0) Absent; (1) present. A small fleshy palp is present on the upper jaw, between the nares, in Cerdale paludicola and C. prolata. The palp can be seen in the illustration of Cerdale in Dawson (1974:fig. 4). The palp is absent in other microdesmids and outgroups. (1.00)

Fleshy projection at lower jaw symphysis (27).—(0) Absent; (1) present. A small, distinct fleshy projection is present at the center of the anterior portion of the lower jaw in Microdesmus affinis, M. dipus, M. dorsipunctatus, and M. longipinnis. Other microdesmids and outgroups do not have this projection. (1.00)

V-shaped lower lip indentation (28).—(0) Absent; (1) present. Cerdale ionthas and C. floridana have a prominent indentation in the lower lip (Fig. 5; Dawson, 1974:fig. 4). Other microdesmids and outgroups lack this indentation; their lips are smooth. (1.00)

Mouth orientation (29).—(0) Mouth horizontal or nearly so; (1) mouth inclined. Most microdesmids have inclined mouths, coded as state one. Gunnellichthys monostigma, G. irideus, G. viridescens have horizontal mouths (Fig. 5); these Gunnellichthys species and outgroups were coded as having state zero. Illustration of the head shapes of G. viridescens (state zero) and G. curiosus
Ichthys, Cerdale reaching beyond posterior naris.

Gape size (30).—(0) Gape long, extending to or beyond posterior naris; (1) gape short, not reaching beyond posterior naris. Paragunnellichthys, Cerdale, and Clarkichthys have short gapes (Fig. 5). In other microdesmids and outgroups, the gape extends beyond the posterior naris.

Narial region laterally expanded (31).—(0) Not expanded; (1) expanded. In state one, the narial region is broadly rounded and expanded, with grooves from the orbits to the mouth delineating the lateral borders of the rounded portion. This state is present in Microdesmus hildebrandi, M. intermedius, M. luscus, and M. multiradiatus (Fig. 5). In other microdesmid species and outgroups, the snout is not expanded and grooves are not present. (1.00)

Anterior naris position (32).—(0) Near posterior naris, not adjacent to mouth; (1) far anteriad of posterior naris, adjacent to mouth, nares widely spaced. State one is present in all microdesmids (Fig. 5). Most outgroups examined exhibit state zero, in which the nares are close together. In two outgroup taxa (Barbulifer ceutothecus and Gobulus crescentalis), state one is present, therefore, this character was coded as ambiguous (0&1) in the composite outgroup taxon. (1.00, 0.0)

Thin, tubular anterior naris expansion (33).—(0) Absent; (1) present. The anterior naris is extended into a short tube of skin in Gunnellichthys curiosus and G. pleurotaenia (Fig. 5). Other microdesmids and most outgroups do not have this extension, however, it is present in a few outgroup taxa (Gobiodon citrinus, Elacatinus janssi, Neogobius fluvatilis, and Eviota prasina). Therefore, this character is coded as ambiguous (0&1) in the composite outgroup taxon. (1.00)

Nasal rosettes in expanded nasal cavity (34).—(0) Absent; (1) present. Most microdesmids have enlarged nasal cavities, with expanded rosettes of tissue present inside the chamber. Gunnellichthys monostigma, G. irideus, and outgroup taxa have simple narial chambers, without these expansions of tissue. (0.50)

Narial size (35).—(0) Nares prominent, posterior nares up to half of eye diameter; (1) nares minute, much less than half of eye diameter. Species of Gunnellichthys have minute nares (Fig. 5).

Eye placement (36).—(0) Eyes lateral, not reduced or covered by skin; (1) eyes dorsolateral, deeply subdermal. Microdesmus hildebrandi, M. intermedius, M. knappi, M. lanceolatus, M. luscus, and M. multiradiatus all have tiny, reduced eyes (Fig. 5; Dawson, 1972:figs. 1–2). Other microdesmids and outgroup taxa have larger, distinct, laterally pointing eyes, not covered by skin. (1.00)

Head shape (37).—(0) Head pointed or slightly rounded; (1) head bluntly rounded. Microdesmus hildebrandi, M. intermedius, M. knappi, M. luscus, M. multiradiatus, and M. lanceolatus all have blunt, square snouts (Fig. 5; Dawson, 1972:fig. 2; Dawson, 1977:fig. 1). Other microdesmids and outgroups have attenuated, slightly rounded heads, not square or anteriorly blunt. (1.00)

Eye bar pigmentation (38).—(0) No bars radiating from eye; (1) bars radiating from eye, one dropping ventrally from orbit and another extending anterovertrally. State one is present in Microdesmus aethiopicus, M. afric anus (Dawson, 1979:fig. 1), M. bahianus (Dawson, 1973b:fig. 1), M. retropinnis, M. carri, and M. suttkusi (Gilbert, 1966:fig. 1), particularly in smaller specimens. In some of the published figures, particularly the photographs, the color is faded and difficult to distinguish, but my examination of specimens confirmed the presence of pigmentation around the eye. Other microdesmids and outgroups lack this pigmentation around the eye. (1.00)

Posttemporal position (39).—(0) Articulating with epioccapitals at rear of neurocranium; (1) not articulating directly with neurocranium, instead contacting epioccapitals by ligament. State one is present in Gunnellichthys and is readily seen both in cleared-and-stained preparations and radiographs. In other microdesmids and outgroups, the posttemporal is in contact with the epioccapitals at its articulation with the rear of the neurocranium. (1.00)

Pectoral fin rays (40).—(0) Usually 15 or more; (1) usually 14; (2) usually 12 or 13; (3) usually 10 or 11; unordered. The character is coded such that states do not overlap in any species. Outgroups, Cerdale prolata, Gunnellichthys monostigma, and G. curiosus exhibit state zero; other states are distributed variously among the other microdesmid taxa. (0.27, 0.33)

Pelvis morphology (41).—(0) Pelvis robust, with small anterior extensions of pelvic intercleithral cartilage (PIC), not deeply cleft; (1) pelvis slender, with PIC deeply cleft, separate along most
of its length. All microdesmids share state one (Fig. 6), in which the entire pelvis is elongate and gracile, with the PIC slender and cleft along most of its length. Outgroup taxa exhibit state zero, in which the PIC is stout and not elongate.

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**Pelvic fin rays** (42).—(0) Five; (1) four; (2) three; (3) two; unordered. The pelvic fins of microdesmids are small and slender. Each pelvic fin bears a single spine laterally and two (Paragunnellichthys), three (Cerdale, Clarkichthys, and Microdesmus), or four (Gunnellichthys) segmented rays (Fig. 6). Outgroup taxa have five pelvic rays, with one exception: Eviota prasina has four rays, and therefore this character is coded as ambiguous (0&1) in the composite outgroup. (1.00, 0.0)

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**Median fin finfold** (43).—(0) Absent; (1) present, fins connected by low finfold. In state one, the result is a continuous finfold around the body joining the dorsal, caudal and anal fins. State one is present in Microdesmus. Other microdesmids and outgroups exhibit state zero, in which the dorsal, caudal and anal fins are distinct. (1.00)

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**Dorsal fin number** (44).—(0) Two; one spiny, the other with rays; (1) one, spiny and rayed portions continuous. Most gobies (including all outgroup taxa examined) have two dorsal fins; microdesmids all have a single continuous dorsal fin, in which the spiny and rayed portions are contiguous. (1.00, 0.0)

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**First dorsal spine pterygiophore spacing** (45).—(0) All pterygiophores evenly spaced; (1) first two pterygiophores more closely spaced than remainder. Gunnellichthys curiosus, G. pleurotaenia, G. irideus, G. viridescens (Dawson, 1968a:fig. 3), Clarkichthys bilineatus (Dawson, 1974:fig. 9), Paragunnellichthys fehlmani and P. springeri share state one, in which the first two dorsal spines are more closely spaced than the remaining spines. In G. monostigma, P. seychellensis (Dawson, 1967:fig. 4), other microdesmids, and outgroups, all the dorsal fin spines are evenly spaced. (0.25, 0.50)

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**First dorsal spine insertion** (46).—(0) At gap between third and fourth neural spines; (1) at gap between fourth and fifth neural spine; (2) posterior to gap between fourth and fifth neural spine; unordered. This character describes posterior displacement of the dorsal fin origin and is also correlated with the presence of highly reduced dorsal fin pterygiophores that do not bear spines or rays anterior to the first spine-bearing pterygiophore. Dawson (1974) refers to these nonspine bearing bones as “predorsal interneurals” in his descriptions; these bones are not equivalent to the “predorsals” of Mabee (1988), rather they are “rayless pterygiophores” (Birdsong et al., 1988). Most of the species in Cerdale and Microdesmus exhibit state one, with the first dorsal spine inserting between the fourth and fifth neural spine. Clarkichthys, Gunnellichthys, Paragunnellichthys, Microdesmus luscus, and outgroups exhibit state zero, with insertion at or anterior to the gap between third and fourth neural spines. The species C. paludicola (7th/8th gap), M. bahianus (10th/11th gap), M. aethiopicus (7th/8th gap), and M. retropinnis (15th/14th gap) all exhibit state 2, describing far posterior displacement of the dorsal fin. (0.40, 0.77)

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**Dorsal fin spines** (47).—(0) 5–7; (1) 11–18; (2) 19–22; (3) more than 23; unordered. This character describes the length of the spinous dorsal fin. States are coded in these groups because in a histogram of species versus range in number of spines, distributions fall into these four groups. Outgroup taxa all exhibit state zero. (0.60, 0.80)

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**Dorsal fin spine pterygiophore expansion** (48).—(0) Present; (1) absent. Gunnellichthys and outgroups exhibit state zero, in which the radials of the first dorsal fin pterygiophores are expanded anteriorly, most prominently in the anterior portion of the fin. Other microdesmid
species exhibit state one: slender pterygiophores without any dorsal expansion. (1.00)

Vertebral number (49).—(0) 47 or fewer; (1) 48 or more. Species of Microdesmus, Gunnellichthys, and Paragunnellichthys have 48 or more total vertebrae and concomitantly elongate bodies, most notably in Microdesmus longipinnis, which may have as many as 66 vertebrae (Dawson, 1962). In outgroups, Cerdale, and Clarkichthys the total vertebral number is 47 or fewer. (0.50, 0.83)

Segmented caudal fin rays (50).—(0) 17; (1) 15. Microdesmus, Cerdale, and Clarkichthys have 17 caudal rays, Gunnellichthys and Paragunnellichthys 15 caudal rays. Outgroup taxa have 17 segmented caudal rays. The caudal skeletons of Cerdale ionthas and Clarkichthys bilineatus were illustrated in Dawson (1974:fig. 7). (0.50, 0.86)

Caudal fin shape (51).—(0) Rounded; (1) elongate, lanceolate. State one is present in Microdesmus lanceolatus, M. hildebrandi, M. luscus, and M. multiradiatus. The lanceolate condition is particularly evident in small specimens but is also present in adults. In the related taxa M. knappi and M. intermedius, even in fairly small specimens, the caudal fin is blunt and almost square. Most microdesmids have a blunt-rounded tail as adults and emarginate tails as larvae and small juveniles. Larval and juvenile emarginate tails and rounded adult tails were illustrated in Gilbert (1966:fig. 1). The lanceolate tail was illustrated in Dawson (1962:fig. 1). Outgroup gobiosids have rounded tails as adults with the exception of Microgobius gulosus and Oligolepis acutipinnis, which have lanceolate tails. This character is coded as ambiguous (0&1) in the composite outgroup taxon. (0.67)

Body elongation (52).—(0) Body depth 10% or more of standard length; (1) body depth less than 10% of standard length. In outgroups and Cerdale, the body depth is 10% or more of standard length; all other genera have variously elongate bodies. For microdesmids, data for this character were taken from the descriptions of Dawson, particularly Dawson (1974). (0.50, 0.80)

Body pigmentation: irregular mottling on dorsal and lateral aspects (53).—(0) Absent; (1) present, resulting in a spotted or stippled appearance on dorsal and lateral aspects. State one is present in Microdesmus carri and M. suttkusi (Gilbert, 1966:fig. 1). Other microdesmids and outgroups have a variety of pigmentation patterns but do not exhibit the condition seen in M. carri and M. suttkusi. (1.00)

Body pigmentation: lateral, chevron-like blotches (54).—(0) Absent; (1) present. Microdesmus dor-sipunctatus and M. dipus share state one, with pigmented blotches roughly following the shapes of the body myomeres (Dawson, 1968b: figs. 1–2). Other microdesmids and outgroups have a variety of pigmentation patterns but do not exhibit the chevron pattern seen in M. dorsipunctatus and M. dipus. (1.00)

Body pigmentation: lateral and dorsal ovoid blotches (55).—(0) Absent; (1) present. State one is present in Microdesmus aethiopicus and M. retropinnis. Variation exists; some specimens are much paler than others, particularly larger specimens. Only one specimen of M. aethiopicus could be examined, but the spots could be seen even though the specimen had faded. Other microdesmids and outgroups have a variety of pigmentation patterns but do not exhibit the ovoid blotches seen in M. aethiopicus and M. retropinnis. (0.50, 0.0)

Spots at dorsal fin margin (56).—(0) Spots absent; (1) row of evenly spaced spots present on distal border of fin membrane. Paragunnellichthys fahlmanni and P. springeri share state one (Dawson, 1969:fig. 4; 1970:fig. 2). Paragunnellichthys fahlmanni additionally has a row of spots on the anal fin membrane. In other microdesmids and outgroups, these spots are absent. (1.00)

Squamation density (57).—(0) Scales imbricate; (1) scales nonimbricate but closely spaced; (2) Scales nonimbricate and sparse; (3) no scales; unordered. Clarkichthys, Cerdale, Paragunnelliclythys, and Gunnellichthys all have nonimbricate but even, fairly continuous squamation. Microdesmus has nonimbricate, irregular sparse scales, particularly on the ventral portion of the body (Dawson, 1968b:fig. 7). Most outgroup gobiosids have imbricate scales, with the exception of Gobiodon citrinus (nonimbricate but closely spaced scales) and Barbularfer ontothecus, Elacatinus janssi, and Gobulus crescentalis, which are scaleless. This character is coded as ambiguous (0&K&3) in the composite outgroup taxon. (1.00)

Gill opening (58).—(0) Not extended into a tube; (1) extended into a tube formed by folds of the branchiostegal membrane. Tubiform gill openings are seen in Clarkichthys, all Cerdale except for C. prolata (Dawson, 1974:fig. 6), and M. knappi (Fig. 5). The gill opening in C. prolata is known from only the holotype. Dawson (1974)
Fig. 7. Strict consensus of three cladograms generated by parsimony analysis of 59 morphological characters for 30 microdesmid ingroup and one composite gobioid outgroup taxa. This cladogram has a consistency index of 0.653, retention index of 0.882, and rescaled consistency index of 0.575. Small numbers at each node are Bremer support indices; selected character state changes are indicated on the branches. Reversed characters are indicated with an “R” after the character number, and homoplasious changes by open rather than solid bars.

Fig. 8. The three alternate most parsimonious reconstructions of relationships within Cerdale. Character state changes are indicated on the branches; reversed characters are indicated with an “R” after the character number. Reconstruction shown in (C) is the same as in strict consensus cladogram shown in Figure 7.

Bremer support values are one or two; because of the morphological simplification and small size of microdesmid fishes, informative characters were not in abundance, but most of the relationships among microdesmid species could be resolved. The three cladograms differ only in the placement of Cerdale fasciata; the three alternate relationships of Cerdale species, with alternate character distributions, are shown in Figure 8. The trichotomy of Microdesmus hildebrandti, M. luscus, and M. multiradiatus is a result of insufficient data, not conflicting data; no characters were found to resolve relationships of these species.

**DISCUSSION**

The phylogenetic hypothesis obtained in this study validates groupings postulated by Dawson (1974): Microdesmidae and all included genera
are monophyletic, Cerdale and Clarkichthys are closely related, and the Indo-Pacific Gunnellichthys and Paragunnellichthys are basal to the American Cerdale, Clarkichthys, and Microdesmus. Characters diagnosing each named genus, and other clades revealed in this analysis, are discussed below. The numbers of the characters, corresponding to the numbering in the data matrix (Appendix), are given in parentheses.

Microdesmidae.—The group is diagnosed by seven characters: presence of an anterior maxillary projection (7), loss of the inner palatine process that articulates with the lateral ethmoid (16), widely spaced nares (32), a slender pelvis with anterior extensions of the pelvic intercleithral cartilage (41), a single dorsal fin (44), an elevated vertebral number (49; reversed in Cerdale and Clarkichthys), and a body depth of less than 10% of standard length (52; reversed in Cerdale).

Gunnellichthys.—The five species in this genus share the presence of a square ventral flange on the ectopterygoid (17; also found in one clade within Microdesmus), minute nares (35), and posttemporals that do not directly contact the epiparietals (39).

Paragunnellichthys, Clarkichthys, Cerdale, and Microdesmus.—This complex is diagnosed by the incomplete ossification of the frontal bones (1), loss of the lacrimal bone (14), slender, simple dorsal fin pterygiophores (48), loss of large, laterally compressed teeth in the outer tooth row (11), complex, expanded nasal cavities (34), and an inclined mouth (29); the last two are also found in some Gunnellichthys.

Paragunnellichthys.—The three species in this genus share an ossified rostral cartilage (6), loss of an anteroventral process on the anguloarticular (21), and the presence of an expanded pouch on the chin (24; also found in some Microdesmus).

Cerdale, Clarkichthys, and Microdesmus: the American clade.—This large clade is diagnosed by a loss of the contact between the frontals and epiparietals (3) and the presence of nonrecurved teeth (9).

Cerdale and Clarkichthys.—These two genera are diagnosed as sister taxa by the presence of biserial teeth, with the inner row spatulate and the outer row conical (10), a low vertebral count (49), and the restriction of the gill opening into a tube (58). Because of the uncertain placement of Cerdale fasciata and specimen limita-
which are found in some or all microdesmids. This morphological reduction and simplification is clearest in comparisons of *Gunnellichthys* and the remainder of the genera, *Gunnellichthys monostigma* and *G. irideus* are relatively large, with more robust ossification, including complete ossification of the frontal bones and presence of a lacrimal. In general, morphological reduction is a derived condition among gobies (Miller, 1973; Hoese and Gill, 1993), but among microdesmid genera this pattern does not hold. Microdesmidae includes *Paragunnellichthys*, species of which are not only small in size, but also feature several skeletal reductions as compared to other microdesmids. This genus is not the most phylogenetically derived; *Paragunnellichthys* is sister to a clade containing *Cerdale*, *Clarkichthys*, and *Microdesmus*, among which species a variety of reductive and less reductive morphologies are manifested. Even though the skeletal structures in microdesmids are simplified, potentially obscuring phylogenetic character data, it was possible to resolve most of the relationships within this group, largely because of the unique specializations in the head skeleton and sensory structures.

Primate features for Microdesmidae are thin, smooth skin around the mouth and on the chin, and no expansion or elaboration of the narial cavity. A variety of complex modifications of the mouth and nares are seen most microdesmids. Within *Gunnellichthys*, *G. curiosus*, *G. pleurotaenia*, and to a lesser extent *G. viridescens* exhibit some of the head modifications seen in the other genera: a more rounded face and jaw, expanded narial cavities and oral papillae. *Paragunnellichthys* and some *Microdesmus* species feature an expanded thin-walled pouch on the chin (24) and *Cerdale* species share the presence of an elongate, thin dentary processes (8). In *Microdesmus*, some species possess lateral expansions at the mouth corners (25), oral papillae (23) and expanded, ridged chins (22); the most striking sensory modification among these species is the reduction of the eyes (36). All of these characters are likely related to enhancement of senses other than vision, possibly related to the burrowing ecology of microdesmid species.

**Outgroup to Microdesmidae and higher classification within Gobioidei.**—Microdesmidae was erected by Reid (1936), and placed in Gobioidei by Gosline (1955), based on skeletal characters in *Microdesmus multiradiatus*, including the absence of parietals, configuration of the caudal skeleton, and the presence of a gap in the suspensorium bordered by the symplectic-metapterygoid strut and the preopercle. Gosline (1955) diagnosed Microdesmidae as elongate gobies that possess a single continuous dorsal fin and an anterior projection on the maxilla which overlies the premaxillary processes but did not make any further hypothesis of relationships, except to note that *Microdesmus multiradiatus* shares similarities in the neurocranium (dorsal extension of the sphenotics) with *Eviota epiphanes*, *Kelloggella oligolepis*, and *Gobiodon rivulatus*. Hoese (1984) united Microdesmidae (as the subfamily Microdesminae) with a group of four described and two undescribed genera (five are now described: *Aioliops*, *Ptereleotris*, *Parioglossus*, *Nemateleotris*, and *Oxymetopon*) assigned to Ptereleotrinae (Rennis and Hoese, 1987). This grouping was based on characters including the “unique specialization” of an elongate posterior process on the pelvis, but Hoese (1984) indicated that further research was needed to evaluate this grouping.

Hoese’s pelvic process character has been a source of confusion in microdesmid systematics. Birdsong et al. (1988) recognized Hoese’s classification but illustrated only the pelvis of *Ptereleotris* to exemplify the microdesmid character state. Harrison (1989) reported that two of the five microdesmid genera (*Cerdale* and *Microdesmus*) lacked the posterior pelvic process. In this study, the latter observation is confirmed and extended to the other three microdesmid genera: the posterior pelvic spine is not present in Microdesmidae (Fig. 6). Hoese (1984) also stated that his two subfamilies share strongly compressed head and body, with lateral eyes, separate pelvic fins without an interspinal membrane, five branchiostegal rays, one epural, loss of the dorsal postcleithrum and endopterygoid, and interlocking of the anterior preopercular process with the dorsal end of the symplectic. The first of these (lateral compression of the head and body) is only present in the microdesmid genera *Gunnellichthys* and *Paragunnellichthys*; the others are present in microdesmids and ptereleotrids but also in other gobiodid taxa. Other widely distributed gobiodid characters he reported as being shared by microdesmids and ptereleotrids are an L-shaped palatine with a short process articulating with the lateral ethmoid (character 16; present in ptereleotrids but not microdesmids) and an expanded dorsal flange of the sphenotic reaching the supraoccipital (character 2; present in microdesmids but not ptereleotrids). Thus, none of the possible diagnostic characters for Microdesmidae sensu Hoese (1984) could be confirmed; additionally, no new character evidence that could
serve to indicate a relationship between Hoese’s microdesmid subfamilies was identified.

This result forces reassessment of some earlier suggestions of the sister group to Microdesmidae. Hoese (1984) suggested a relationship between Xenisthmidae and Microdesmidae (sensu Hoese, 1984), but this was based on a character present only in his ptereleotrine genera (presence of an interneural gap between dorsal fins). Similarly, Hoese and Gill’s (1993) suggestion that the electrotrid genera Grahamichthys and Thalasseleotris might be related to Microdesmidae is based on characters shared by these genera and Hoese’s Ptereleotrinae. The lack of evidence for a relationship between Microdesmidae and Ptereleotrinae sensu Hoese (1984) removes Microdesmidae (sensu Dawson, 1974) from consideration as sister taxon to Xenisthmidae or Eleotrididae.

Harrison (1989) proposed that microdesmids might be the sister taxon to a monophyletic group containing sicydine and gobionelline gobiods. Harrison’s assertion was based on the morphology and relative positions of the quadrate and ectopterygoid; further work by Parenti and Thomas (1998) on pharyngeal jaw morphology among sicydines indicates that sicydines are sister to the genera Tukugobius and Rhinogobius but did not exclude the possibility that sicydines, Tukugobius, and Rhinogobius may be related to microdesmids. A member of Sicydiinae (Sicydiu multipunctatum) was examined in this study as part of the survey of gobiod outgroups; the sicydine shares one derived character state with Microdesmidae (sensu Dawson, 1974) is recognized. Ptereleotrinae is accorded family rank; Ptereleotrinae is excluded from Microdesmidae and Microdesmidae sensu Dawson (1974) is recognized. Ptereleotrinae is sister to Microdesmidae is premature. Based on these results, Hoese’s (1984) Ptereleotrinae may be the sister taxon to a monophyletic group containing sicydiine and gobionelline gobiods. Harrison’s assertion was based on the morphology and relative positions of the quadrate and ectopterygoid; further work by Parenti and Thomas (1998) on pharyngeal jaw morphology among sicydines indicates that sicydines are sister to the genera Tukugobius and Rhinogobius but did not exclude the possibility that sicydines, Tukugobius, and Rhinogobius may be related to microdesmids. A member of Sicydiinae (Sicydiu multipunctatum) was examined in this study as part of the survey of gobiod outgroups; the sicydine shares one derived character state with Microdesmidae (sensu Dawson, 1974) is recognized. Ptereleotrinae is accorded family rank; Ptereleotrinae is excluded from Microdesmidae and Microdesmidae sensu Dawson (1974) is recognized. Ptereleotrinae is sister to Microdesmidae is premature.

Material Examined

Institutional acronyms follow Leviton et al. (1985). Taxa are listed alphabetically, with microdesmid taxa first, followed by outgroup taxa. The number of specimens in each lot is indicated in parentheses. An asterisk after a lot number indicates the lot was cleared and stained, and if only part of a lot was cleared and stained, the number following the asterisk indicates the number of cleared-and-stained specimens. An “x” following a lot number indicates the lot was x-rayed.

**Microdesmidae**

*Cerdale fasciata*: GCRL 10702 (1)*.

*Cerdale floridana*: ANSP 80576 (1), ANSP 81371 (1), ANSP 82101 (4)*-2, ANSP 105753 (1), ANSP 105769 (1), ANSP 117426 (1), ANSP 119021 (1), ANSP 119022 (1)*, ANSP 119023 (1)*, ANSP 119024 (1), ANSP 144666 (1), ANSP 144956 (1), ANSP 147840 (1), ANSP 147841 (1), ANSP 147842 (1), GCRL 4615 (1)*, UMMZ 186215 (1), UMMZ 187105 (1), USNM 116991 (1).

*Cerdale ionthas*: GCRL 6562 (24)*-3, GCRL 11413 (9), GCRL 6024 (1)*, MCZ 44829 (1), USNM 205072 (5), USNM 207504 (2).

*Cerdale paludicola*: GCRL 6590 (2), GCRL 6592 (1)*, UF 223461 (1), USNM 209217 (1)x.

*Cerdale prolate*: ANSP 134100 (1)x.

Clarkichthys bilineatus: FMNH 41647 (3), GCRL 4109 (1), GCRL 4229 (1)*, GCRL 6558 (2), MCZ 44831 (1)*, MCZ 44832 (1), MCZ 44834 (1), USNM 101685 (1), USNM 206435 (1).

Gunnellichthys curiousus: ANSP 109662 (1), ANSP 109665 (1)*, ANSP 109666 (1), ANSP 109667 (1)*, ANSP 109668 (1), BPBM 6402 (1)*, BPBM 11262 (2), BPBM 54399 (1), USNM 312893 (1).

Gunnellichthys irideus: USNM 171757 (1)x.

Gunnellichthys monostigma: ANSP 128113 (30)*-5, ANSP 128114 (10), ANSP 128435 (10), BPBM 5596 (4), BPBM 5598 (5), BPBM 29173 (4), BPBM 31842 (4), BPBM 32880 (1), USNM 201383(10).

Gunnellichthys pleurotaenia: ANSP 109663 (24)*-5, ANSP 109664 (1), BPBM 6548 (1), BPBM 27904 (1), USNM 171758 (2), USNM 210868 (3), USNM 219493 (2), USNM 223117 (1), USNM 235751 (3).

Gunnellichthys viridescens: ANSP 108569 (1), ANSP 10867 (10), ANSP 108669 (1), BPBM 6548 (1), BPBM 27904 (1), USNM 171758 (2), USNM 210868 (3), USNM 219493 (2), USNM 223117 (1), USNM 235751 (3).

Microdesmus aethiopicus: AMNH 17145 (1)*, UF 221308 (1)x.

Microdesmus affinis: GCRL 2718 (11)*-3, GCRL 6574 (2), USNM 084300 (1)x.
Microdesmus africanus: AMNH 29404 (1)x, GCRL 16026 (1)*.

Microdesmus bahianus: ANSP 103427 (1), GCRL 10711 (1), GCRL 10715 (13), GCRL 10716 (2)*, GCRL 11101 (2)*, MZUSP 9852 (5), USNM 209537 (2), USNM 274853 (1).

Microdesmus carr: ANSP 102210 (2), GCRL 2412 (47), GCRL 3704 (42)*, GCRL 4607 (1)*, GCRL 4608 (2)*.

Microdesmus dipus: ANSP 111199 (3), GCRL 2302 (83)*, GCRL 2304 (47), GCRL 4616 (1)*, USNM 202429 (5), USNM 205753 (7).

Microdesmus dorsipunctatus: ANSP 111200 (2), GCRL 2311 (42)*, GCRL 6582 (30), USNM 202427 (4).

Microdesmus hildebrandi: GCRL 1780 (1)x, USNM 086547 (1)x.

Microdesmus intermedius: CAS 146293 (1), USNM 082680 (2)x.

Microdesmus knappi: ANSP 117497 (1), GCRL 7816 (1)*, GCRL 7817 (4)x, UF 229864 (1), USNM 206507 (1), USNM 206508 (1).

Microdesmus lanceolatus: GCRL 1651 (1)x, USNM 195976 (1)x.

Microdesmus longipinnus: ANSP 133205 (1), ANSP 144350 (1), GCRL 286 (50), GCRL 2408 (1)*, GCRL 13883 (34), GCRL 22109 (1)*, MZUSP 49212 (12), USNM 117614 (2), USNM 121990 (1), USNM 196615 (1), USNM 207751 (3).

Microdesmus luscus: GCRL 14237 (1)*, ANSP 133205 (1), USNM 198261 (1).

Microdesmus multiradiatus: GCRL 1781 (1), ANSP 144350 (1), GCRL 286 (50), GCRL 2408 (1)*, GCRL 13883 (34), GCRL 22109 (1)*, MZUSP 49212 (12), USNM 117614 (2), USNM 121990 (1), USNM 196615 (1), USNM 207751 (3).

Microdesmus suttkusi: GCRL 1784 (3), GCRL 6583 (23)*, USNM 205755 (1), USNM 206432 (1), USNM 209532 (5)*.

Paragunnellichthys fehlmani: USNM 203831 (1)*, USNM 209382 (2)x.

Paragunnellichthys seychellensis: ANSP 103610 (1), ANSP 103615 (2)*, ANSP 103656 (1), BPBM 9828 (1).

Paragunnellichthys springeri: USNM 204613 (1)x.

Gobiod outgroup taxa

Family Ptereleotridae

Nematolepis magnifica: BPBM 6084 (1), BPBM 9618 (1)*, BPBM 12006 (1).

Ptereleotris eides: MCZ 64324 (3)*.

Family Gobiidae, Subfamily Gobionellinae

Gnatholepis thompsoni: LACM 20636 (2)*, Oligolepis acutipinnis: UMMZ 218768 (46)*, UMMZ 218769 (28).

Tridentiger bifasciatus: LACM 45686-1 (6)*, LACM 45688-1 (7).

Family Gobiidae, Subfamily Gobiinae

Asterropteryx semipunctatus: LACM 33723-13 (46)*.

Bathygobius lineatus: LACM 43690-27 (107)*.

Barbulifer centotheus: LACM 6024 (66)*.

Chirolepis minutus: LACM 20058 (2), LACM 20148 (4)*.

Corypholetrus personatus: UMMZ 176549 (6)*.

Elatineus jannsi: LACM 32524-46 (40)*.

LACM 32524-47 (1)*.

Eviota prasina: UMMZ 186039 (22)*.

Gobiodon cirrus: LACM 37393-8 (3), LACM 42491-69 (5)*.

Neogobius fluvatilis: LACM 44708-1 (30)*.

Gobulus crescentalis: LACM 32547-54 (4), LACM 32562-49 (9)*.

Lophogobius cyprinoides: LACM 7847 (85)*.

Microgobius gulosus: UMMZ 158862 (69)*.

Pomatoschistus microps: UMMZ 201313 (152)*.

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DAWSON. 1985. A new wormfish (Gobiidae: Microdesmidae) from the northern Red Sea. Ibid.


### Taxonomy by Character Matrix for Microdesmid Gobies and Outgroups

<table>
<thead>
<tr>
<th>Taxon</th>
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