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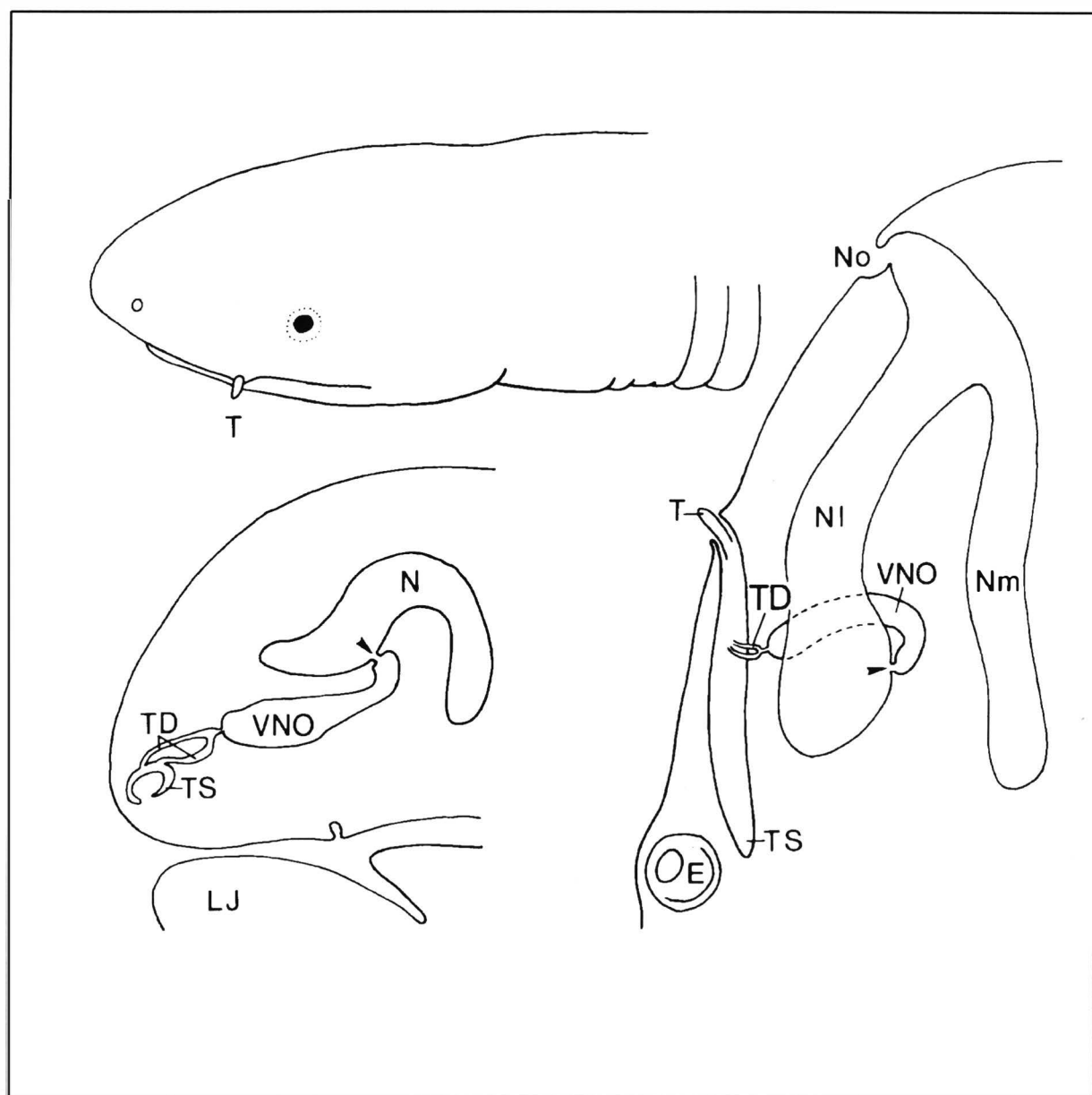
SENSORY BASIS OF FORAGING BEHAVIOUR IN CAECILIANS (AMPHIBIA, GYMNOPHIONA)

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The caecilian *Ichthyophis kohtaoensis* is able to localize prey objects by chemical cues only. On the surface of the ground *I. kohtaoensis* moves faster and on a more direct path towards prey than does the newt *Triturus alpestris*. Blocking the tentacles in the caecilian does not impair this ability. Within artificial tunnels, however, caecilians with blocked tentacles took longer to reach the prey than control animals did. Blocking the nostrils led to complete failure of prey localization on the surface of the ground.

INTRODUCTION

Compared to other amphibian groups, caecilians (Gymnophiona) are rather poorly investigated. The subterranean mode of life makes these limbless tropical animals relatively inaccessible. It is extremely difficult to observe their behaviour and to study sensory physiology. We keep *Ichthyophis kohtaoensis* (Family *Ichthyophiidae*) in our laboratory and have begun to investigate sensory functions involved in feeding behaviour. As in other caecilian species the eyes of *I. kohtaoensis* are rather small (about 0.5 mm in diameter) and they are covered by skin. Vision does not guide feeding; the only visually guided behaviour in *I. kohtaoensis* is a negative phototaxis (Himstedt & Manteuffel, 1985). In front of each eye caecilians possess a tentacle. This organ is unique among vertebrates and is possibly involved in tactile and chemoreceptive functions. The structure of the tentacle skin suggests a
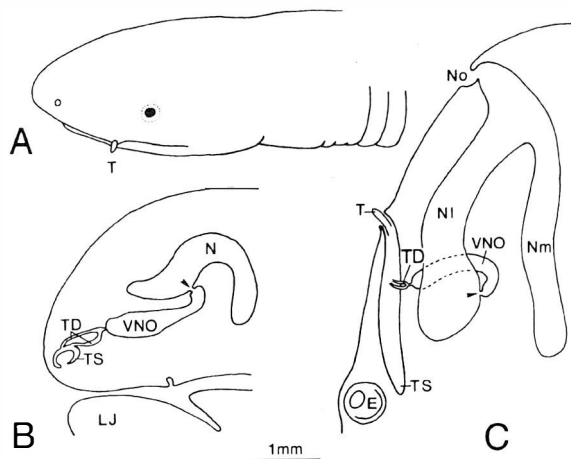

FIG. 1. Anatomy of nasal cavities and tentacle apparatus in *Ichthyophis kohtaoensis*. A. Lateral view of the head; between eye and nostril, the tentacle is visible. B. Cross section at the level of the tentacle ducts. C. Dorsal view of the nasal cavities. Abbreviations: E = eye; LJ = lower jaw; N = nasal cavity; Nm = nasal cavity, medial part; Nl = nasal cavity, lateral part; No = nostril; T = tentacle; TD = tentacle ducts; TS = tentacle sac; VNO = vomeronasal organ: The arrowhead points to the connection between nasal cavity and vomeronasal organ.

tactile function (Fox, 1985). During development, the tentacle is constructed from parts of the eye muscles and nerves, and of the accessory eye glands (c.f. Engelhardt, 1924; Billo & Wake, 1987; Wake, 1993.) Tentacle ducts connect the tentacle sac to the vomero-nasal organ (Fig. 1) and it is presumed that by means of this path substances from the surrounding medium may be transported to the olfactory epithelium (c.f. Badenhorst, 1978; Billo, 1986). Until now, however, there is no experimental evidence for function of the tentacle. Therefore it was the aim of this study to investigate a possible role of the tentacle in identifying and localizing prey objects.

MATERIAL AND METHODS

Adult specimens of *I. kohtaoensis* were collected in north-eastern Thailand and kept in terraria in moist soil and moss at about 27°C and a 12 hr : 12 hr light-dark cycle. They were fed earthworms and pieces of meat. For experiments, 10 specimens (about 18 to 20 cm total length) were kept individually in perspex boxes measuring 25 x 20 cm, 13 cm height filled with soil 10 cm deep. The soil was covered by a perspex plate with a central hole 1 cm in diameter. This hole was the only exit to the surface. During experiments, animals were fed daily at the beginning of the dark phase, with one piece of meat (bovine heart) weighing 0.05 g. This meat was placed on top of the perspex surface, and during four to five weeks the caecilians learned to search for food outside their burrows on the surface after "sunset". During experiments the perspex plate was covered by a sheet of paper and the piece of meat was placed in one corner of the rectangular surface, 12 cm away from the central hole. The corners were changed in random sequence, and the paper was replaced after each trial.

Searching and feeding behaviour were observed and recorded under infra-red illumination, by means of an infra-red sensitive video camera (Fig. 2). The paths of the experimental animals could be tracked on a monitor screen so that the time and the length of path from the exit hole to the target were recorded. In control experiments each animal was presented with a prey target 10 times. Subsequently, the tentacles were
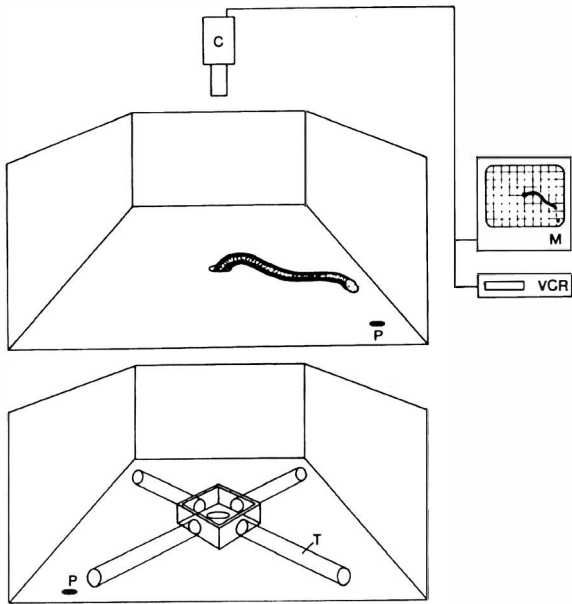
FIG. 2. Diagram of the experimental set-up to test chemical orientation. Above: on the surface of the ground. Below: in a tube system. C = Video camera; M = monitor; P = prey object; T = glass tubes; VCR = video cassette recorder.

blocked by closing the tentacle opening with a surgical glue (Histoacryl®). After three days, the glue scaled off the skin and the tentacles could be protruded as before. Experiments with blocked tentacles were likewise performed 10 times on each animal. In other experiments, the nostrils were blocked by filling the external and internal nostrils with a two-component polyvinyl (Dentagum®, a dentist's material for taking impressions). The tentacle and vomeronasal organ were not influenced by this treatment. After an experiment the plugs were removed with fine forceps.

In order to compare the ability of *Ichthyophis* to localize prey objects by means of chemical cues, with that of other amphibians, adult terrestrial newts of the species *Triturus alpestris* were tested in the same experimental situation. Ten newts were fed in darkness with pieces of meat as described above for *Ichthyophis*. During experiments, a newt was placed in the center of a rectangular box, with the prey object in a corner 12 cm away from the animal's head.

In another series of experiments caecilians were not tested on the surface of the ground but within tubes (Fig. 2, below). Here a situation was simulated in which a caecilian follows a prey within its tunnel. After leaving the exit hole, the animal had the choice to enter one of four glass tubes leading to the four corners of the test box. One of the tubes was scented by pulling the piece of meat through it so that the inner wall of this tube was contacted by the odorous substances. After each trial the tubes were cleaned thoroughly. In this setup each of the ten experimental animals was tested 10 times as controls and 10 times after blocking the tentacles.

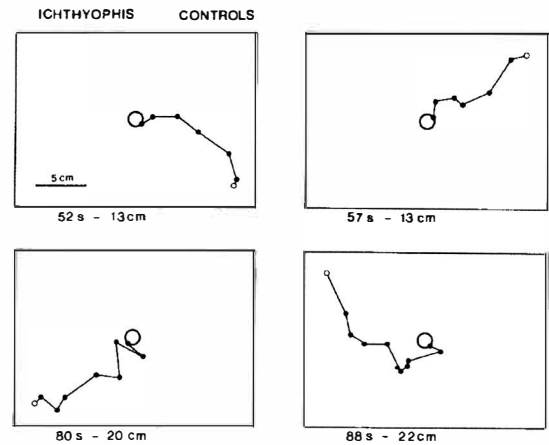The Wilcoxon matched-pairs signed-ranks test was used to compare samples.

FIG. 3. Examples of paths of four control animals (*I. kohtaoensis*). The position of the animal's head was marked by a dot every 10th second. The total time from leaving the exit until reaching the prey and the length of the path are indicated.
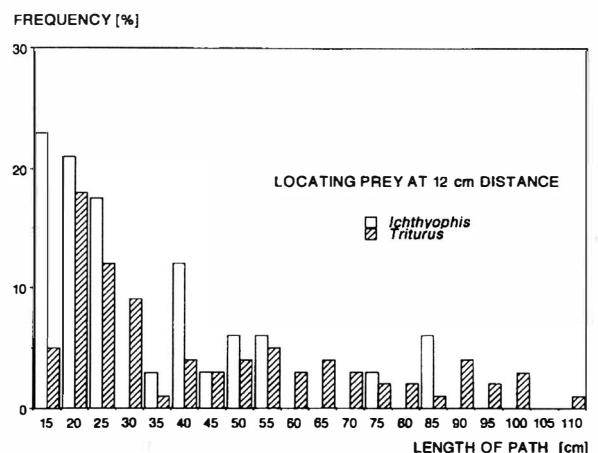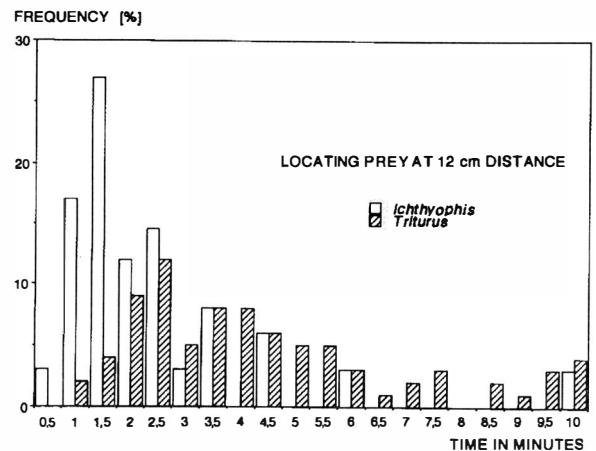

FIG. 4. Comparison of chemical orientation in the caecilian *I. kohtaoensis* and in the newt *Triturus alpestris*. Above: Time to reach the prey. Below: Length of the path.

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newts exceeded this path length. The differences between *Ichthyophis* and *Triturus* regarding the time as well as the length of path are significant ($P < 0.01$).

Caecilians with blocked tentacles showed normal feeding behaviour one day after surgery. These animals behaved much like the controls in the experiments. The movements during searching from the exit hole toward the piece of meat appeared not to be affected by the restriction of the tentacles. Indeed, as can be inferred from Fig. 5, neither the length of path nor the searching time is longer in animals with blocked tentacles. Regarding the length of path, there is a slight predominance of blocked individuals at the intervals from 15 to 25 cm, suggesting that without tentacle use the path might be even more straight. This difference, however is not significant ($P > 0.3$).

Differences occurred, however, if *Ichthyophis* had to follow a scented track within the glass tube system. Generally, the caecilians responded quite precisely and quite quickly in this situation. In 100 trials respectively, control animals entered the scented tube 79 times, blocked animals entered it 78 times. So the frequency of errors in the first orienting decision was nearly the same in animals with and without blocked tentacles. But the velocities within the tube differed significantly ($P < 0.01$). After entering a scented tube, caecilians with functioning tentacles moved distinctly faster than those with blocked ones. As can be seen in Fig. 6, the proportion of controls that reach the target within the first minute, is nearly three times that of the blocked animals.

Blocking the nostrils resulted in remarkable effects. These experiments were performed on the surface of the ground only, but not in the tube-system. As can be seen in Fig. 7, the paths were no longer directed towards a target but were totally random. None of the 10 animals, which again were tested 10 times each, seized the prey object. Even if the path led close to the prey the caecilian did not turn towards it but passed by.
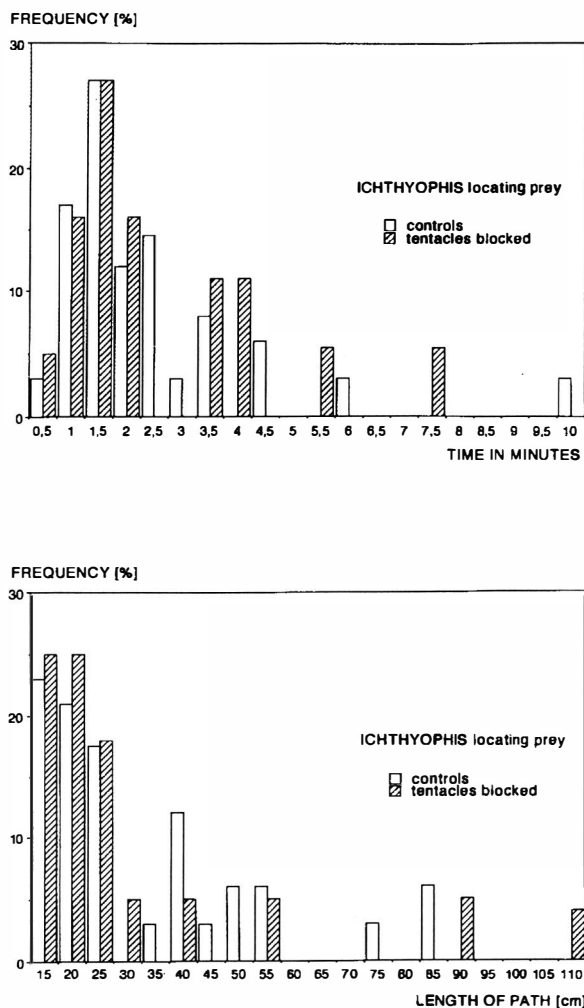
FIG. 5. Comparison of chemical orientation in caecilians with functioning tentacles (controls) and with blocked tentacles. Above: Time to reach the prey. Below: Length of path.

RESULTS

The movements of *I. kohtaoensis* on the surface, toward the prey object, appeared rather straight and fast. Fig. 3 shows four typical paths of control animals which reached the targets without many detours and within quite a short time. The direct distance from exit to prey object was 12 cm, and in these four examples the length of the path ranged from 13 cm to 22 cm, while the time elapsed until seizure of the meat ranged from 52 s to 88 s. In Fig. 4 the responses of *Ichthyophis* are compared to the data for *Triturus*. It is clear that *Ichthyophis* moved faster to the target; most animals reached it within one to two minutes, while only a few newts seized the prey so soon. Only six caecilians needed more than 5 min to reach the target, whereas 24 newts were counted in the intervals from 5.5 to 10 min. The lengths of the path also clearly differed. Most caecilians (61%) went 25 cm or less whereas the newts walked longer distances, making more detours. Only 35% of the newts needed 25 cm or less; 9% of the caecilians covered more than 60 cm, but 25% of the
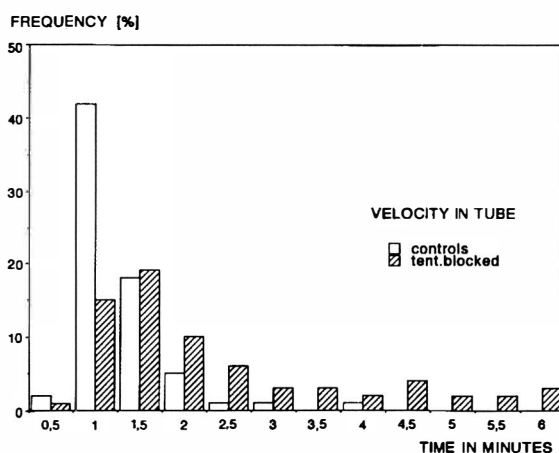
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FIG. 6. Reactions of caecilians with functioning or blocked tentacles following a scented path within the tube system.
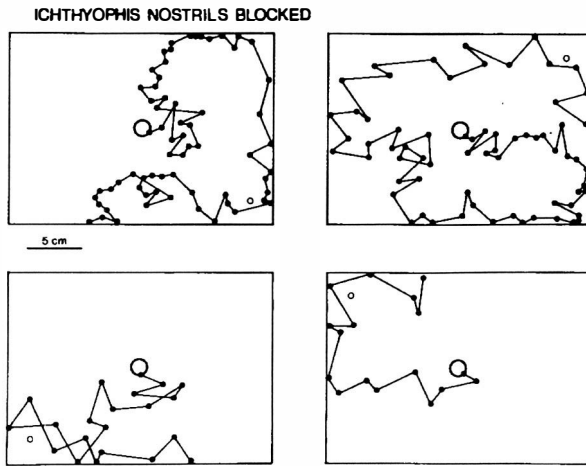
ICHTHYOPHIS NOSTRILS BLOCKED

FIG. 7. Examples of paths of four caecilians with blocked nostrils. As in Fig. 3. the position of the animal's head was marked every 10th second.

DISCUSSION

The experiments reported here show that the caecilian *I. kohtaoensis* is able to localize prey objects by chemical cues only, quite precisely. Compared to terrestrial newts the caecilians reached a prey object on the ground surface within a shorter time and by a more direct route. The fact that *Ichthyophis* in this situation reached the target faster, does not necessarily indicate greater sensory abilities but might also be a result of a different mode of locomotion. The fact, however, that the newts took courses with larger deviations (resulting in longer paths) may be interpreted in terms of better chemical orientation by the caecilians. Presumably *I. kohtaoensis* is able to detect smaller differences in odour concentration reaching the left or right olfactory epithelia.

Blocking the tentacles had no effects on behaviour on the surface, so we conclude that feeding on the surface of the ground is guided by olfaction with the nose. In the experiments with blocked nostrils, the tentacles and the vomeronasal organs were not influenced. But these organs were apparently unable to detect the prey and to guide the animal to it. In this situation, the tentacles probably have no function. Indeed, they are so short that a protruded organ does not touch the ground when *Ichthyophis* is moving horizontally on a flat surface. This is different in a subterranean tunnel.

Burrows built by *Ichthyophis* consist of tubes with a lumen that matches the body diameter of the animal. Within them, the moving tentacles can contact the substrate and might pick up odour molecules and transport them towards the olfactory epithelia. This may explain the results of our experiments in the glass tube system. Here, animals with blocked tentacles reached the target after a significantly longer time than the controls with functioning tentacles. We conclude that within a tube the tentacles may support olfactory orientation when the molecules to detect are not only gaseous but also dissolved in substrate humidity. In

reptiles, the vomeronasal organ is involved in chemoreception during tongue-flick behaviour which may pick up odorants from the substrate but also may sample air (c.f. Simon, 1983; Halpern, 1992). Whether or not the tentacles in *Ichthyophis* are involved in detection of air-borne odorants is an open question and has to be tested.

With tentacles blocked, the caecilians in the tubes seemed not to be seriously handicapped. They still reached their prey within a rather short time. The role of the tentacles in chemical orientation probably might be more important if caecilians have to burrow in the soil. In our experiments, animals moved within premade tubes, like caecilians travelling through their gallery-system. In terraria *I. kohtaoensis* does not dig new tunnels continously. When placed in fresh soil they spend about two weeks burrowing and from then on move within the same tubes.

During burrowing in the soil the external nostrils are closed, and half a century ago Marcus (1930) presumed that the physiological function of the caecilian tentacle is not only to serve as a tactile sense organ but also to provide a side-path for breathing and olfaction during burrowing behaviour. Marcus thought that gaseous scents enter the tentacle opening and that the movements of the tentacle itself had the function of removing soil particles from the opening. Badenhorst (1978) suggested that particles clinging to the moist tentacle are deposited into and dissolved in the secretions of the orbital glands covering the tentacle and conveyed via the tentacle ducts to the vomeronasal organ. He also postulated that the tentacle opens a bypass in the event of closure of the external nostrils, while burrowing. This hypothesis was adopted by recent anatomists such as Billo (1986) and Schmidt & Wake (1990).

Our data are consistent with this hypothesis: In our tube experiments, the tentacles might have transported dissolved substances which they could not do on the ground surface where only gaseous scent was present.

The function of the tentacles during burrowing must be investigated in further experiments. In contrast to Ramaswami (1941), who reported that *Ichthyophis* is no burrower but lives under decaying vegetation, our own observations show that *I. kohtaoensis* stays in tunnels built by burrowing. Not only does it live in subterranean burrows in terraria; in the natural habitat in Thailand as well, most specimens were found about 10 to 20 cm deep in the soil, although some stayed on the surface under wood or leaves. Also Ducey, *et al.*, (1993) reported that *I. kohtaoensis* in terraria was not detectably a less effective burrower than caecilians of other genera. We therefore presume that chemical orientation mediated by the tentacles might be of biological significance in this species while moving in existing tunnels as well as during burrowing in the soil.

A possible function of tentacles and vomeronasal organs in caecilians might also be detection of pherom-

ones. In salamanders, chemosignals in courtship behaviour and territorial interactions are mainly perceived by the vomeronasal organ (c.f. Dawley & Bass, 1989; Houck, 1986). Until now, these behaviours have not been observed and studied in caecilians.

ACKNOWLEDGEMENTS

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