

BEHAVIORAL AND MORPHOLOGICAL ADAPTATIONS TO
BURROWING OF TWO SPECIES OF DACTYLOSCOPIID
FISHES FROM THE NORTHERN GULF OF
CALIFORNIA

by

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ABSTRACT

Dactylagnus mundus and M. opercularis differ in body form and modes of burrowing. Burrowing of the fusiform D. mundus is accomplished by a side to side movement while resting on its ventral surface, whereas the attenuated M. opercularis burrows by thrusting head first into the sand and vigorously undulating its body. D. mundus possesses curved pectoral fin rays which aid in its burrowing and a ventral integument which is considerably thicker than that of M. opercularis. The primary digging tool of M. opercularis is the fleshy extension of the lower jaw which has a greatly thickened epidermis. The epidermis of the lateral body wall of the two species is similar in thickness, but the dermis of D. mundus is notably thicker. This greater dermal thickness of the lateral body wall of D. mundus may be correlated with the coarser sand of its habitat.

Although feeding postures of both species are similar, capture of prey is different. D. mundus never leaves the sand but lurches its head upward capturing the prey as it swims overhead. When feeding, M. opercularis leaves the sand completely then reburrows immediately. This feeding behavior may be related to the different modes of burrowing.

The most conspicuous gross morphological adaptations to burrowing in these two species are the fimbriae on the mouth and operculum preventing the entrance of sand into the oral cavity and gill chamber.

Males of both species have significantly longer pectoral fins than females and the third and fourth anal fin rays are directed anteriorly rather than posteriorly as in females. These sexual dimorphisms are correlated to the egg-carrying behavior displayed by males of both species.

INTRODUCTION

The family Dactyloscopidae (sand stargazers) is a little known group of burrowing Perciform fish which is represented by at least 11 species in the Gulf of California (Walker and Norris, M.S.). Recently the Dactyloscopidae have been placed in the suborder Trachinoidei (Greenwood, et al., 1966) which is composed chiefly of small, shallow-water, marine fishes exhibiting burrowing behavior. The dactyloscopids are closely related to fishes of the Asiatic family Leptoscopidae and the Uranoscopidae (electric stargazers), and may be a degenerate branch of the latter (Jordan and Evermann, 1898).

The two most abundant species of Dactyloscopidae at Puerto Peñasco, Sonora, Mexico, are Myxodagnus opercularis Gill and Dactylagnus mundus Gill. In the Gulf of California the known ranges of these two species extend from Puerto Peñasco to Cape San Lucas, but the complete ranges extend much farther south. M. opercularis have been collected along the coast of Peru (Fowler, 1944) and D. mundus have been collected in Panama Bay (Meek and Hildebrand, 1928).

Studies on the burrowing habits of the dactyloscopids are completely lacking, but studies of other burrowing fishes have been made. Rao (1939) reported on the burrowing

habits of the gobioid fish Taenioides cacculus which lives in the mudflat area in the Andamans (India). He found that the mode of burrowing depended on whether the mud was hard or soft. If hard, the mud was removed by biting into it and forcefully ejecting it through the opercular openings; if soft, it was shovelled away with the head. Nayer (1951) observed that Symbranchus bengalensis and Taenioides cirratus probably only burrowed when a low tide occurred or when they were disturbed. The mode of burrowing of T. cirratus was very similar to that of T. cacculus.

Dahlgren (1927) studied the burrowing behavior and morphological adaptations of Astroscopus guttatus (Uranoscopidae). Burrowing was accomplished by side to side motions of the fish while resting on its ventral surface. Both pectoral and pelvic fins performed shovel-like movements, causing the sand beneath the fish to be removed. At the same time the body motions caused the extended caudal and anal fins to dig a trough in the sand. This species was observed to burrow as deep as 12 inches into the sand when frightened but usually was found just below the surface with eyes protruding from the sand.

Dahlgren (1927) described four major anatomical adaptations to burrowing in A. guttatus. He noted the flattened head area and dorsal location of the eyes allowing maximum protection and unobstructed vision; the position and

strength of the pectoral and pelvic fins for burrowing; a connection between the mouth cavity and the nasal openings, presumably for the intake of water when buried; the possession of fleshy papillae on the lips, the interdigitation of which allows water to be strained into the mouth without also sucking in sand.

There are a few studies on the morphological adaptations of the integument to burrowing. Jakubowski (1958) studied the morphology of Misgurnus fossilis, the Pond-Loach. He found a considerably thickened integument, the epidermal thickening primarily due to a large number of mucous glands. Jakubowski (1960) also examined the integument of Pleuronectes flesus luscus, a marine flounder, and found it to be thick but not as thick as that of the Pond-Loach. Liem (1967) reported that the integument of Monopterus albus, a burrowing Synbranchoid fish, consisted of an epidermal layer several cells thick and a dense dermal layer.

Little is known about reproductive adaptations in burrowing fishes. According to Breder (1966) no information on the reproductive habits of the dactyloscopids is available, but Meek and Hildebrand (1928) collected one large Dactylagnus mundus in Panama Bay between May 12 and 15, 1911, which had "attached" to its abdomen a cluster of eggs containing embryos. They concluded that the embryos were

carried until hatching. The sex of the egg-carrying specimens was not given. Sexual dimorphism has been noted in the pectoral and anal fins of Dactyloscopus amnis and others (Miller and Briggs, 1962; Böhlke and Caldwell, 1961) but the purpose for these anatomical differences in males and females has remained obscure.

Stargazers live most of their lives below the sand surface. This specialized mode of existence must place different stresses on these animals than if they were pelagic or even bottom dwelling. The present study was undertaken to correlate burrowing behavior of the two dactyloscopid species Dactylagnus mundus and Myxodagnus opercularis with gross anatomical and integumental morphology, and to elucidate the specialized reproductive habits and sexual dimorphisms in these species.

MATERIALS AND METHODS

Myxodagnus opercularis and Dactylagnus mundus were collected at various times during 1966, 1967 and once during 1968 at Norse Beach, Puerto Peñasco, Sonora, Mexico. Collecting was attempted during the morning and evening low tides during 1966, but in 1967 it was limited to the evening low tides since this was found to be most profitable. The collecting apparatus consisted of a 20-foot beach seine which was dragged along the sand in water approximately 1-3 feet deep. Occasional digging in the sand at the water's edge was attempted but without much success.

The fish to be used for histological studies were immediately preserved in Bouin's fixative upon capture. Those intended for behavioral studies were transferred to aquaria at the Puerto Peñasco Marine Research Station where they were maintained until being transported to the University of Arizona. Aquaria at the University of Arizona were equipped with bottom filters and contained sand from the natural environment of the animals.

External morphology of 13 male and 13 female M. opercularis and 8 male and 13 female D. mundus was studied to determine gross anatomical adaptations to the different modes of burrowing employed by each species.

Histological slides of the integument of five M. opercularis and five D. mundus were made. Sections were taken from the lateral body wall and the unscaled ventral area posterior to the pelvic fins but anterior to the anus. The scaled lateral body wall was decalcified in 5% HNO₃ prior to dehydration. The fleshy papilla of the lower jaw of M. opercularis and the fleshy papillae (fimbriae) of the mouth of both species were also sectioned. Tissue was cut at 7 μ , and sections of each area were stained in Harris' hematoxylin and eosin after the method of Davenport (1960); and P.A.S. and Alcian Blue after the method of Mowry (1963).

Burrowing behavior of M. opercularis and D. mundus was studied by uncovering the fish in sand-filled aquaria and by placing the fish either in stack dishes or aquaria without sand and observing their behavior. Fifteen specimens of each species were observed in both the sand and sandless situations. These fish had been collected at various times during 1967. Both mature and immature specimens were observed.

Since M. opercularis adults were collected only in fine sand areas and D. mundus adults were collected only in coarse sand areas, sand samples for both areas were analyzed for particle size in graded sieves according to the method of Faure-Fremiet (1951). To determine if the sand

type was a factor in restricting adults of these two species to their specific sand habitats, sand preference tests were conducted. Immature and mature fish of both species were tested individually in aquaria, half of which contained two inches of coarse sand and half of which contained two inches of fine sand. Fish were dropped into the aquaria at the division line between the two sand types. The fish were periodically disturbed to see into which of the sands they had burrowed. Fish were then replaced at the sand division line. Each fish was observed over a three day period and disturbed three times a day. For this study 20 members of each species were used, 10 mature and 10 immature individuals.

Feeding behavior of both species was observed. Members of each species were divided into four groups, each consisting of three individuals. Each group was maintained in well-aerated five gallon aquaria which contained two inches of sand from the natural habitat. All groups were fed once a day with live brine shrimp. They were observed during daylight hours and in the evening with a minimum of light.

Data on the reproductive activity of D. mundus and M. opercularis was gathered both in the field and laboratory. The length of the pectoral fin was determined by caliper measurement from the base of the pectoral fin to the tip of

the longest fin ray. Standard lengths were also measured. Student's t test was used to determine if a significant difference existed between the pectoral fin to standard length ratio of males and females of both species.

RESULTS

Habitat

The area at Puerto Peñasco where D. mundus and M. opercularis have been collected is in the low intertidal zone bounded by a reef of conglomerate rock extending in a north-south direction about 75 yards from the high tide line. During low tides the reef is exposed and therefore separates this area from the open water of the Gulf of California (Fig. 1). The presence of the reef ameliorates wave action and during low tides causes a lagoon-type situation. Infrequently, during high tides with an onshore wind, the water is turbulent with breaking waves approximately two feet high.

A sand bar between the reef and shore occurs at low tide. Usually the bar is oval in shape and approximately 50 yards in length, but when extremely low tides occur, it can extend at least 200 yards southward.

M. opercularis and immature D. mundus were collected along the perimeter of the sand bar in water ranging from a few inches to several feet. The fish can be found throughout the area between the sand bar and the reef during low tides. M. opercularis has been collected in the sandy area directly adjacent to the reef.



Figure 1. Collection area of M. opercularis and D. mundus at Norse Beach, Puerto Penasco, Sonora, Mexico, during high tide (above) and low tide.

Mature D. mundus (7.0 to 10.5 cm.), were usually collected in the area between the sand bar and shore on an incoming tide at a water depth of at least two feet. They were also collected in this area when the sand bar was completely flooded at a water depth of at least four feet. The sand in this area is of a coarser nature than that found on the perimeter of the sand bar, and this coarse, sandy area is close to shore where breaking waves are common. Figure 2 shows the difference in sand consistency of the two areas.

At no time were mature D. mundus captured in the fine sand area peculiar to the immature forms of both species and to adult M. opercularis, and at no time were the immature D. mundus or any stage of M. opercularis collected in the coarse sand area singular to adult D. mundus.

In addition to the coarser sand, the area in which adult D. mundus were collected is usually covered by one to five inches of water during low tides and is completely drained only during exceptionally low tides. This area is also exposed to more surf action than the fine sand area. Table 1 shows that in each of the sand preference tests, the sand from the natural environment of the particular species and stage was usually preferred over the other sand type. Although the results are not conclusive due to the

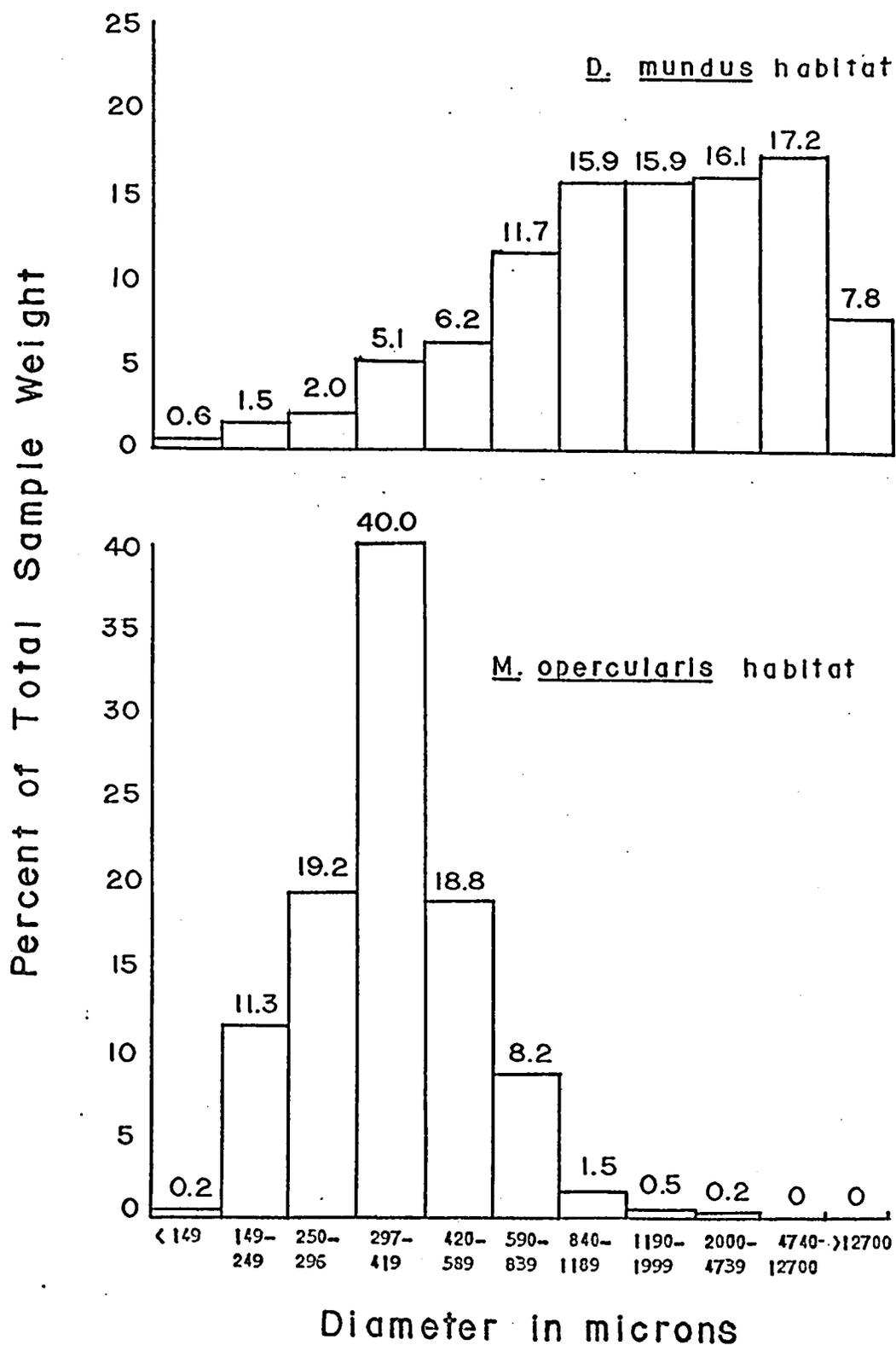


Fig. 2 A comparison of sand samples from the habitats of D. mundus and M. opercularis.

Table 1. Sand preference experiment. Each individual was observed nine times over a three day period.

Species	Sample No.	Total No. of Observations	Coarse Sand No. of times chosen	Fine Sand No. of times chosen
<u>D. mundus</u> immature	10	90	10	80
<u>D. mundus</u> mature	10	90	84	6
<u>M. opercularis</u> immature	10	90	3	87
<u>M. opercularis</u> mature	10	90	11	79

small sample size, they indicate that sand type may be one of the limiting factors in the local distribution of species.

Water temperatures at the sand surface in the collection area were taken during the times when fish were collected (Table 2). Temperatures were the same in both coarse and fine sand areas. The temperature range was approximately 15°C to 31°C during the time period studied.

External Morphology

The external gross morphology of both species was examined for adaptations to burrowing. Both species possess fimbriae on the upper and lower lips (Fig. 3). These fimbriae are arranged so that when the mouth is partially open they interdigitate creating a sieve-like apparatus through which water can pass. Fimbriae are also found on the postero-dorsal area of the opercular flaps (Fig. 3). They originate from the opercular membrane and extend posteriorly so that their distal ends slightly overlap the proximal dorsal area of the pectoral fins and cover the dorsal opening of the operculum.

The opercular membranes of both species extend laterally, and ventrally overlap each other at the mid-ventral area. They also extend anteriorly in the ventral area forming two folds of tissue between the dentary.

The pectoral fins of D. mundus are angled dorsally and are slightly concave due to the dorsal curvature of the

Table 2. Water temperatures in the collection area at Norse Beach, Puerto Peñasco, Sonora, Mexico, between May 1966 and June 1968.

Date	Temperature (°C)
May 5, 1966	20
June 15, 1966	29
July 15, 1966	29
Oct. 1, 1966	28
Oct. 16, 1966	24
Nov. 25, 1966	20
Jan. 25, 1967	15
Feb. 25, 1967	15
April 21, 1967	20
May 6, 1967	22
May 20, 1967	25
June 15, 1967	28
July 20, 1967	30
Aug. 6, 1967	30
Oct. 7, 1967	31
Oct. 12, 1967	28
June 10, 1968	28



Figure 3. Fimbriae of the operculum (above) and mouth of D. mundus.

fin rays. Gill (1862) noted that the oblique levator muscles of the pectoral fin rays of D. mundus were greatly developed and caused the fin rays to curve upwards at their distal ends. The pectoral fins of M. opercularis are not arranged in such a manner (Fig. 4).

The jugular pelvic fins of both species consist of three fin rays each connected by membranous tissue. When the fish are not active, the pelvic fins are fully expanded and lie almost perpendicular to the long body axis. In this position the dorsally curved fin rays move the ventral portion of the opercular membranes laterally thus allowing an easy exit for water from the gill chambers but protecting this area from the invasion of sand.

The body shape of M. opercularis is greatly attenuated resembling that of *Amphioxus*. The lower jaw of this species is extended by the presence of a fleshy papilla.

The body form of D. mundus is fusiform but slightly depressed in the head region. No fleshy papilla extends the lower jaw region in this species.

Modes of Burrowing

The burrowing process of D. mundus is quite different from that of M. opercularis. M. opercularis primarily utilizes its head during burrowing. D. mundus, on the other hand, accomplishes its burrowing by lateral body



Figure 4. Pectoral fins of D. mundus (top) and M. opercularis.

movements while resting on its ventral surface and by extensive use of the pectoral, pelvic, and anal fins.

In D. mundus the movement of the pectoral fins, which are the main digging tools of this species, is coordinated with the side to side body movement of the fish. The motion of the pectoral fins can best be described by dividing it into two stages and referring only to the fin of one side. In the first stage the pectoral fin is pulled medially toward the lateral body wall and the fin rays compress. At this time the fin is angled dorsally. In the second stage the fin rays separate; the ventral-most rays move downward and the fin moves ventrally, digging into the sand. Now the fin moves outward from its medial position scooping sand by means of the concavity produced by the ventral-most curved fin rays. At the same time the fish moves its body laterally in the same direction as the pectoral fin, thus lending impetus to the scooping or shovelling action of the fin.

The pectoral fins work in an alternating manner. When the fin of one side is moving downward and outward, the fin of the other side is moving against the lateral body wall and dorsally. Due to this alternation of fin movements, the side to side body movement of the fish is always aiding the pectoral fins to push sand away. There is no wasted motion.

The pelvic fin movements are coordinated with those of the pectoral fins. While at rest the jugular pelvic fins are fully expanded with the dorsally curved rays of each fin almost perpendicular to the anterior-posterior body axis. When burrowing, as the pectoral fin of one side moves upward against the body wall, the pelvic fin of the same side moves posteriorly in an arc to a medial position so that the pelvic fin rays are close together and the fin lies almost in an anterior-posterior direction.

As the pectoral fin begins to move downward and out the pelvic fin moves from the medial position sweeping forward in an arc which places it once again perpendicular to the long body axis. This movement of the pelvic fin complements the outward movement of the pectoral fin by transporting sand from beneath the gill chamber area. In completing the forward motion the pelvic fin rays are in a position such that they are overlapped by the long ventral rays of the pectoral fins, thus extending the surface area of the pectoral shovel.

The anal fin also works in conjunction with the pectoral and pelvic fins. The anal fin remains extended at all times during the burrowing process, therefore aiding in the pushing of sand from under the fish and digging a trench when the fish moves from side to side.

M. opercularis burrows by thrusting its head first into the sand. The protruding lower jaw with the fleshy papilla comes in contact with the sand first. As the fish enters the sand the body undulates so as to forcefully drive the fish deeper. The main burrowing equipment of this animal is the pointed lower jaw which acts as a digging tool and the eel-like body which enables it to easily penetrate the substrate. The fins do not seem to be used to any great extent in the burrowing process.

When M. opercularis enters the sand it does not continue to burrow at the same angle at which it began. Instead the fish arches its body causing the anterior region to move toward the surface. The fish comes to rest either completely below the sand surface or with its head protruding slightly above the sand.

Neither species was observed to burrow very deeply in aquaria. Usually they burrowed to a depth of one and sometimes two inches. Even when frightened by a constant prodding they did not seek the refuge of the depths. In their natural habitat they were not collected more than one or two inches below the sand surface.

Integumental Histology

The integument of D. mundus and M. opercularis is composed of three layers; the epidermis, corium, and subcutis. The ventral area anterior to the anus, the fleshy

extension of the lower jaw of M. opercularis, and the fimbriae of the lips of both species are unscaled, whereas the lateral body wall of both species is scaled. Table 3 is a summary of the mean thickness of the epidermal and dermal layers of these areas from both species.

In the ventral area of D. mundus, the epidermis has a mean thickness of 14 μ and the dermis a mean thickness of 46 μ (Fig. 5). The epidermis is composed of three cell layers. The basal layer is made up of large cuboidal cells with large nuclei. The middle layer is very similar to the basal layer. The outermost epidermal layer is composed of cells which are slightly flattened or spindle shaped; these cells also possess large nuclei. The dermis is composed of dense fibrous connective tissue. No distinction could be made between the stratum laxum and the stratum compactum. Sections stained with P.A.S. and Alcian Blue revealed no mucous glands.

The ventral area of M. opercularis is composed of an epidermis two cell layers thick with a mean of 7 μ and a dermis with a mean thickness of 13 μ (Fig. 6). The basal epithelial layer consists of large oval cells containing large nuclei. The cells of the outer layer are somewhat flattened. Staining of this area showed the presence of large mucous cells which are P.A.S. positive. The dermis is composed of dense fibrous connective tissue. Both the

Table 3. The mean thickness of various epidermal and dermal areas of D. mundus and M. opercularis. Data are based on five individuals of each species.

Area of Integument	Mean Thickness (μ)	
	<u>D. mundus</u>	<u>M. opercularis</u>
Ventral, anterior to anus		
epidermis	14	7
dermis	46	13
Lateral body wall		
epidermis	7	6
dermis	38	17
Fimbriae of mouth		
epidermis	24	22
Fleshy papilla of lower jaw		
epidermis (at tip)	--	78
epidermis (rest of papilla)	--	35

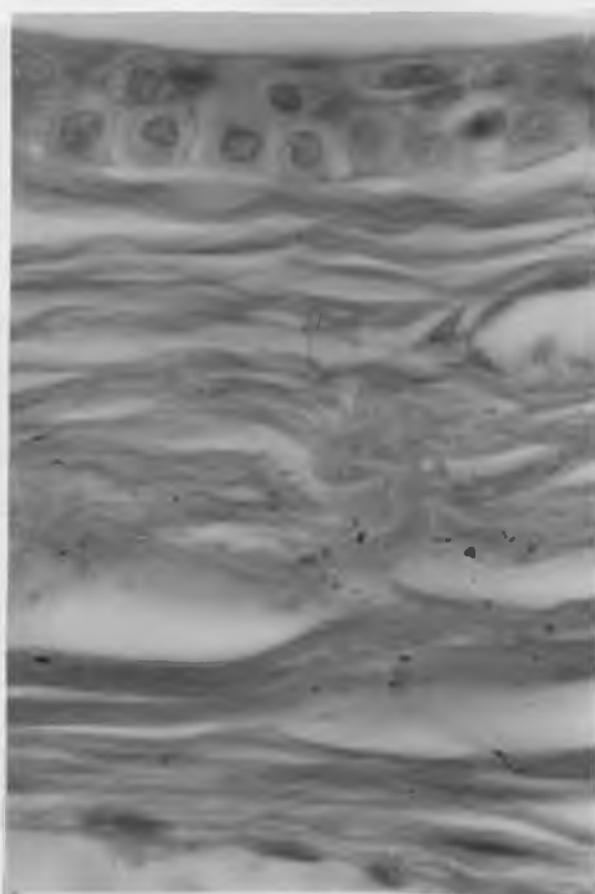


Figure 5. Ventral integument of *D. mundus* stained with Harris' hematoxylin and eosin (1000x).

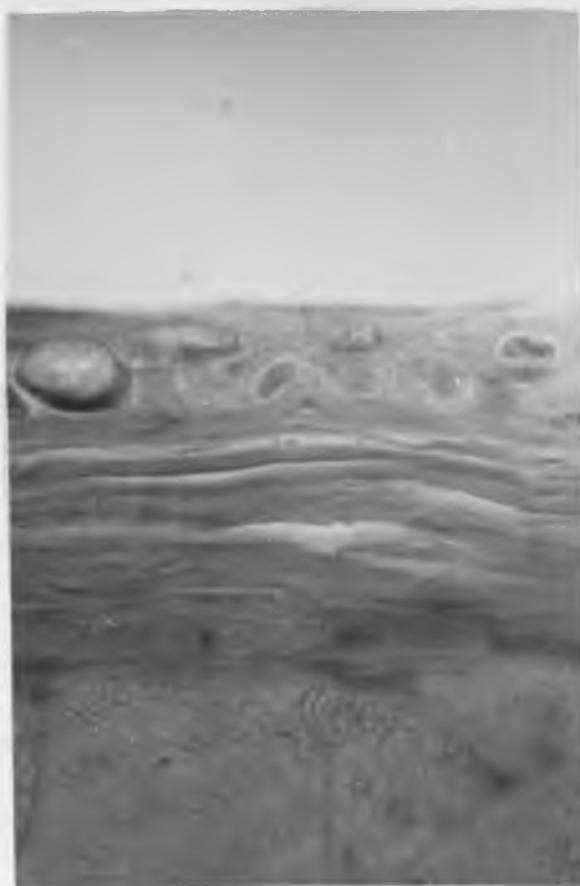


Figure 6. Ventral integument of *M. opercularis* stained with Harris' hematoxylin and eosin (1000x).

dermis and epidermis of the ventral area of M. opercularis are considerably thinner than the corresponding layers of D. mundus.

On the other hand, the lateral body wall epidermis of both species is similar. In both species the epidermis is two cell layers thick and composed of large cuboidal cells. Staining with P.A.S. showed mucous cells to be present. The lateral body wall epidermis ranges from 5 to 8 μ thick in both M. opercularis and D. mundus. The dermis of this area is composed of dense fibrous connective tissue in both species. However, a great difference is observed in the thickness of the dermis. In D. mundus the dermis has a mean thickness of 38 μ , while in M. opercularis the mean thickness of the dermis is 17 μ . Figure 7 shows the lateral body wall integument of D. mundus.

Sections of the fleshy papilla of the lower jaw of M. opercularis revealed that it consists of epithelial cells from 4 to 16 layers thick and ranging from 33 μ to 80 μ thick. The greatest thickness is found at the anterior-most tip of the papilla (Fig. 8). The basal layer is composed of small rounded cells while the outer layers are columnar with nuclei located at the base of the cells.

The fimbriae on the mouth of both species are similar in construction. They are composed of epithelial

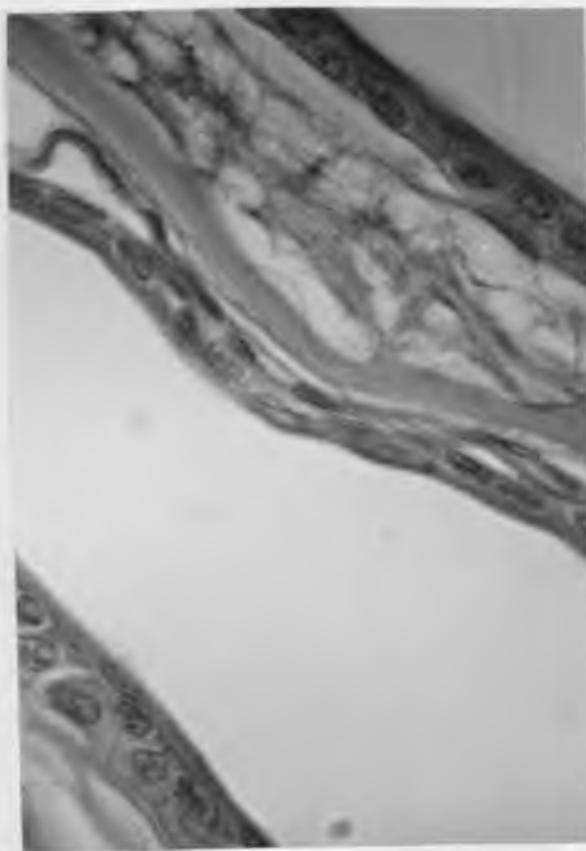
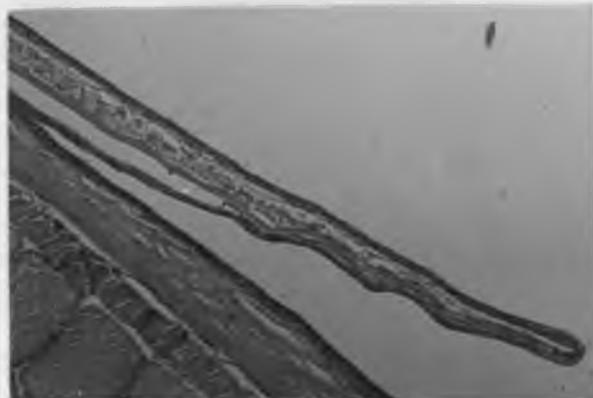


Figure 7. Lateral body wall of *D. mundus* stained with Harris' hematoxylin and eosin (160x above; 1000x below).

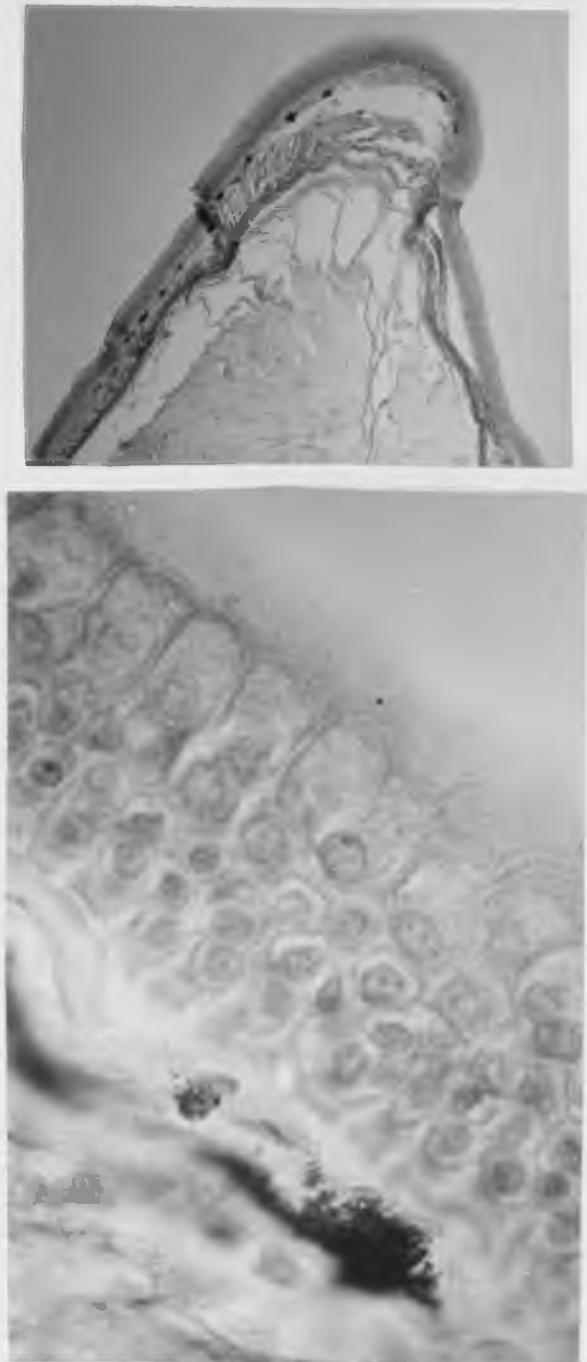


Figure 8. Longitudinal section of fleshy extension of lower jaw of M. opercularis (160x above; 1000x below).

cells beneath which is a dense network of connective tissue. The epidermis is four cell layers thick. The cells of the basal layer are columnar while the middle layers are rounded with large nuclei. The outermost layer has distinct columnar cells with nuclei at the base of the cells. The mean thickness of the epidermal layers is essentially the same for both species (Table 3).

Feeding Behavior

Observations of M. opercularis and D. mundus indicate that they have a nocturnal behavioral pattern. M. opercularis and D. mundus were consistently more active in the evening than in the daytime, and some of these nocturnal activities are feeding activities.

All groups of both species were relatively inactive during the day. The fish were usually completely buried beneath the sand; only rarely were fish observed to have their heads above the sand. When live brine shrimp were introduced into the aquaria during the day feeding was observed only occasionally.

In the evening both species move about frequently and assume characteristic feeding postures. When stationary, M. opercularis is burrowed with its head exposed. Depending on the individual the entire head region or just the eyes are above the sand. The most common movement of M. opercularis is leaving the sand completely, then quickly

burrowing a few centimeters from its original position. Less frequently an individual would swim to the water surface and either return to the bottom and burrow immediately or suddenly become limp and fall to the bottom where it would remain for a short time, then burrow.

The behavior of D. mundus is different from that of M. opercularis probably because of the different method of burrowing employed by this species. Although quite active at night, D. mundus seldom completely leaves the protection of the sand environment but shifts its position either by "walking" through the sand using its pectoral fins or by body undulations. This type of behavior is exhibited when the fish is completely covered with sand or when only its head is exposed. This movement usually takes the fish a few centimeters from its original position. When stationary, D. mundus is burrowed with only the eyes and a small portion of the head exposed above the sand surface in a manner similar to that of a stationary M. opercularis (Fig. 9). Occasionally, like M. opercularis, D. mundus would swim to the water surface and subsequently reburrow. When either species was fed in the evening, they commenced taking food shortly after it was placed in aquaria. Although feeding postures of the two species are similar, the actual capture of prey is different. M. opercularis leaves the sand to capture brine shrimp, after which it immediately burrows



Figure 9. Feeding posture of D. mundus.

again with its head partially out of the sand. D. mundus, on the other hand, never leaves the sand. When a shrimp comes within range it lurches upward to capture the prey with most of its body remaining below the sand. Following the capture D. mundus resumes its original posture.

The stomach contents of five D. mundus and five M. opercularis were examined. In some stomachs of both species collected during February, small "opposum shrimp" (order Mysidacea) were found. Small isopods, Tylos latreilli were found in D. mundus collected during August. In one D. mundus an unidentifiable fish was found.

Reproductive Activity

The reproductive activities of M. opercularis and D. mundus seem to be confined to early May through early October (Table 4). No spawning or gravid specimens of either species were collected from November to April.

Spawning M. opercularis were captured in the same areas where they had been found previously throughout the year. Spawning D. mundus were collected in the coarse sand close to shore. No spawning D. mundus were ever collected in the fine sand areas and no spawning M. opercularis were found in the coarse sand areas.

On several occasions during the spawning period male D. mundus were captured carrying either unfertilized eggs or eggs containing embryos (Fig. 10). The egg masses

Table 4. Gravid or spawning species collected at Norse Beach.

Collection Date	Species	Temperature (°C)
May 5, 6, 1966	<u>M. opercularis</u>	20.5
Oct. 1, 1966	<u>D. mundus</u>	28
May 6, 1967	<u>M. opercularis</u>	22
May 20, 1967	<u>M. opercularis</u>	24.5
June 10, 1967	<u>M. opercularis</u>	25
June 15, 16, 1967	<u>M. opercularis</u> <u>D. mundus</u>	27
July 20, 1967	<u>D. mundus</u>	30
Aug. 7, 1967	<u>M. opercularis</u>	31
Oct. 7, 1967	<u>D. mundus</u>	31



Figure 10. *D. mundus* male carrying eggs using pectoral, pelvic and anal fins (dorsal view above; ventral view below).

were held to the lateral and ventral body walls primarily by the pectoral fins. The expanded fins covered the eggs pressing them against the lateral body wall on each side. Ventrally the egg mass was not encased by the pectoral fins and it is thought that the eggs in this area are secured by the dorsally curved pelvic fins and the anal fin. The third and fourth anal fin rays of this species are directed anteriorly on males whereas in the females all anal fin rays are posteriorly directed (Fig. 11).

A male M. opercularis was observed carrying eggs on one occasion. The individual had been in captivity for at least two months and was being maintained in a 15 gallon aquarium with other fish of the same species. The eggs appeared to be held to the lateral and ventral body walls. Laterally the pectoral fins secure the eggs while ventrally it is thought that the pelvic and anal fins aid in the attachment of the egg mass. As in D. mundus males of this species possess an anal fin in which the third and fourth fin rays are anteriorly directed (Fig. 12).

M. opercularis was never seen carrying eggs when collected from its natural environment. This is probably because when stressed M. opercularis and D. mundus release the egg masses, the former doing this more readily than the latter. Occasionally egg masses were found in the seine lying close to M. opercularis males.



Figure 11. *D. mundus* showing sexual dimorphism in third and fourth anal fin rays (female above; male below).



Figure 12. *M. opercularis* showing sexual dimorphism in third and fourth anal fin rays (male above; female below).

Measurements of the pectoral fins of males and females of both species showed that a sexual dimorphism exists. The males of both species possess a significantly higher pectoral fin to standard body length ratio (Table 5).

The eggs of both species are opaque and demersal. The diameter of the eggs is approximately 1 mm for both species. They are attached to one another by fine strands of adhesive material and a thicker adhesive thread is located in the central portion of the egg mass. This is probably the primary means for keeping the egg mass together. The adhesive nature of the eggs may also assist in holding the eggs to the body wall. An egg count revealed that a D. mundus mass contained 3,342 eggs, whereas a M. opercularis mass contained only 404 eggs.

Very few opportunities to observe the egg-carrying individuals were presented; however, three D. mundus were successfully brought back to the laboratory and their burrowing behavior was observed. These egg-carrying individuals appeared to be less skillful in burrowing. This was probably due to the fact that their most powerful digging tools, the pectoral fins, could hardly be used effectively. They waddled into the sand in a fashion similar to that of non-egg-carrying specimens but body undulations were much more pronounced and more time was needed for the fish to completely cover itself with sand.

Table 5. Ratio of pectoral fin length to standard length in males and females of the species M. opercularis and D. mundus.

Species	N	$\bar{X} \pm \bar{sx}$	Range	t	P
<u>M. opercularis</u> males	13	.309±.0102	.225-.353		
				16.8	<.001
<u>M. opercularis</u> females	13	.163±.0053	.131-.184		
<u>D. mundus</u> males	8	.275±.0074	.240-.300		
				7.4	<.001
<u>D. mundus</u> females	13	.224±.0032	.202-.238		

The burrowing of an egg-carrying M. opercularis was only observed once. It appeared to have no difficulty in burrowing since extensive use of the fins is not necessary.

DISCUSSION AND SUMMARY

Certain aspects of ecology, gross anatomy, behavior, integumental histology, and reproductive habits of M. opercularis and D. mundus have been studied. Some adaptations to burrowing in sand are shared by both species, while other adaptations appear to be related to the different modes of burrowing utilized by these two species, and to the different sand environments in which adults are found.

The fleshy fimbriae of the mouth possessed by both species are obvious adaptations to living in the sand. Their function is to filter sand from the stream of water entering the mouth for respiration. Dahlgren (1927) also believes this to be the function of the fimbriae in the Uranoscopidae. The fimbriae located on the postero-dorsal border of the operculum may have a similar function; they may prevent sand from entering the dorso-lateral opening into the gill chamber as water is expelled.

The extensive opercular flaps also appear to be adaptations to living in the sand. Ventrally the flaps overlap each other protecting the gill chamber openings from abrasion. This is especially important in D. mundus which burrows by waddling on its ventral surface. The pelvic fins are used in conjunction with the opercular flaps.

When at rest the pelvic fins lie perpendicular to the longitudinal body axis with their rays extended. In doing this the fins push the opercular flaps slightly laterally permitting the exit of water from the gill chamber but at the same time protecting the area by partially covering exposed portions.

The curvature of the ventral fin rays of the pectoral fins is clearly related to the particular mode of burrowing of D. mundus. It is the curvature of the fin rays which produces the concave outline of the fin and this concave shape is essential for shovelling sand from beneath the fish efficiently. The pectoral fins are the most important digging tool of this species. It has been noted that burrowing is not as efficient when males of this species carry eggs with the pectoral fins. Curved ventral rays of the pectoral fin are not present in M. opercularis which does not use these fins extensively in burrowing.

The flattened head of D. mundus may also be related to its life under the sand. With a flattened head and dorsally situated eyes this species is able to have its eyes above the sand and yet have its anterior region completely covered. If the head were not depressed particles would roll off as the fish approaches the sand surface, leaving that portion of the fish uncovered and unprotected.

The attenuated body shape and fleshy extension of the lower jaw of M. opercularis are clearly related to the mode of burrowing displayed by this species. The streamlined body allows the animal to get into the sand with a minimum of abrasion occurring to the body surface. The fleshy extension adds to this streamlined outline and provides a means to dig into the sand.

Integumental differences do exist between D. mundus and M. opercularis and appear to be related primarily to the different modes of burrowing. This is particularly evident in unscaled areas. It is obvious that the manner of burrowing utilized by D. mundus subjects the ventral area to considerable abrasion by the coarse sand particles in its environment. Probably the burrowing method of M. opercularis does not place as much stress on the ventral surface, but indeed subjects the fleshy papilla of the lower jaw to a great amount of abrasion and pressure.

The integument of D. mundus is thicker than that of M. opercularis in the ventral unscaled area anterior to the anus. The epidermis is approximately twice as thick and the dermis over three times thicker than that of M. opercularis in this region. The greater abrasion on this surface apparently necessitates the thicker ventral integument of D. mundus. The greater epidermal thickness is primarily related to an additional cell layer. It is interesting to

note that the integument of M. opercularis in this region contains large mucous cells which are absent in D. mundus. Mucous may serve as a lubricant for M. opercularis in its particular mode of burrowing.

M. opercularis is more dependent on body undulations when burrowing in the sand than is D. mundus. However, sections of the scaled lateral body wall of both species demonstrate that the epidermis is essentially the same thickness. The presence of scales and mucous cells in this region may preclude any further adaptations to abrasion and pressure. The dermis of D. mundus is much thicker than that of M. opercularis in this region. The dermis may be thicker over the entire body of D. mundus giving the added resiliancy necessitated by living in a coarse sand environment.

The fleshy papilla of the lower jaw of M. opercularis which is the main digging tool of this species possesses the thickest epidermis of the areas studied on both species. This is clearly an adaptation to the mode of burrowing of M. opercularis. It is the papilla which pushes the sand aside as the body violently undulates into the sand, and hence it is the papilla which receives the greatest abrasive action of the sand. The thickness of this area is due to additional cell layers and enlarged outer cells.

The unscaled fimbriae of the jaws of both species have thick epidermal areas. The mean thickness is

approximately the same in both species. The current created when the fish is taking water into the mouth through this sieve-like arrangement causes sand particles to constantly rub against the fimbriae, thus necessitating a thick epidermis.

It is interesting to note that the fresh water burrowing forms Misgurnus fossilis and Monopterus albus both have much thicker integuments than either of the dactyloscopid species investigated in this study (Jakubowski, 1958; Liem, 1967). Jakubowski found the epidermis of M. fossilis to be 331 μ and the dermis 423 μ thick. Most of the epidermal thickness was due to mucous glands some of which reached a height of 220 μ . Liem found the epidermis of M. albus to be 50-100 μ and the dermis 300-500 μ thick. However, both of these species reside in areas where the substrate is a fine silty mud and each of these species is subject to dessication at various times of the year. The numerous large mucous glands increasing the thickness of the epidermis may represent an adaptation to dessication and low oxygen tension rather than to a burrowing mode of life.

Jakubowski (1960) studied the integument of the flounder Pleuronectes flesus luscus. He found the mean thickness of the epidermis to be 35 μ , and the epidermis of the lower surface constantly thicker than the upper surface.

This thickness is closer to those found for the epidermis of D. mundus and M. opercularis in this study.

Laboratory sand preference data agree with field collections. Although far from conclusive, the sand preference tests indicate that at least locally the various stages of the two species may be restricted to a particular sand type. The fine sand preference of immature D. mundus and all stages of M. opercularis may be related to the size of these fishes and the mode of burrowing of the latter. Thrusting head first into a sand composed primarily of large shell and stone armed only with a fleshy papilla and body undulations as weapons is no small task. In fact it was observed under laboratory conditions that M. opercularis had considerable difficulty attempting to burrow into the coarse sand. Size may be the major deterrent to burrowing in coarse sand for immature D. mundus. Not having the powerful pectoral fins of an adult, pushing away large shell fragments may be a near impossibility.

The sand preference of adult D. mundus may again be related to size. The smaller particle size of the fine sand may clog the oral cavity and gill apparatus of this larger fish when it opens the fimbriae to take in water. These large individuals were found only during the spawning season. It may well be that during spawning there is a greater oxygen need for this fish. The larger sand size would afford

a greater circulation of water and therefore a greater oxygen concentration especially in areas where water is turbulent.

M. opercularis and D. mundus exhibit different methods of capturing prey. The difference in method of capture is apparently related to the dissimilar methods of burrowing. It may be that M. opercularis cannot just half leave the sand when capturing prey as D. mundus does because it cannot effectively reburrow itself by waddling into the sand. Although this feeding behavior may seem to be hazardous for this species the amount of time M. opercularis is exposed to the non-sand environment appears to be no greater than the exposure of D. mundus when feeding.

The complete reproductive periods of either species is not known. M. opercularis have been captured with eggs as early as May 5 and as late as August 6. D. mundus have been captured with eggs no earlier than June 15 and as late as October 7. It seems likely that the spawning period of D. mundus extends through September although no collections were made during this month.

The egg-carrying behavior displayed by males of both M. opercularis and D. mundus is unique. The eggs are not only guarded by the parent but also are buried with the parent where predation on the eggs is almost impossible. Since males were collected with egg masses containing

highly developed embryos and on one occasion the embryos hatched while in captivity, it is believed that these eggs are carried for the complete gestation period.

The anatomical sexual dimorphisms previously noted in several species of this family serve as egg-carrying devices in males of M. opercularis and D. mundus. The enlarged pectoral fins in males of both species hold the egg masses to the fish, and the anteriorly directed third and fourth anal fin rays and the pelvic fins are apparently used for this same purpose. The reproductive behavior of M. opercularis and D. mundus may be similar for all members of this family in which these same sexual dimorphisms are present.

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