Fishes, as well as birds, build bowers

Article · January 2001

Jay Richard Stauffer
Pennsylvania State University

George F Turner
Bangor University

Ad Konings
El Paso Community College

Tetsu Sato
Ehime University

Fishes, as well as birds, build bowers

Kenneth R. McKaye, University of Maryland Center for Environmental Science, Appalachian Labortory, 302 Braddock Road, Frostburg, Maryland 21532 and Universidad Centroamerican, Managua, Nicaragua (e-mail: mckaye@al.umces.edu); **Jay R. Stauffer, Jr.**, School of Forest Resources, Pennsylvania State University, University Park, Pennsylvania 16802; **George F. Turner**, School of Biological Sciences, University of Southampton, Bassett Crescent East, Southampton SO16 7PX, England, United Kingdom; **Ad Konings**, 417 Valplano Dr., El Paso TX 79912, USA; and **Tetsu Sato**, Department of Biology, University of Malawi, P.O. Box 736, Zomba, Malawi

ABSTRACT

Cichlid mouthbrooding fishes build display structures that function solely as a site for courtship and spawning. They are constructed independently of the need to care for eggs and young. The female deposits eggs and immediately picks them up in her mouth, where they are fertilized. Eggs are then brooded solely in the mouth of the female. Males engage in no parental care. The use of the word bower for these cichlid structures acknowledges their similarity to display sites built by bowerbirds. Both are elaborate display characters, which are presumably costly to construct, yet appear to serve little adaptive function enhancing the survival of the male, female or offspring. Hence these bowers are not nests, as recently proposed, since they are not designed to "meet the needs of the young." The diversity of cichlid bowers, the linguistic origin of the word bower and justification for retaining the decade old use of bower for cichlids display sites are discussed.

INTRODUCTION

Diversity of Male Cichlids Spawning Structures.

All of the cichlid fishes endemic to Lake Malawi are, as far as is known, maternal mouthbrooders. Some species spawn on the surface of rocks, or in caves excavated beneath rocks, while others spawn in the water column. However, during the breeding season, males of the majority of species living over sandy or muddy substrates aggregate on communal display grounds, or leks, where they construct display and spawning structures, which have been termed 'bowers' (McKaye et al., 1990). In Lake Malawi, bowers vary dramatically between species in size, form and position (McKaye et al., 1990; McKaye, 1991). McKaye (1991) divided the spawning structures of Lake Malawi cichlids into ten types (Fig. 1) ranging in size from giant craters 3m in diameter (Fig. 2, 3), to small depressions in the sand (Fig. 4) and to sand castles (Bass, 1988) with base diameters of 1m (Fig. 5-7, McKaye, 1984). Bowers of similar form can be found in Lake Tanganyika as well (Figs.7-9). Often these mounds can be slanted (Fig. 10). Some can be craters with mounds inside them (Fig. 11), and can be constructed under a log (Fig. 12). These structures can be built on rocks (Fig. 9), in weed beds (Fig. 13), and over the open sand. The spawning platforms of many species incorporate an over-hanging ledge (Fig. 14-15), or a side with a rock wall (Fig. 16), a rock within the bower (Fig. 17), or in a crevice with walls on all sides except the entrance (Fig. 18). These structures can involve the construction of craters with heaps of sand on the side (Figs. 21-22). Other complex platforms have a central heap of sand at which all courtship takes place and protects the females from intruders (Fig. 23). Males of certain species have over 20 "decorative" mounds around this central courtship mound (Fig. 24). Often objects other than rocks, such as large snail shells of the genus

Lanistes (Fig. 25) or wood (Fig. 26) can be found in bowers.

THE FUNCTION OF BOWERS

Males must expend considerable energy moving sand to build these structures (Fig. 20). This must be costly, in terms of loss of energy available for growth and survival, so it is likely to have some selective benefit. When a spawning site is concealed among rocks (Figs. 14-18), protected on one side by a piece of wood or other object in the bower (Fig. 12,26), built with a mound that blocks entry from one side (Fig. 23), or dug as a pit (Figs. 2-3,11, 21-22), the risk of stolen fertilizations might be reduced. However, it is not as easy to imagine how it might be safer to spawn in the open on a high platform (Fig. 5-9), in full view of any fish in the water column, nor to envisage what benefit could be provided by constructing a series of bumps in the sand a few centimeters away. Perhaps, although higher and in full view of fish in the water column it may be more difficult for intruding males to come from the side. Most mounds have a lip or depression inside of them. By being in a raised position a male may be able to see a competing male easier, though this position makes them clearly more vulnerable to territorial egg eaters that hover above the breeding arena. (McKaye, 1984).

Nevertheless, in other groups of organisms, sexual selection by female choice is generally invoked to explain the evolution of apparently costly and arbitrary courtship traits (Gilliard, 1969; Borgia, 1995; Andersson, 1994). Such features may evolve simply because most females prefer them and thus mating with males possessing such traits is likely to confer an advantage on the male offspring of such matings, since they will be more likely to attract females than are the sons of males not exhibiting the trait (the Fisher, 1930 hypothesis). Alternatively, the costliness of the traits may provide a test of the male's ability to bear the cost, which is an indication of his overall vigor and health (Zahavi, 1975; Taylor et al., 1998, the handicap principle).

Theoretical studies have suggested that the Fisher process is more likely to generate variability between species in their courtship traits. By contrast, it is to be expected that once a species has hit on a particularly informative 'handicap', selection should lead to an increase in the costliness of the trait, and suppress the adoption of additional traits which are likely to be less informative in the early stages of their evolution. Recent research has demonstrated that closely related, but genetically and morphologically distinct, populations may differ in bower form (Fig. 19, McKaye et al., 1993; Stauffer et al., 1993). This suggests that bower form may often diverge rapidly, as predicted by the Fisher theory. It also indicates that it might be a useful character in the identification of cryptic species, and may also be a significant feature in the maintenance, and perhaps the origin, of reproductive isolation between species.

APPLICATION OF THE WORD BOWER

These sites were originally referred to as nests, even by the present authors (Fryer and Iles, 1972; Keenleyside, 1979; McKaye, 1983, 1984; McKaye and Stauffer, 1988; Konings 1989; Turner et al. 1991). Nevertheless, it became clear to us that this was an inappropriate designation because: "A nest is a special construction forming a bed or receptacle in which eggs and young develop... and are designed by evolution to help parents meet the needs of their young" (Collias and Collias, 1984: 1). Since there was no care of young or eggs on these structures, nor any convergence to an "optimum" adaptive form designed for care of young, the word nest was inaccurate (McKaye et al., 1990).

The term bower was first used to describe display structures built by birds, because they reminded Gould (1840) of mid 19th century English gardens. Nevertheless, the use of bower in the ornithological literature has evolved in the past century and a half, as the following definitions demonstrate: "We define a bower as a construction adapted to facilitate the mating relationship, independently of care of eggs or young, and provide some screening from possible interference" (Collias and Collias, 1984, p. 74); "Avian display courts that have been constructed using brought- in materials are usually called bowers" (Johnsgard, 1994). These definitions fit precisely the mating structures we have described in some cichlid fishes.

McKaye et al. (1990) proposed that the term bower be used to describe these courtship structures because of their similarities in function to the courtship structures built by bowerbirds (Gilliard, 1969)

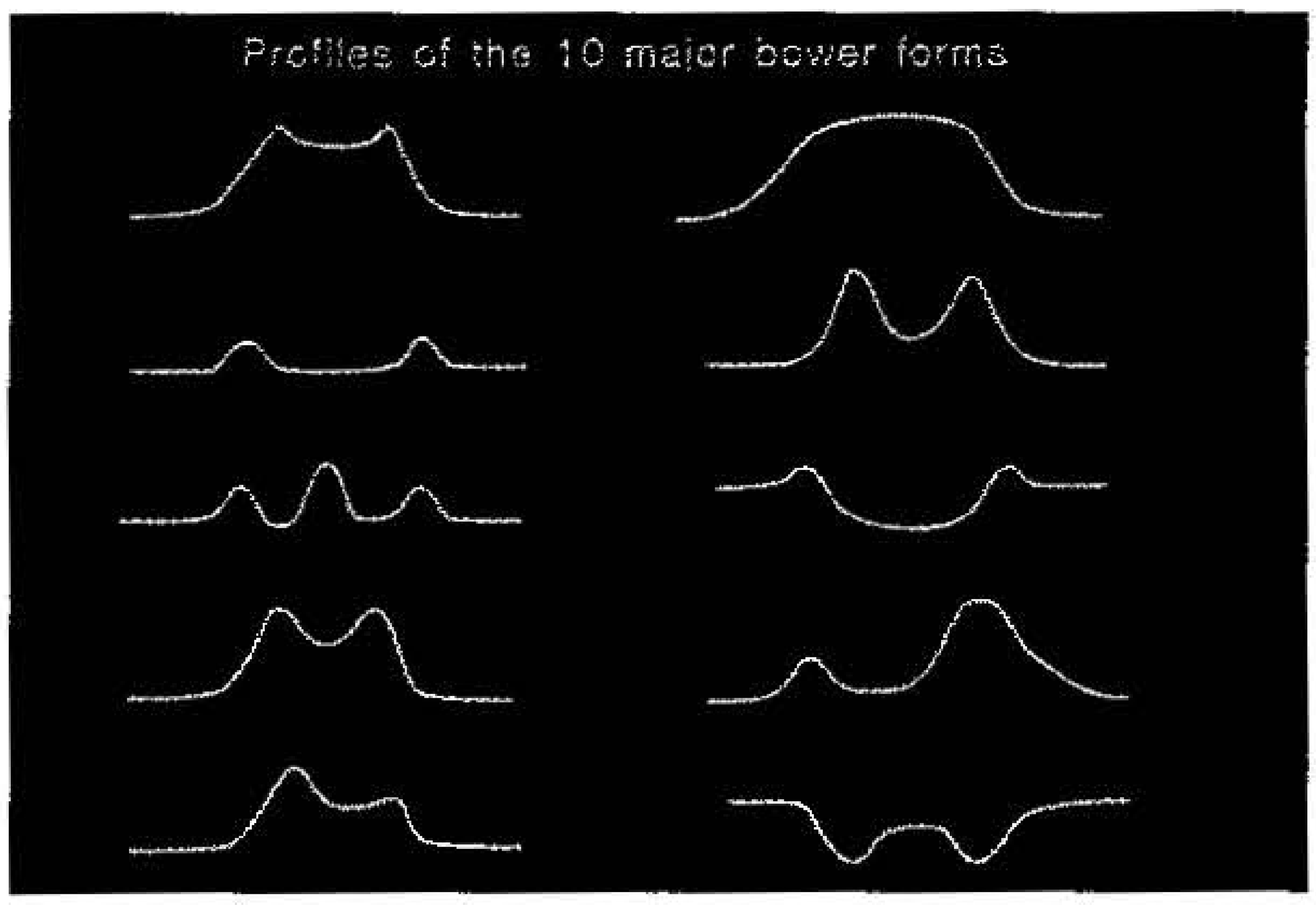

Figure 1. Profiles of the ten major bower forms in Lake Malawi. Left to right then top to bottom. *Tramitichromis* spp.; *Protomelas* cf. *marginatus; Taeniolethrinops* cf. *furcifer*; *Trematocranus* spp.; *Lethrinops* cf. *auritus*; *Dimidiochromis kiwinge*; *Copadichromis* spp.; *Buccochromis atritaeniatus; Protomelas kirkii; Oreochromis* spp. (From McKaye, 1991).

Figure 2. *Dimidiochromis kiwinge*

Figure 3. *Taeniolethrinops preaorbitalis*

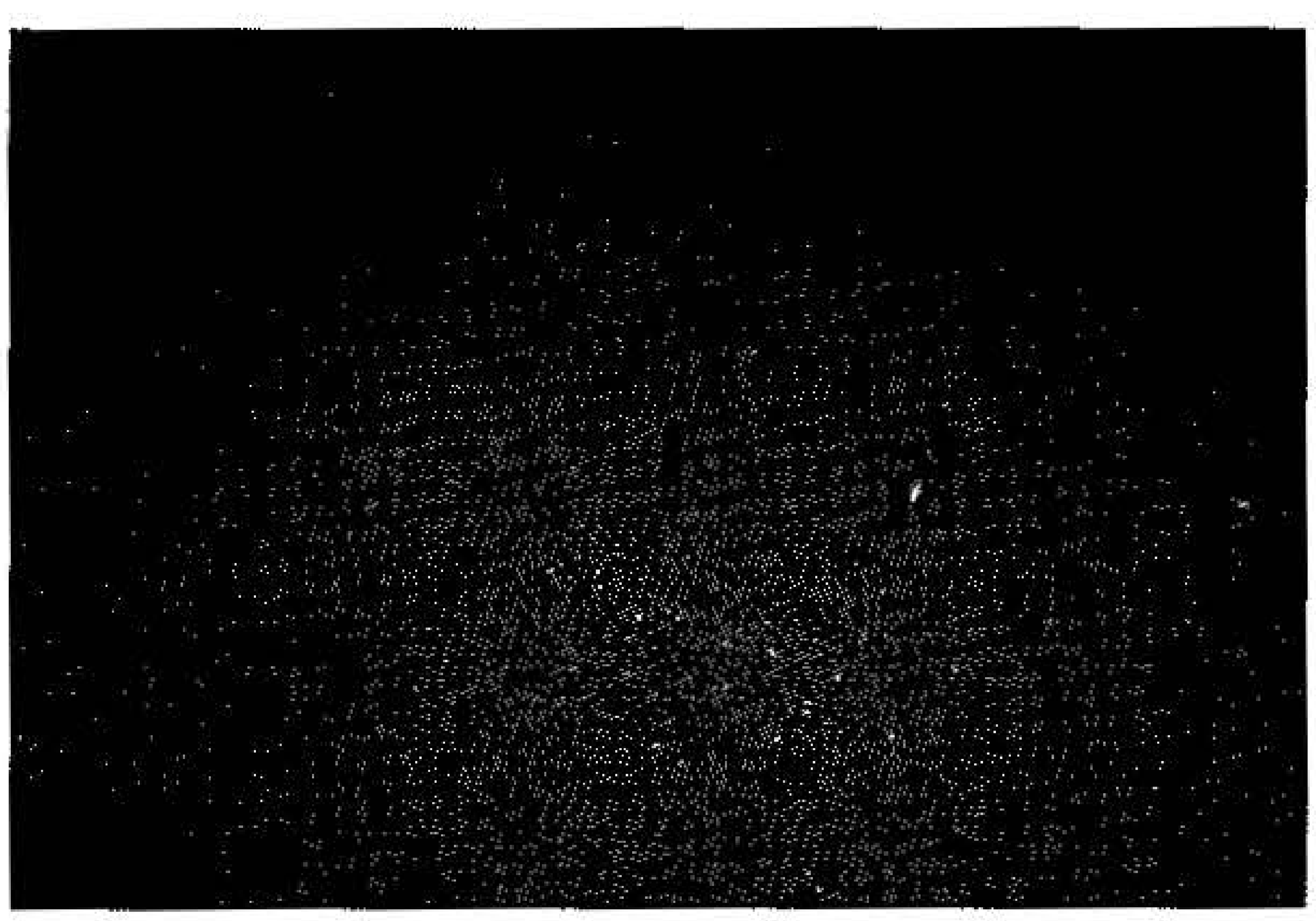

Figure 4. *Otopharynx* cf. *argyrosoma*

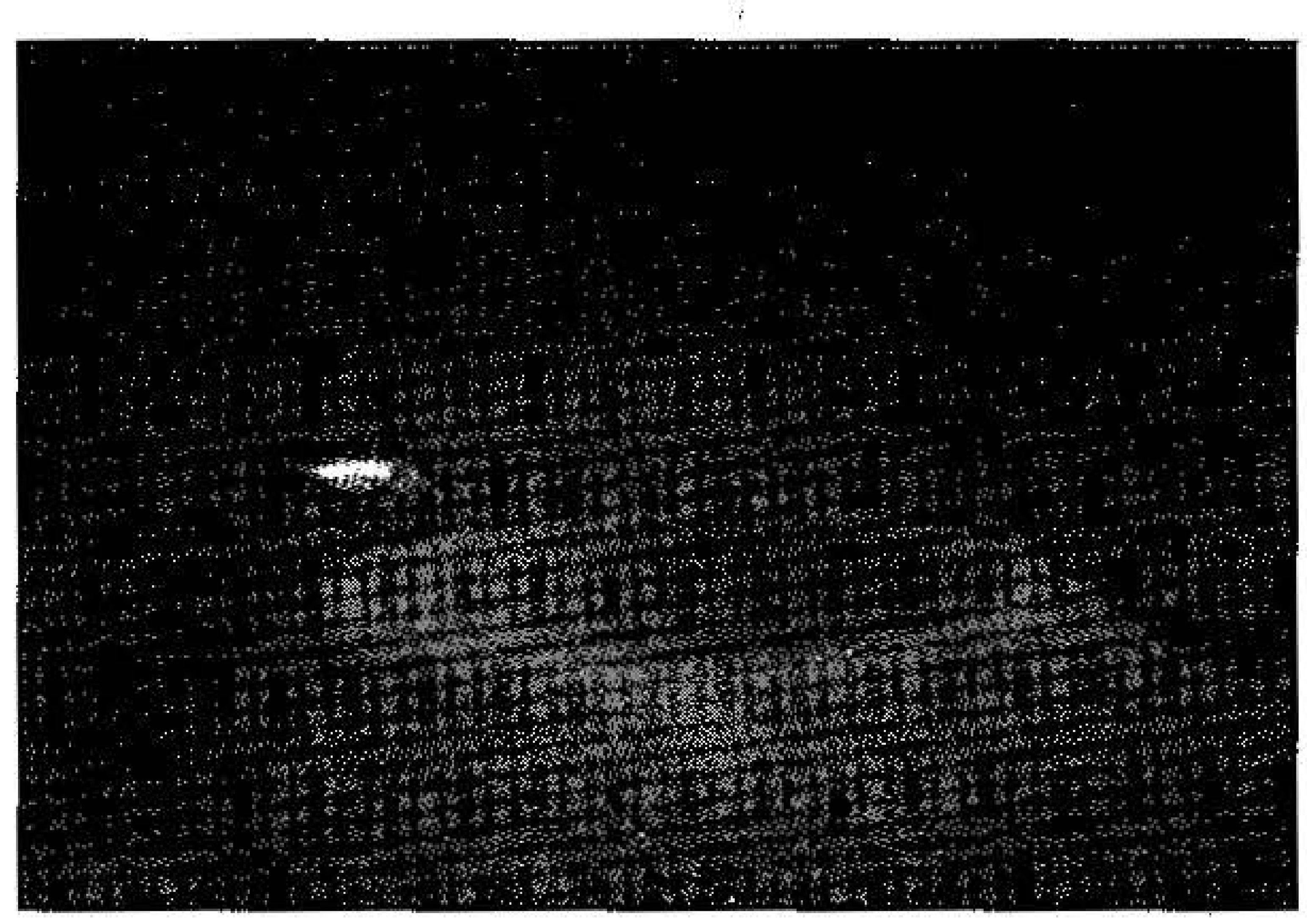

Figure 5. *Trematocranus microstoma*

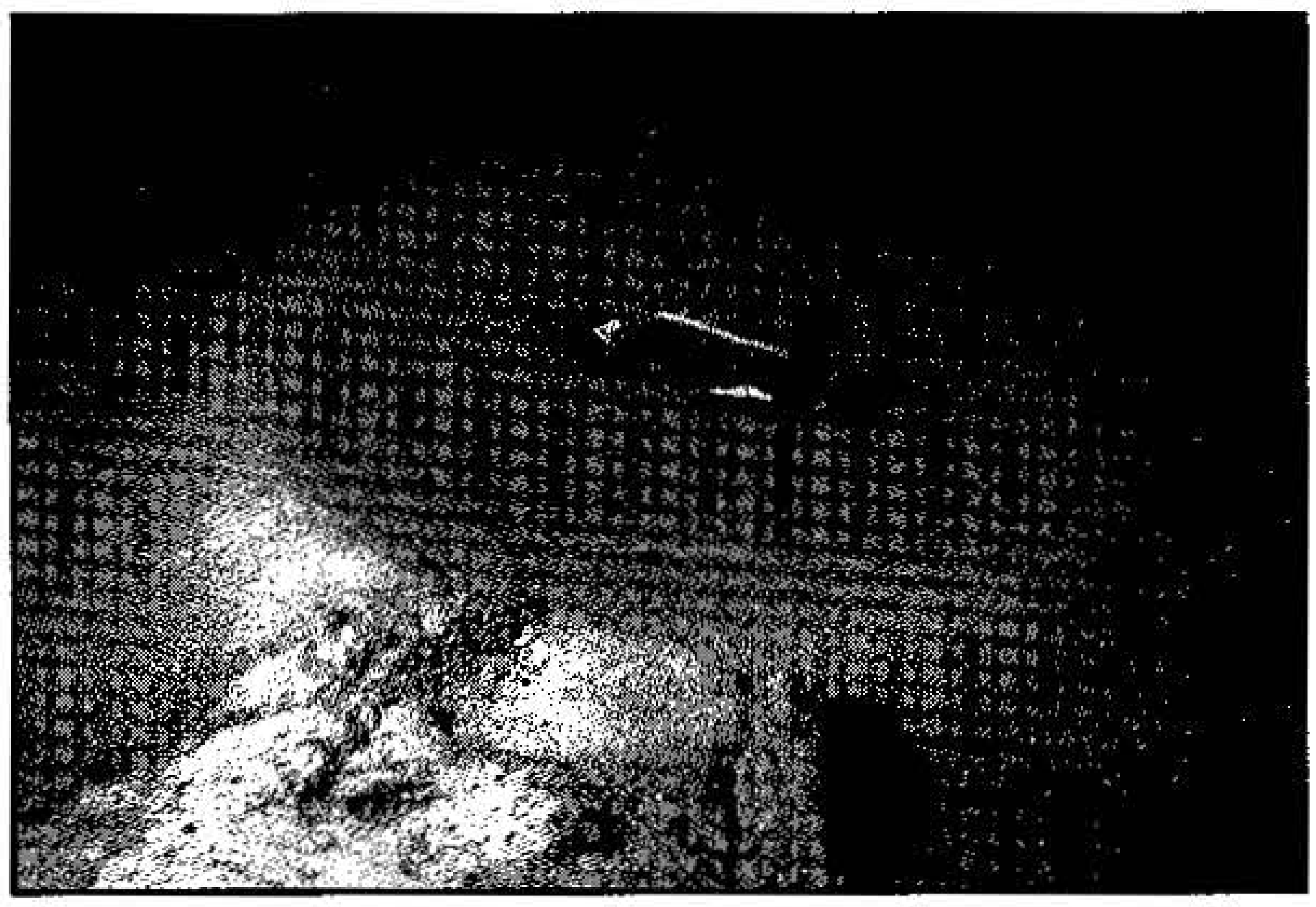

Figure 6. *Copadichromis* sp. "Likomae masinje"

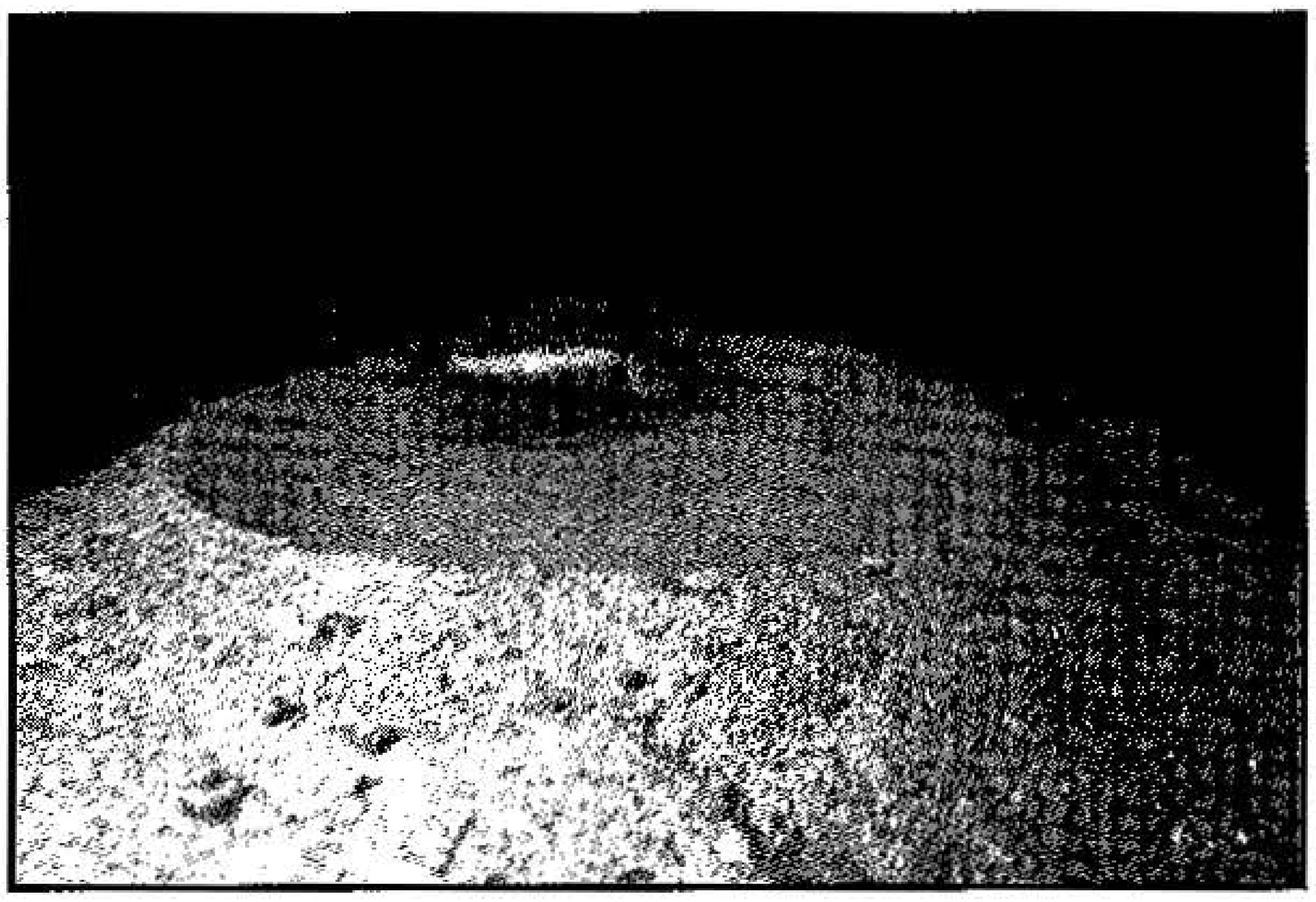

Figure 7. *Cyathopharynx foae*, Lake Tanganyika

Figure 8. *Aulonocranus dewindti*, Lake Tanganyika

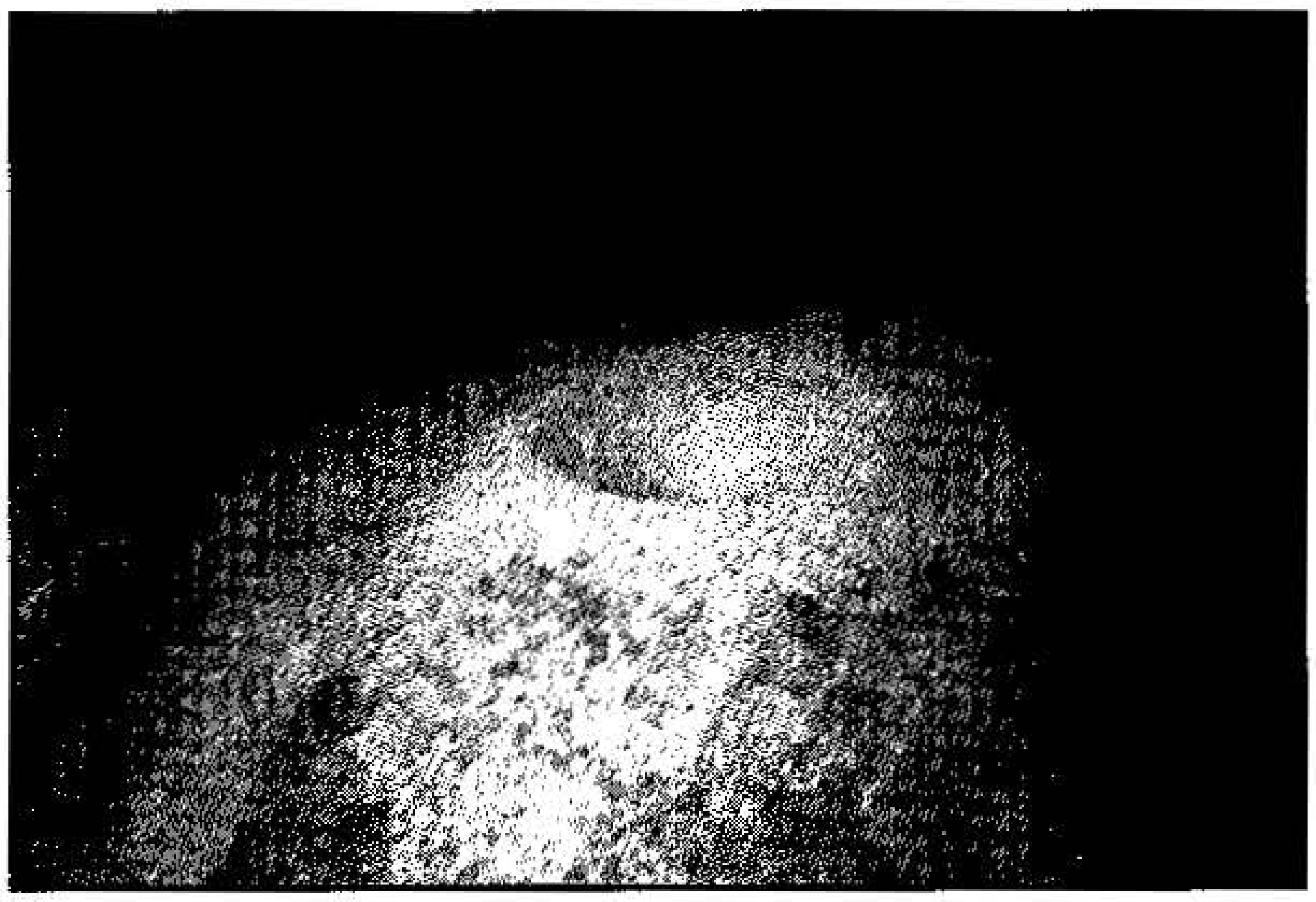

Figure 9. *Ophthalmotilapia nasuta*, Lake Tanganyika

Figure 10. *Nyassachromis microcephalus*

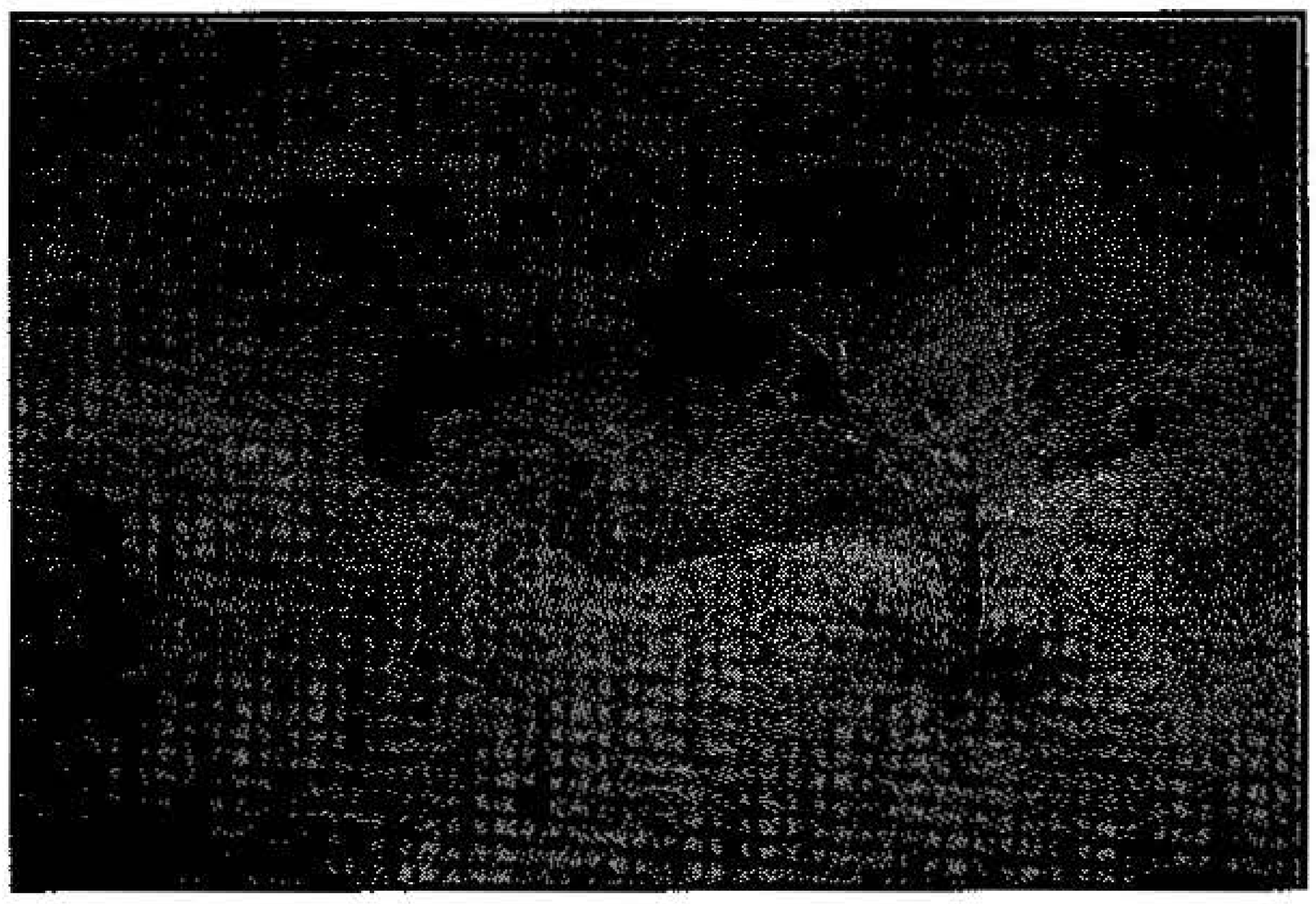

Figure 11. *Oreochromis* sp.

Figure 12. *Oreochromis* sp.

Figure 13. *Protomelas kirkii*

Figure 14. *Copadichromis ilesi*

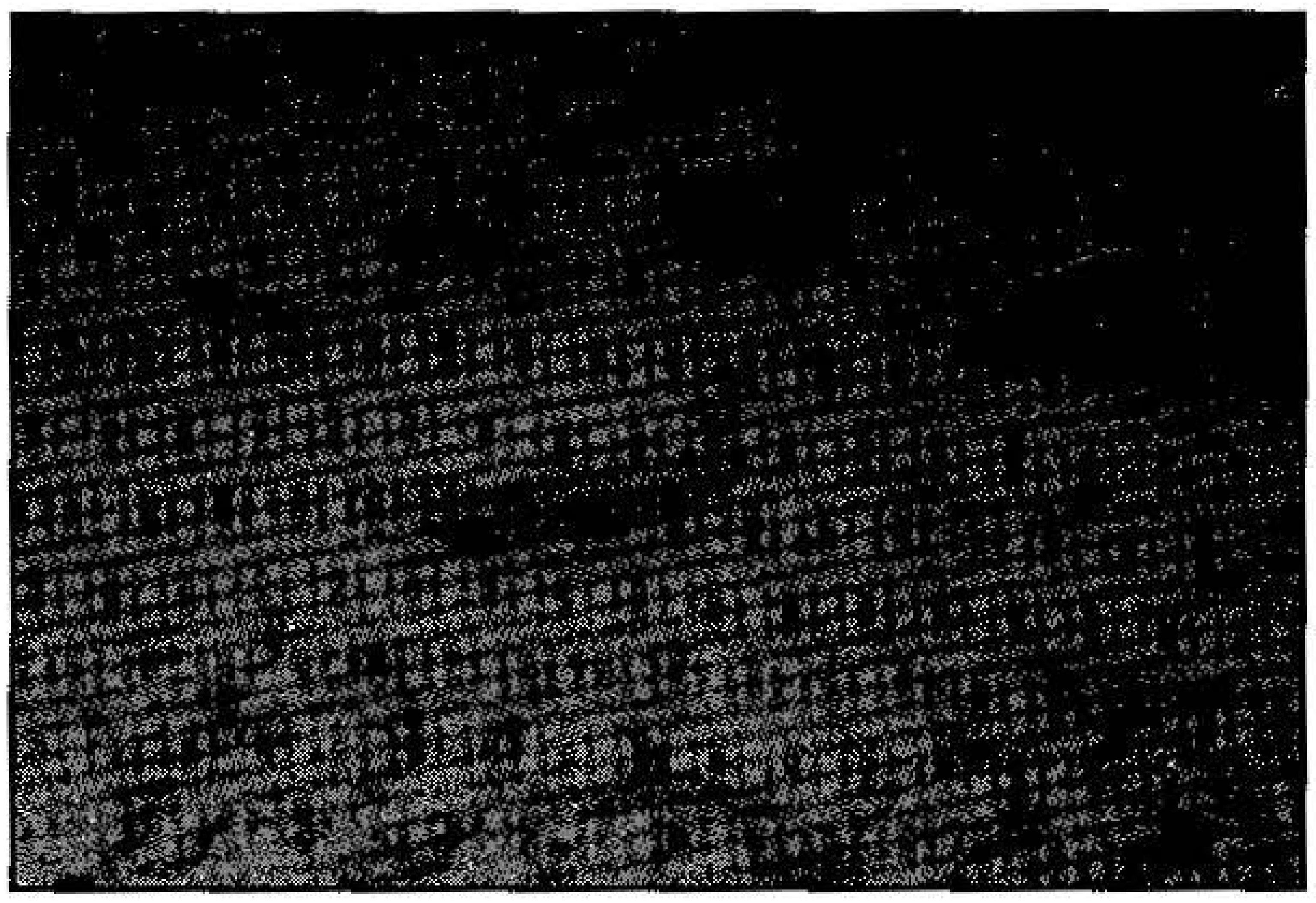

Figure 15. *Copadichromis* sp. "kawanaga"

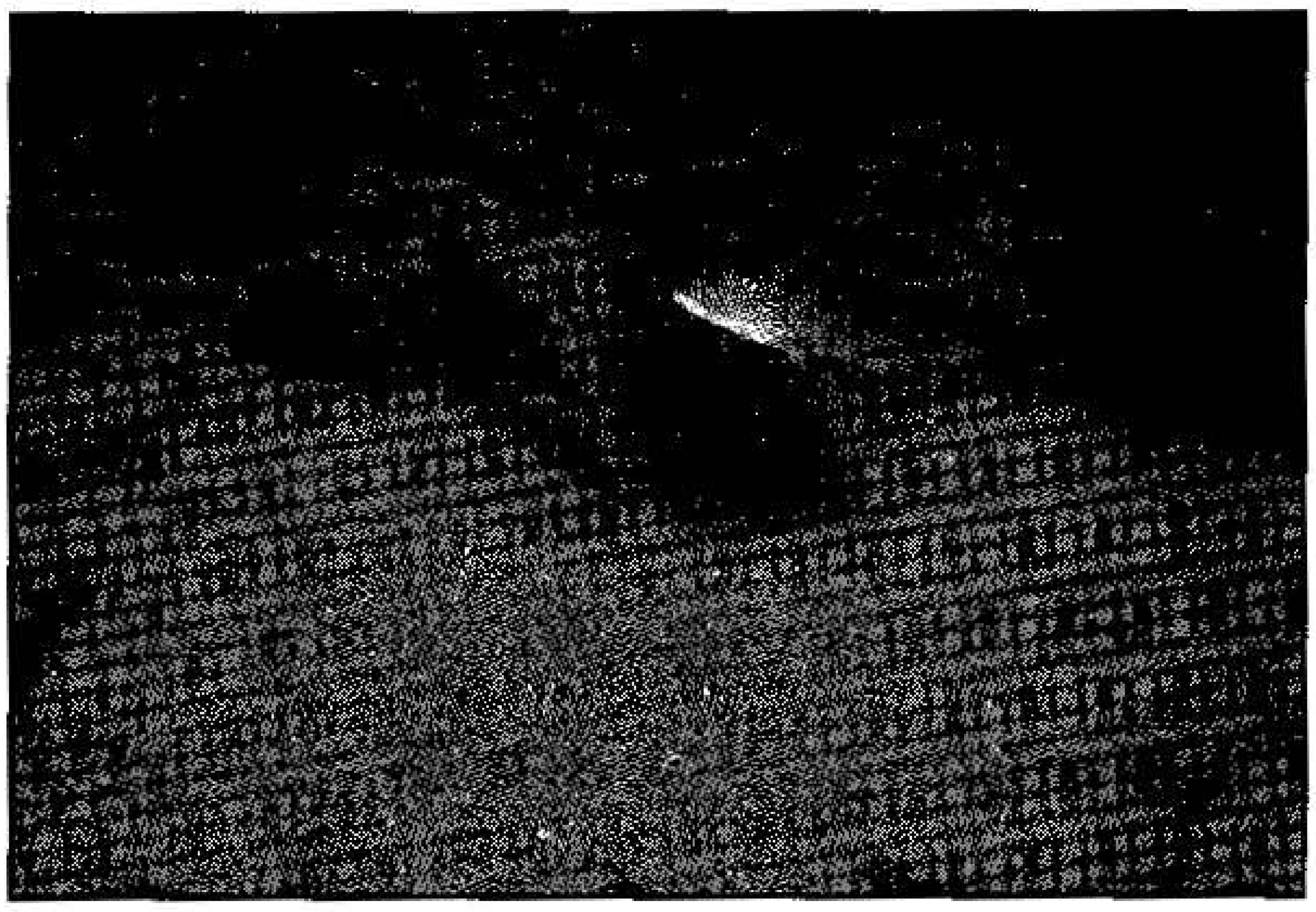

Figure 16. *Tyrannochromis macrostoma*

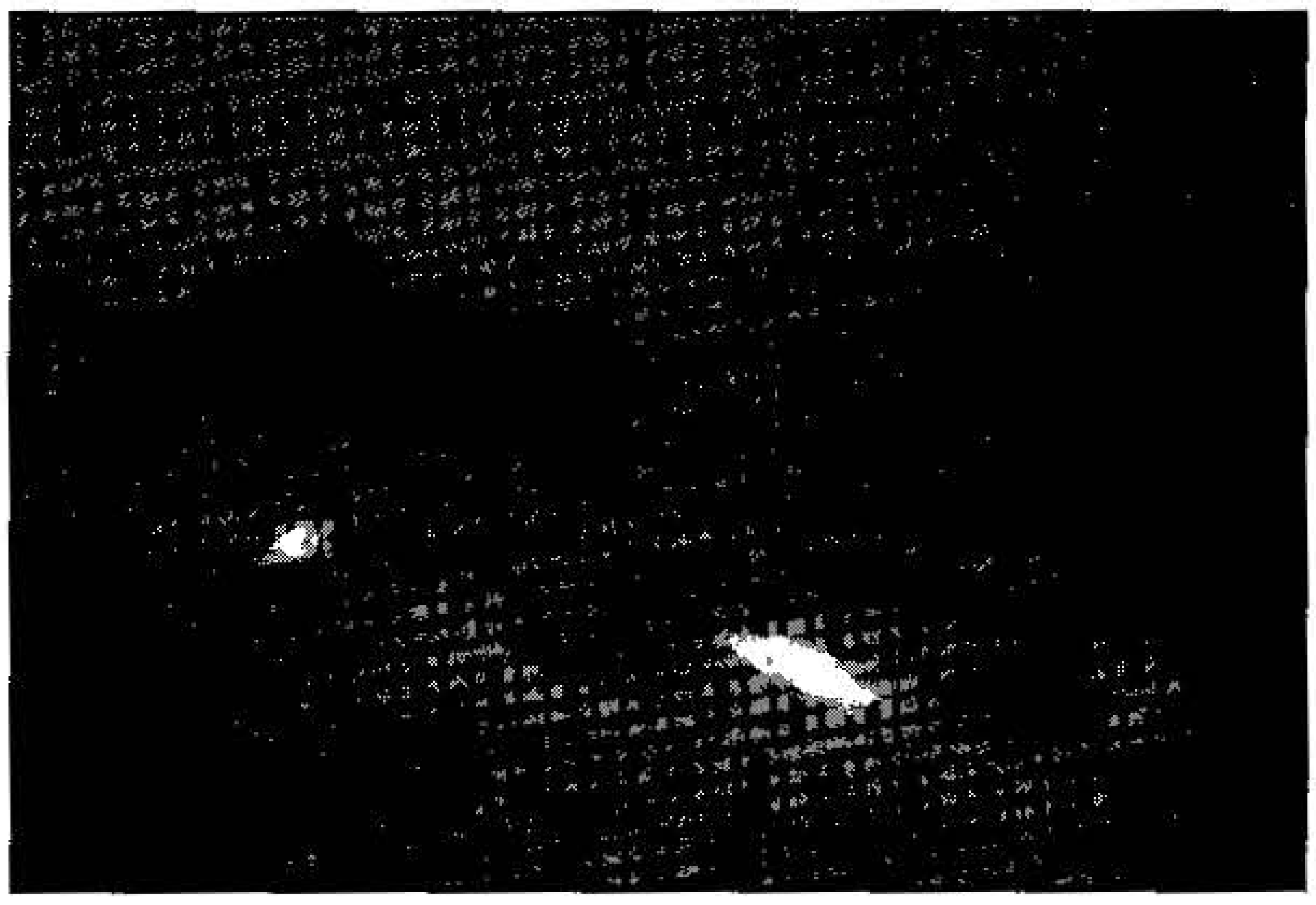

Figure 17. *Tramitichromis* sp.

Figure 18. *Protomelas ornatus*

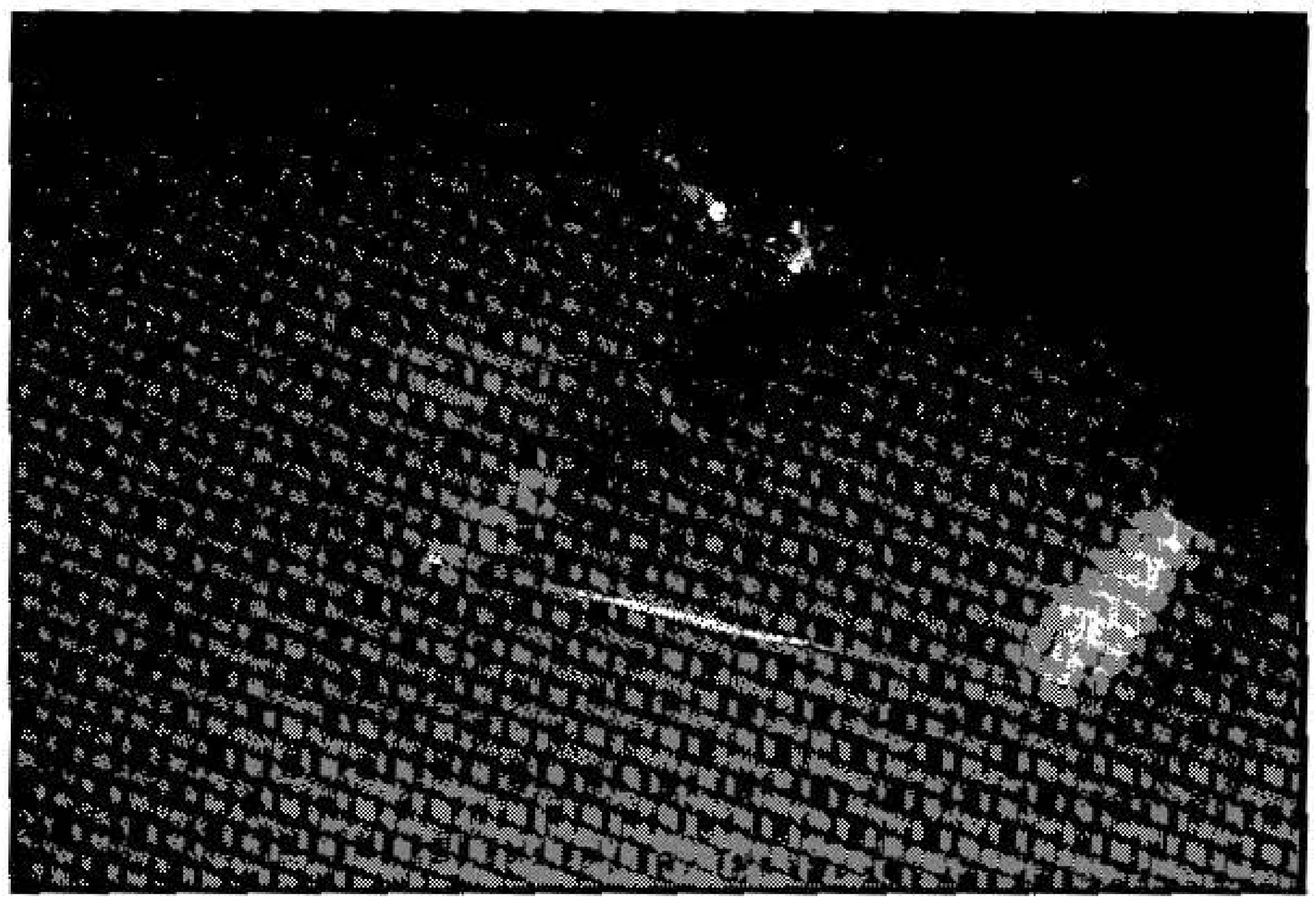

Figure 19. Measuring the bower of *Lethrinops* cf. *furcifer*

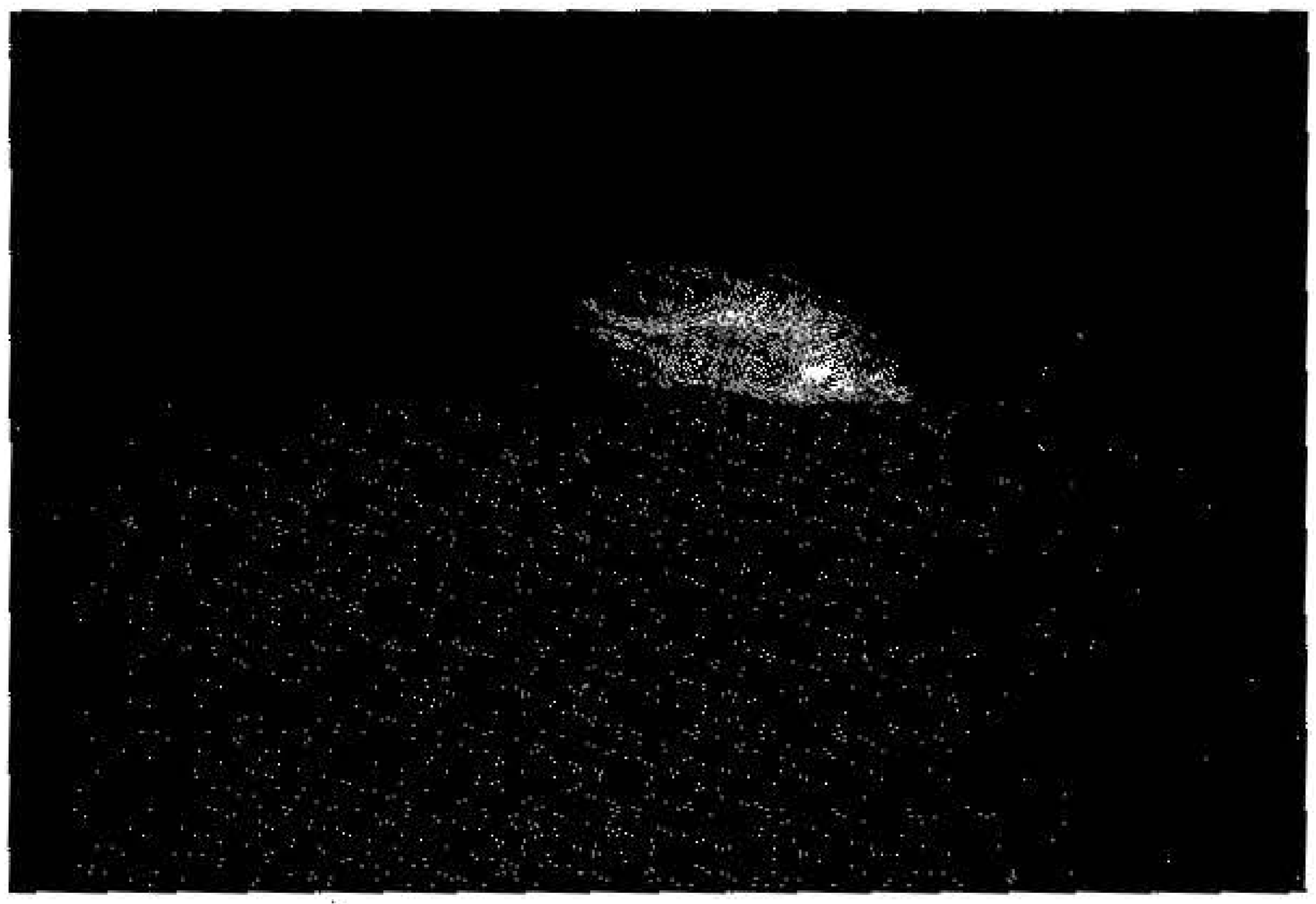

Figure 20. Male *Lethrinops* cf. *furcifer* at Cape Maclear moving sand at edge of bower.

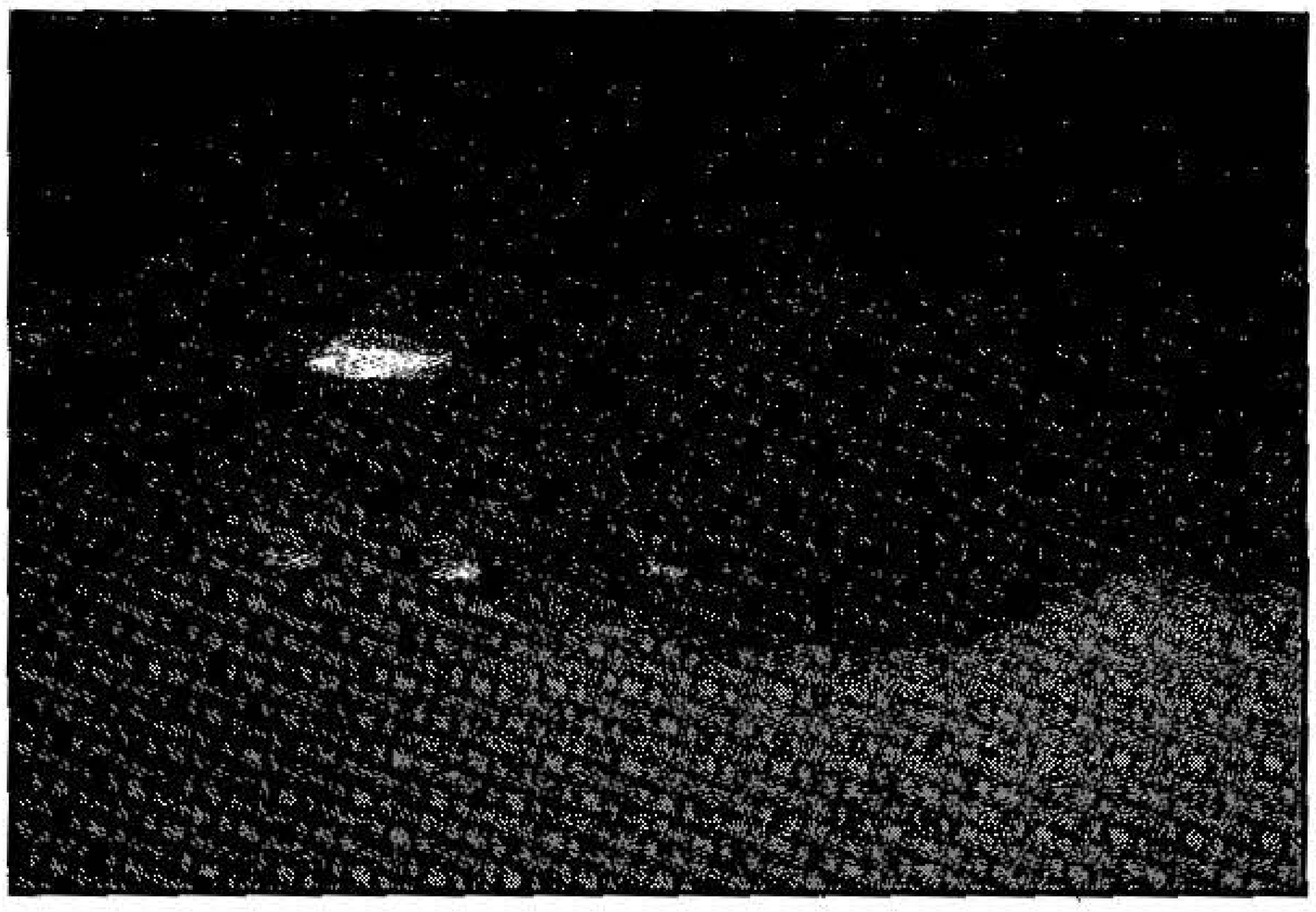

Figure 21. *Lethrinops* sp. "longimanus likoma"

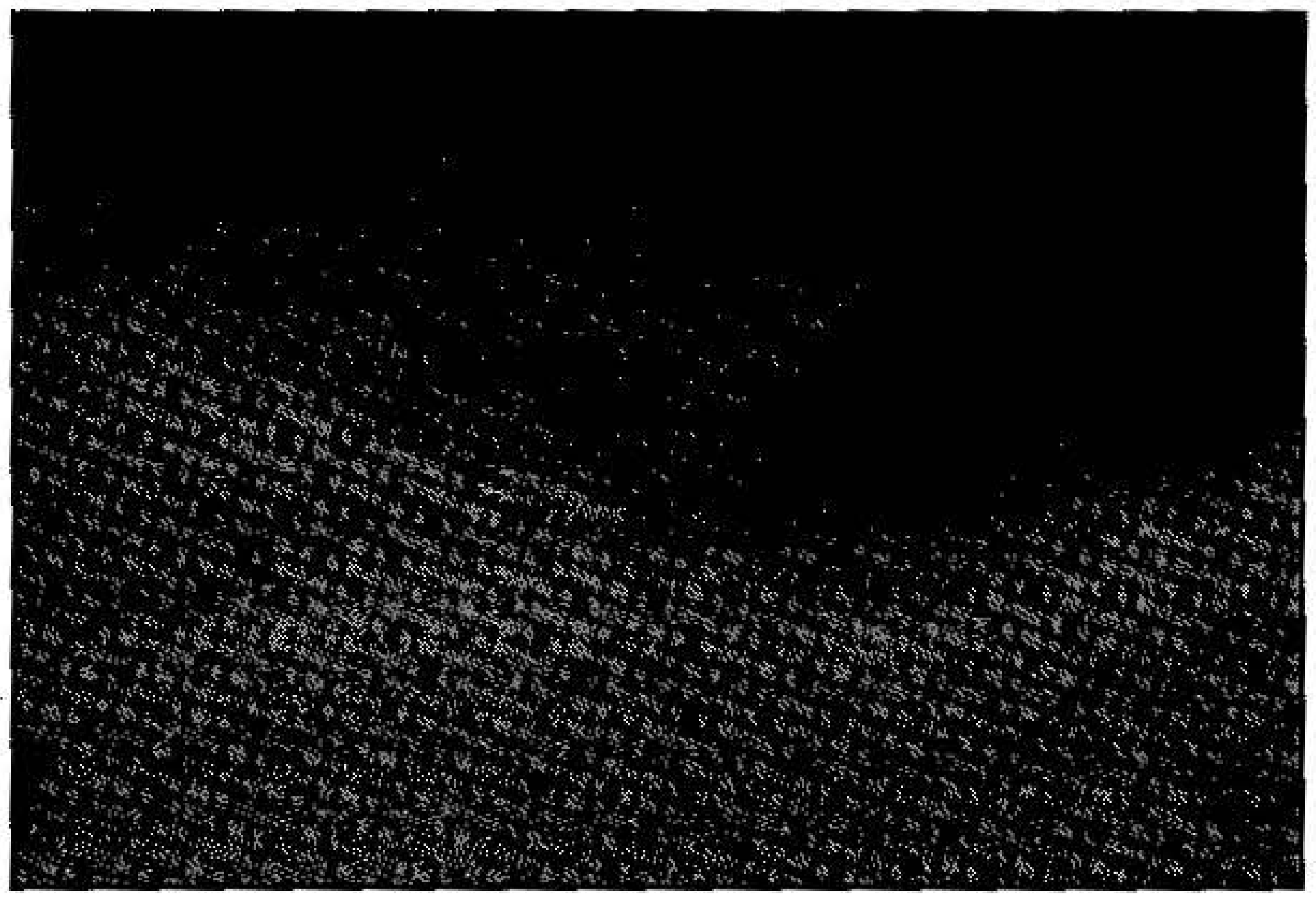

Figure 22. *Lethrinops* sp. "longipinnis ntekete"

Figure 23. Male *Lethrinops* cf. *auritus* above central courtship mound in bower.

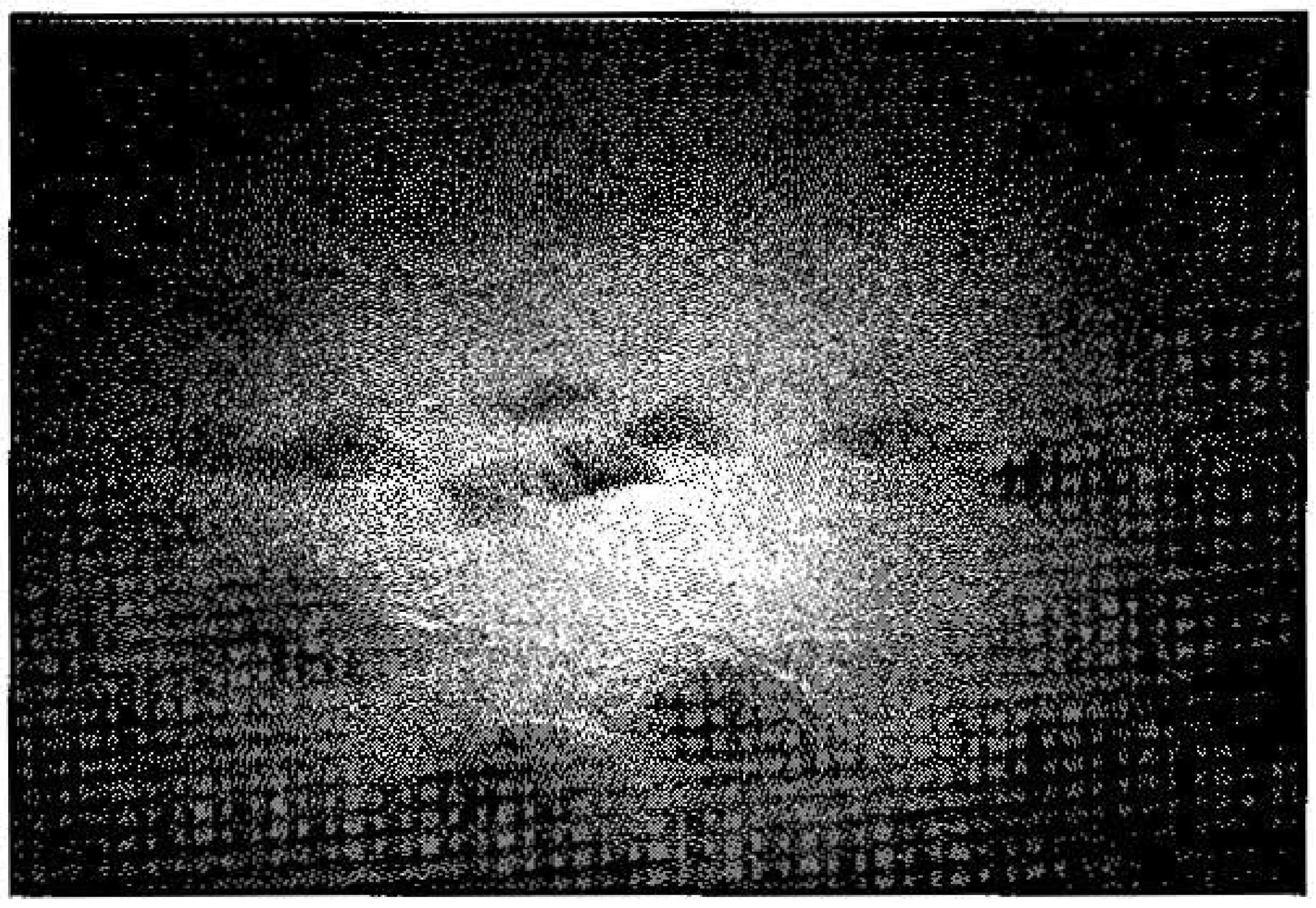

Figure 24. *Lethrinops* cf. *auritus* bower with many "decorative" mounds surrounding central courtship mound.

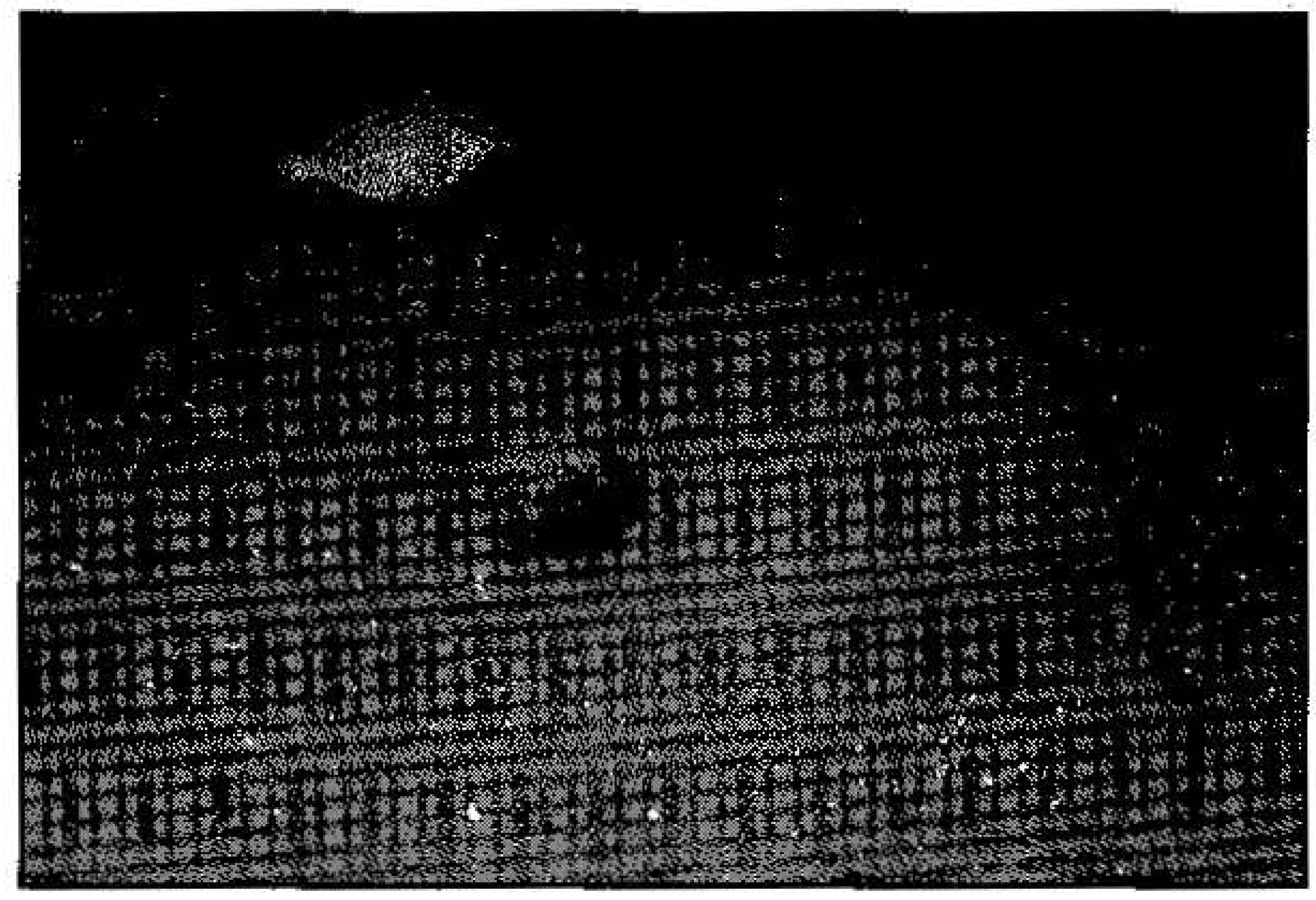

Figure 25. *Lanistes* shell in bower of *Otopharynx* cf. *heterodon.*

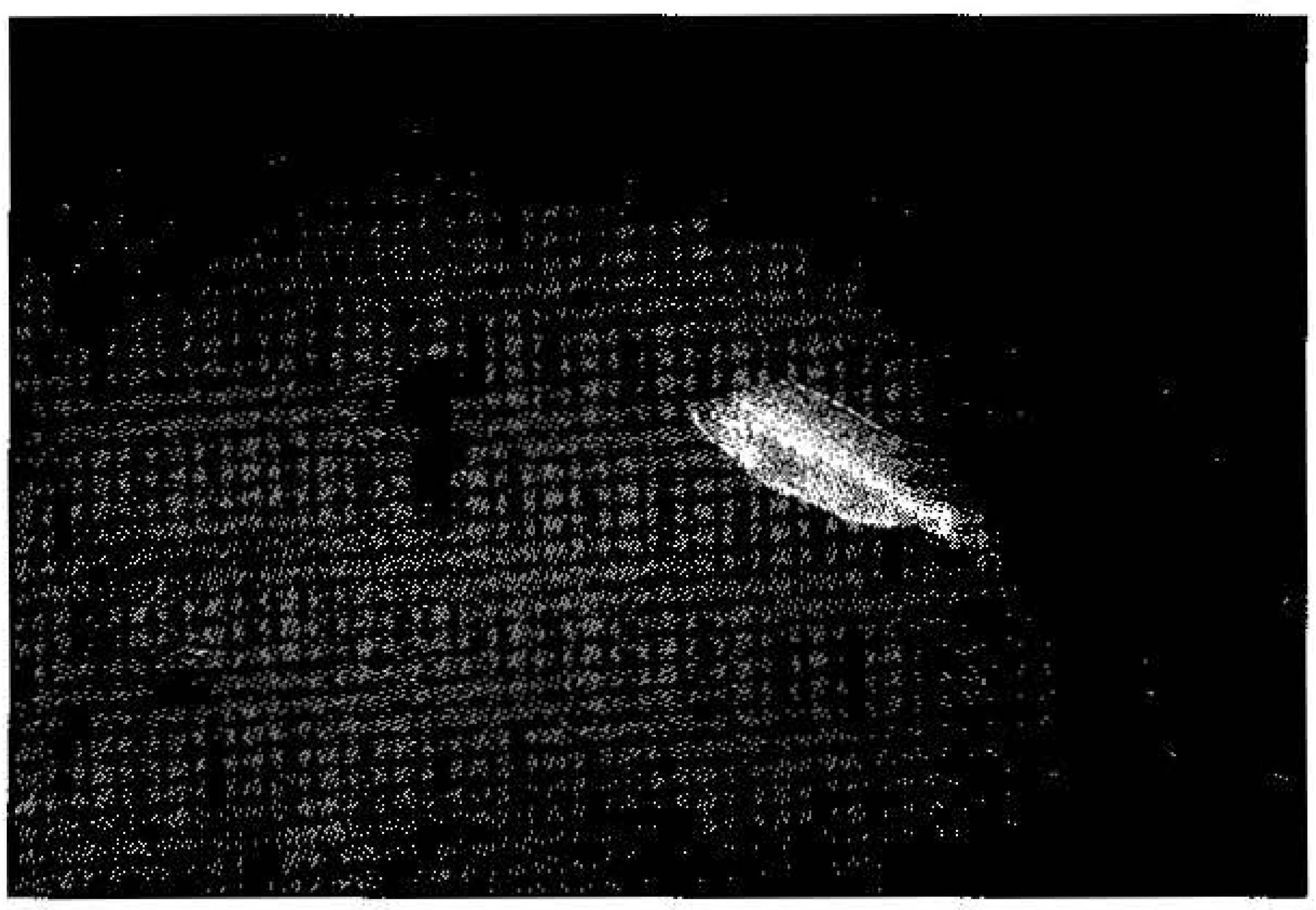

Figure 26. *Protomelas* cf. *pleurotaenia* with knot in rope in bower.

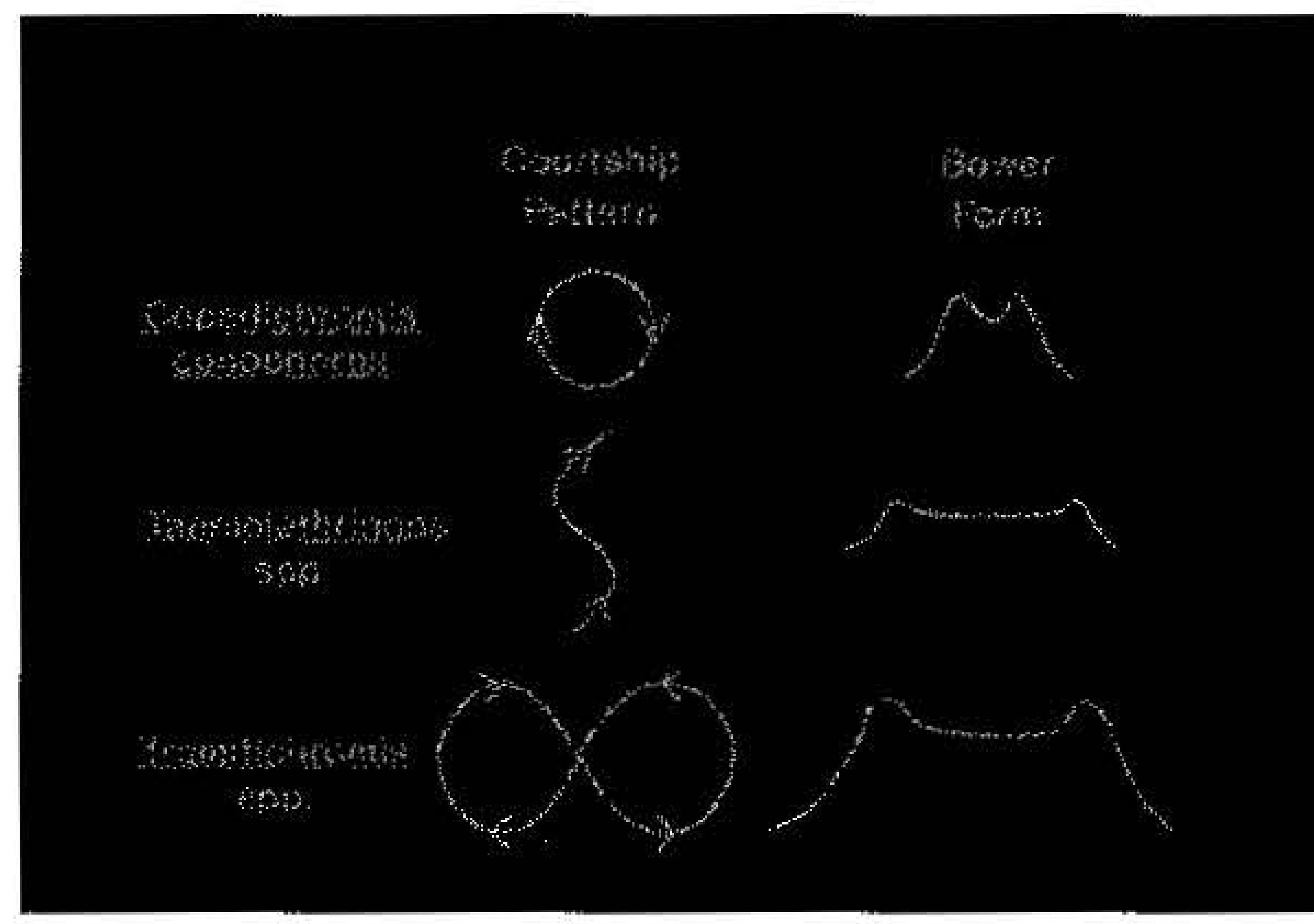

Figure 27. Courtship dance pattern for several lineages of Malawi cichlids

and widow birds (Andersson, 1991). This term was adopted and has been applied to these cichlid breeding structures in both lakes Malawi and Tanganyika (Bass, 1989; Karino, 1996, 1997; Konings, 1991; Stauffer et al., 1993; Stauffer and Kellogg, 1996; Taylor et. al., 1998, Kellogg et al., 2000).

Despite the fact that these structures by definition (see Collias and Collias, 1984) are not nests, Tweddle et al. (1998) proposed to reinstate the term "nests". They state "It is unacceptable to use the word bower for the cichlid structure because it is not a bower as defined in ornithological literature, and it is used for egg laying as well as display."

We disagree. Language is not static and continually evolves. The word bower originates from the old German *buan* meaning to dwell (Merriam-Webster's Collegiate Dictionary http://www.m-w.com/cgi-bin/dictionary). Before the 13th century the old English derivative meant an attractive dwelling or retreat. The verb *to embower* dates from 1580 and means to shelter or enclose.

A formal system for determining functional relationships does not exist in evolutionary biology and often one has to argue by analogy (Williams, 1966). Clearly, when possible, parallel terminology should be utilized to describe similar functional attributes rather than unique phylogenetic history. Most notable is the wing of a bird versus the wing of a bat. Wing is used to denote the function of flying. Wings have led to parallel evolution in other anatomical and physiological features such as a reduction in weight and high metabolism in both birds and bats (Young, 1981). Nevertheless the movable scapula, which permits the control of the angle of the wing is unique to bats (Young, 1981).

Likewise, the term eye is used to depict analogous organs in both vertebrates and arthropods, although this structure has evolved independently in the two groups. Similar arguments can be made for the term fin in Cetaceans and fish. "The designation of something as the *means* or *mechanism* for a certain *goal* or *function* or *purpose* will imply that the machinery involved was fashioned by selection for the goal attributed to it" (Williams, 1966). Therefore, linguistically or scientifically there is no *a priori* reason that a word used for bird behavior or structures built by birds should not be utilized for functionally similar fish behavior or artifacts.

SIMILARITY OF BOWER-BUILDING BIRDS AND BOWER-BUILDING CICHLIDS

The greater similarities between the function and evolutionary consequences of the structures built by bowerbirds (Gilliard, 1969; Borgia, 1985, 1995a,b) and those of maternal mouthbrooding cichlids justifies the use of the term bower. This congruence of characteristics will be shown not to be the case for the structures built by "nest-building" cichlids in relation to those of "bower-building" cichlids.

Bower-building birds, bower-building cichlids and nest building cichlids build structures. Amongst bower-building species, there are a wide variety of bowers constructed with materials often brought in from the outside (Figs. 2-26, Johnsgaard, 1994; McKaye, 1991). Cichlid nests, on the other hand, are excavations in which parents hide their eggs and larvae, but can become complex with 8 or more openings arranged in a flower shape as is found in Lake Tanganyika, while in Lake Xiloá some species, *Amphilophus longimanus*, *Amphilophus rostratus*, and *Hypsophrys nicaraguensis* have 3-40 holes or depressions between which they move their larvae.

In bower-building cichlids and birds, only males build bowers (Gilliard, 1969, McKaye 1991). In contrast, nesting cichlid females usually assist in either building the nest or evicting other residents from the nest (Alonzo et al., 2000; McKaye, 1977a, b, 1986). *Lamprologus callipterus*, however, has a mating system where the females visit the male's nest to spawn and take care of young.

Male bowerbirds vigorously court as the female nears or enters the structure. This is also true for cichlid males who circle or perform complex figure 8 movements to entice the female to the bower (Fig. 27). Fertilization amongst bowerbirds and bower cichlids is internal. Bower cichlid eggs are fertilized in the female's mouth. Although the eggs are briefly on the bower, they are quickly sucked into the female's mouth before they are fertilized. With nest-building cichlids the eggs, larvae, and young can remain in the nest for over a month (Keenleyside, 1991). There is no parental care on cichlid or bird bowers. Females care for young away from the structure (Gillard, 1969; Fryer and Iles, 1972), and in the case of some Malawi cichlids the females go to the nests of catfish to rear their young (McKaye and Oliver, 1980; McKaye, 1985). The structure of the bower in both cases may serve to reduce the probability of forced fertilizations. In the case of bowerbirds, the structure is hypothesized to reduce the risk of a forced copulation with the owner (Borgia, 1995, Borgia and Presgraves, 1998). In the case of the cichlids, it reduces the probability of other males stealing fertilizations, as in many nest-building fishes.

In both bowerbirds (Borgia, 1985; Borgia and Muller, 1992) and bower cichlids (McKaye et al., 1990; Nelson, 1995; Taylor et al., 1998; Kellogg et al., 2000) females choose among males and the choice of males is correlated with characteristics of his bower such as size, shape and location in the arena (McKaye, 1991; McKaye et al., 1990; Taylor et al., 1998, Kellogg et al., 2000). Among nesting cichlids, there is presently no evidence that the form of the structure has an influence on female choice. Possibly, where either the female or male alone establishes a territory, the quality of the territory might play a role in choice (Hale and McKaye in prep). Our *in situ* observations, however, are that the male and female usually work together to establish a territory for nest construction. The female invariably does most of the work in digging the nest (Rogers, 1998; McKaye, 1986; Alonzo et al., 2000).

If a bower-building male absents himself from a large or high quality bower, another male will occupy the structure (Gilliard, 1969; McKaye, 1991; Karino, 1997). Abandoned or destroyed structures are