Observations on the Biology of Cave Planarians of the United States

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SUMMARY

Observations are made on the biology of several species of cave planarians (mostly of the family Kenkiidae) collected alive from over 50 caves in 14 states. Most of these species were maintained in laboratory cultures at 12°C±3°C. Food caten was extremely variable. Functions of the anterior adhesive organ included food capture, locomotion, defense against predators, and probably chemoreception, mechanoreception, and as a holdfast in strong currents. Predators probably consist of fishes, crayfishes, and salamanders. Sporozoan and ciliated parasites were found occasionally. Cocoons were found in winter, spring, and summer; they hatched in about 3 months and contained 2 to 17 young.

INTRODUCTION

About 50 species of planarians are recognized from the United States, and nearly half of them have been found in caves. Some of these cave dwellers are more often found outside caves and are considered troglophiles (facultative cavernicoles) rather than troglobites (obligatory cavernicoles).

Although many other species will be mentioned and compared, this paper deals primarily with the troglobilic planarians, consisting of about 20 species in the genera Sphalloplana, Macrocotyla, and Kenkia; all are presently assigned to the family Kenkiidae (Kenk, 1975). The taxonomic status of the kenkiids has changed several times since the family was erected by Hyman in 1937. For discussions of this status see Ball (1974), Beauchamp (1961), Carpenter (1971), Hyman (1937), Kenk (1969, 1970, 1972, 1975, 1977), and Mitchell (1968).

The number and identification of the species in my study

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are somewhat controversial. The genus Sphalloplana creates the greatest problem because populations have been found in over 200 caves in at least 16 states; many populations are very similar in appearance so the determination of species becomes very difficult. In addition, there is some debate among taxonomists concerning the validity of several described species. If live specimens are observed it is usually quite easy to identify them to subgenus. This was one of the main reasons I erected three subgenera of Sphalloplana as follows (Carpenter, 1971): (1) subgenus Sphalloplana contained S. percoeca, S. georgiana, S. virginiana, and S. kansensis: (2) subgenus Speophila contained S. pricei, S. buchanani, S. hubrichti, and S. weingartneri; and (3) subgenus Polypharyngea contained S. mohri. Kenk (1977) has added seven new species to this genus as follows: S. evaginata, S. californica, S. culveri, S. consimilis, and S. subtilis (all in the subgenus Sphalloplana); and S. holsingeri and S. chandleri (both in the subgenus Speophila).

Considering the relatively large number of species of troglobitic plonarians and their wide geographic range, it is surprising that almost nothing but their systematics has been studied. It is the purpose of this paper to report basic biological information on the troglobitic planarians I observed periodically from 1968 to 1978.

MATERIALS AND METHODS

Cave planarians were collected alive from over 50 caves in 14 states: subgenus Sphalloplana from West Virginia, Kentucky, Tennessee, Alabama and Georgia; subgenus Speophila from Pennsylvania, West Virginia, Virginia, Ohio, Indiana, Illinois, Missouri, Kentucky, and Tennessee; subgenus Polypharyngea from Texas; Macrocotyla from West Virginia, Iowa, and Missouri: Dendrocoelopsis americana from Oklahoma; Phagocata bursaperforata from Alabama; and Phagocata morgani from Pennsylvania, West Virginia, Virginia, Kentucky, and Alabama: and Phagocata gracilis from Pennsylvania, Virginia, Ohio, Indiana, Kentucky, and Missouri. Many of these specimens were photographed alive, then maintained in cultures for observation. They were kept in refrigerators that fluctuated between 9° and 14°C. Most sexually mature worms were preserved by modifications of the rapid freeze technique described by Carpenter (1989). In order to compare internal morphologies, serial secctions were prepared, by standard histological procedures, from about 150 specimens.

RESULTS

Habitat.

As might be expected, not all species of cave planarians are found in the same type of habitat. Perfectly quiet water such as that of many cave rimstone pools is apparently preferred by S. percoeca (Fig. 1), S. mohri (Fig. 3), D. americana (Fig. 5), and P. bursaperforata (Fig. 8). In these quiet pools the worms are sometimes found crawling on the underside of the surface film. Some pools inhabited by S. percoeca may dry up during summer, and it is not known exactly how the planarians survive; presumably, they remain in an inactive state imbedded in moist mud. Barr and Kuehne (1971) concluded that they survive such dry periods by encysting in mud. But I have kept S. percoeca, D. americana, and P. bursaperforata in culture for over a year without any signs of encystment such as is found in the surface planarian Phagocata velata (Kenk, 1944). Because most caves have a very high relative humidity, cave planarians can probably live out of water for some time. Buchanan (1936) noted in his behavioral studies on S. percoeca that when agitated the animals showed a tendency to leave the water and creep about above the water level. «I have noticed the same tendency, and sometimes the worms leave the water without being agitated. If they are not forced back into it, they sometimes remain out long enough to die from desiccation: I had to check some culture dishes once or twice a week to find such strays before they died.

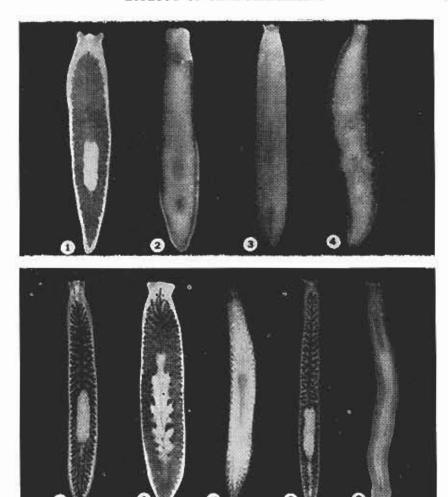
Small, slow moving trickles of water in caves are frequently occupied by S. percoeca and the common surface planarians P. morgani (Fig. 7) and P. gracilis (Fig. 6). Streams of medium to large size are more often occupied by M. glandulosa (Fig. 4), P. gracilis and the species of subgenus Speophila I have observed: S. pricei (Fig. 2), buchanani, S. hubrichti, and S. weingartneri. However, this habitat separation is by no means absolute. For instance, S. percoeca is occasionally found in streams, and the speophila species are sometimes in quiet pools. It is not known to what extent various species occupy interstitial habitats, but P. gracilis and P. morgani are common inhabitants of springs in some areas, and Speophila species have been found in a few springs.

Regardless of habitat, planarians may sometimes be seen in the open, but more often they are found under rocks. Buchanan (1936) suggested that it is "probable that the flatworms are located on the nether side of rocks because they are deposited there by water currents and because the same currents deposit under the rocks the materials which furnish their subsistence". I have never observed their showing any preference for the nether sides of rocks, nor is there any indication the worms are often carried downstream by currents. Even surface planarians can crawl about on the surface of rocks in very strong currents because the force of the current approaches zero very near the substrate (Macan 1961).

It is not unusual for two or more species to live in the same microhabitat in a cave. Especially noteworthy is the stream in Blowhole Cave. Pendleton County, West Virginia, where many specimens of *Macrocotyla hoffmasteri* and *P. Morgani* were found along with one of *S. percoeca* and two of the alloeocoels *Geocentrophora cavernicola* (Fig. 9). This slow moving stream was particularly high in organic debris (Carpenter, 1970).

Although the stream in Blowhole Cave did not seem to be heavily polluted, other caves that are definitely polluted (by many human standards) sometimes contain large populations of planarians. The thousands of worms I saw in Bat Cave, Adair County, Oklahoma, were obviously not affected adversely by the large deposits of bat guano. Holsinger (1966) reported the effects of human organic pollution on the invertebrate fauna in Banners Corner Cave, Russell County, Virginia. In my visit to this cave on 14 July 1969, these effects were still noticeable. An extremely large population of P. gracilis was found in the pool fed by the polluted water; the large population of worms was probably related to the great number of tubificid worms also inhabiting the pool. No S. pricei were found in the polluted pool, but two specimens were found in unpolluted rimstone pools in another part of the cave. Since I have found S. pricei and P. gracilis cohabitating in other caves, the absence of the former in the polluted pool suggests a low tolerance to human organic pollution. This is substantiated by observations in Mill Creek Cave near Nashville, Tennessee; McRitchie (1959) reported that Speophila were found in this cave in 1953, but when I visited the cave on 17 July 1969, it was rather badly polluted and no worms could be found.

Water temperature in various planarian caves is extremely varied. For istance, the water in Devil's Hole, Nye County, Nevada, where Dugesia diabolis lives is about 35°C (Halliday, 1935); in Ezell's Cave, Hays County, Texas, where S. mohri lives it is about 23°C (Hyman, 1939a); in most caves east of the Mississippi River it usually ranges around 10° to 14°C, but planarians have been found in a few places where the water was near 0°C. This



Figs, 1.9

1. Live Sphalloplana (Sphalloplana) percoeca from Mammoth Cave, Edmonson, County, Kentucky, with food (blood) in intestine. 2. Live Sphalloplana (Speophila) pricei from Cathedral Cave, Edmonson County, Kentucky. 3. Live Sphalloplana (Polypharyngea) mohri from Ezell's Cave, Hays County, Texas. 4. Live Macrocotyla glandulosa from stream by Connor's Cave, Boone County, Missouri. 5. Live Dendrocoelopsis americana from Bat Cave, Adair County, Oklahoma, with food (blood) in intestine. 6. Live depigmented Phagocata gracilis from Banners Corner Cave, Russell County, Virginia, with food (blood) in intestine. 7. Live Phagocata morgani from Flatworm Cave, Jackson County, Alabama, 8. Live Phagocata bursaperforata from Eudy Cave, Marshall County, Alabama, with food (blood) in intestine. 9. Live Geocentrophora cavernicola, a cave alloeocoel (not a planarian) from Blowhole Cave, Pendleton County, West Virginia.

does not mean that most cave planarians are tolerant of wide ranges in temperature. Those found in relatively warm water are usually tolerant to cold temperatures as well, but worms normally living in cold water are seldom tolerant to warm temperatures. Buchanan (1936) kept two *S. percoeca* at 24°C for 3 hours without injurious effect. Although I did not perform extensive experiments, I found that some species (especially stream dwellers such as *S. pricei*) cannot live very long at temperatures much above 14°C. Worms sent through the mail died in less than 48 hours if the temperature was not kept low by the use of a vacuum bottle.

Although cave planarians (including S. percoeca) are sometimes found in the twilight zone of caves and some species are found in springs, their tolerance to sunlight is low. Both Buchanan (1936) and McRitchie (1959) noted that a brief exposure to strong sunlight resulted in writhing and eventually in death and disintegration of species of Sphalloplana.

Food

Although cave planarians often will not feed as readily as many surface species and they frequently reject commonly used planarian food such as liver, they will sometimes feed on a variety of foods in the laboratory. For convenience, I usually gave them dried blood, but other foods taken include Trichoptera larvae and pupae, black fly (Simulium) larvae, adult house flies, juvenile scorpions, earthworms, crickets, raw beef, hot dogs, isopods, and amphipods. Crayfish and marine shrimp are reported as good food sources by Kenk (1977). Cave planarians are probably not very selective in their choice of food in caves, where the variety of food available is usually limited by the environment. Only rarely have I observed cave planarians feeding in caves except for times I used bait to attract them. At the bottom of the 40 m Graham Pit, Jackson County, Alabama, I found hundreds of S. percoeca in a pool about 1.8 m in diameter; most of them had red, gray, or black food particles in the gut; 10 were found feeding on a large June beetle. No other living animals such as isopods or amphipods were seen in the pool, so there is no doubt that the large population of worms was supported by animals that accidentally fell into the pit. The area surrounding the pool had many live salamanders, millipedes, and insects that survived the fall but probably eventually would die in the pool. In other caves where accidentals do not contribute significantly to the diet of planarians, terrestrial cave animals may be the main source of food. Mitchell (1968) reported seeing a Texas cave worm (S. mohri) feeding on a cave

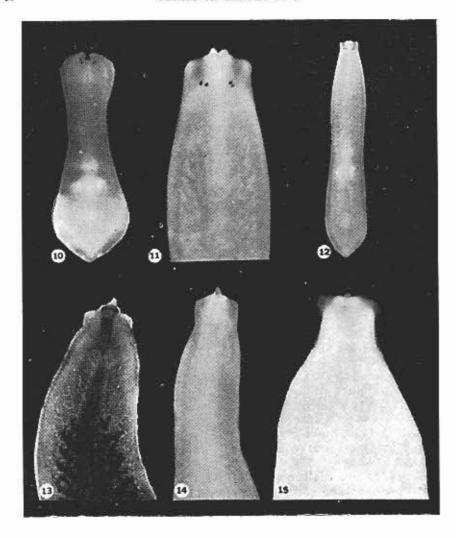
cricket of the genus Ceuthophilus. I observed P. morgani feeding on a cave millipede in Mauldin Cave, Powell County, Kentucky; and in Sauta Cave, Jackson County, Alabama, I found several dead millipedes in pools containing S. percoeca.

In most caves aquatic isopods and amphipods live together with and probably contribute to the diet of the worms. Amphipods and isopods that I crushed were eaten by S. percoeca and S. pricei, and Mitchell (1968) reported seeing a Texas cave worm feeding on the amphipod Stygonectes russelli. However, I maintained isopods and amphipods alive in culture dishes with S. percoeca and S. pricei for several months without signs of predation. Therefore, it appears that only sick, dead, or very young crustaceans are eaten by planarians. If this were not true, where both the worms and crustaceans are confined to a small pool, all the prey would soon be eaten by the predator, which would then die of starvation. It is a good general rule that part of the prey population must be immune to predation in order for both predator and prey to survive.

It is peculiar that while most surface planarians gradually become very small if they are starved for several weeks, I have maintained some starved Sphalloplana in cultures for several months without their losing any weight; occasionally, they have even become sexually mature during these periods. This indicates that either their metabolic rates are extremely low or, perhaps more likely, that they feed on microscopic organisms or organic debris in the cultures. This possibility is substantiated by the fact that worm populations are significantly higher in areas of caves where bat or cricket guano falls into the water. Levengood (1940) observed that D. americana «appeared to be feeding on bat feces which were abundant in the water there». Although it is possible that the worms feed only on guano-eating crustaceans, the distinct possibility remains that they feed directly on the guano. Furthemore, when I fed planarians crushed cruntaceans in the laboratory, their pharynges could be seen ingesting the intestinal contents of the prey, which presumably contained mostly organic debris.

Function of anterior adhesive organs.

Many cave planarians have an anterior adhesive organ of considerable taxonomic value, but there have been few observations on the use of this organ. In American cave planarians there appear to be two basic types: one found only in D. americana, the other in the genera Sphalloplana, Macrocotyla, and probably Kenkia.



Figs. 10 . 15

10. Live Procotyla fluviatilis in leech-like movement, x 7, 11. Live Procotyla fluviatilis with adhesive organ protruded in preparation for grasping prey, x 15, 12. Live P. fluviatilis with adhesive organ retracted; note similarity to Fig. 5 of Dendrocoelopsis americana, x7, 13. Preserved Sphalloplana percoeca from Sauta Cave, Jackson County, Alabama; adhesive organ protruded, x 15, 14. Live Macrocotyla lawisi from Tom Moore Cave, Perry County, Missouri; adhesive organ protruded, x 15, 15. Live Sphalloplana mohri from Ezell's Cave, Hays County, Texas (from a trasparency lent by R. W. Mitchell); adhesive organ protruded slightly (this is the normal position during regular gliding movements, x 7.

The adhesive organ of *D. americana* is similar to, but smaller than, that of the relatively common surface planarian *Procotyla fluviatilis* (Figs. 10-12) and some other dendrocoelids. There have been no significant studies on the *D. americana* adhesive organ except Hyman's descriptions of the species (1939a, 1939b), and the only significant study of the *P. fluviatilis* adhesive organ (or grasping organ) was made by Redfield (1915). This type of adhesive organ is shaped somewhat like a pair of lips that can grasp food and other objects as described by Redfield (1915) and Chandler (1968). *Dendrocoelopsis americana* also appears to grasp its prey with the adhesive organ while trying to subdue it. However, *D. americana* is surely less effective in food capture than is *P. fluviatilis* because it has a much smaller and apparently weaker adhesive organ.

Redfield (1915) and Chandler (1968) performed experiments on *P. fluviatilis* that indicated the adhesive organ contains chemoreceptors and mechanoreceptors that help find food. In addition, both *D. americana* and *P. fluviatilis* use the adhesive organ for rapid forward movements similar to those of leeches or inchworms. This leech-like movement can be observed in nearly all freshwater planarians regardless of the normal presence or absence of an adhesive organ. The only exception I am aware of is *Planaria occulta*, which Kenk (1969) said displays no such movement.

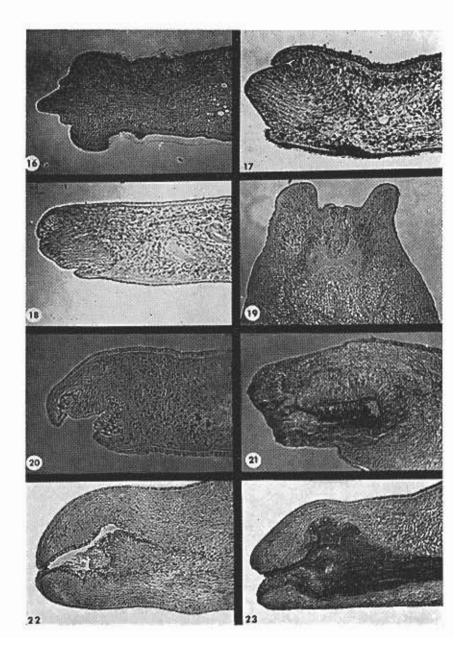
The adhesive organ of Sphalloplana and Macrocotyla differs considerably from the Dendrocoelopsis and Procotyla type. Instead of having a pair of lip-like structures that can grasp prey, this type has a single tongue-like structure (Figs. 13-27) protruding through a relatively small opening at the anterior end. In S. percoeca (Figs. 19-20) and S. mohri (Fig. 15) the tip of the relatively small adhesive organ is normally held near the opening; in members of the subgenus Speophila (e.g., S. pricei) and in Macrocotyla the adhesive organ is larger and is either held near the opening or, more frequently, it is rather deeply invaginated like the finger of a glove turned partially inside out (Figs. 22-23). In all cases the organ can be rapidly extended considerably past the anterior margin of the head where it is employed in a variety of ways. Its most obvious function is in the leech-like movements already described where it is extremely quick and efficient. Mitchell (1968) suggested that; *this type movement is probably most often used as an escape action removing the animal quickly from the mechanoreceptive and chemoreceptive range of predators». I preserved several cave planarians by the rapid freeze technique not only with the adhesive organ in a normal position but also in various phases of the leech-like movement (Figs. 13, 18, 24, 25, 26, 27).

Hyman (1937) suggested that the adhesive organ of Sphatloplana is probably used in food capture, but most investigators who have examined live cave planarians have had no success in feeding them (e.g., Buchanan, 1936; Mitchell, 1968), As mentioned, most of the time I fed my cave planarian cultures on dried blood because of convenience. However, in order to examine the possible use of the adhesive organ in food capture, I fed some planarians live food. On one occasion a live Trichoptera pupa was placed in a culture dish containing two S. percoeca from Mammoth Cave, while I watched through a dissecting microscope. Both planarians approached the pupa, and while still a body length away, they started moving their adhesive organs in and out rather rapidly. When they were only about 2 mm away, they lunged at the pupa with their adhesive organs fully extended. They then crawled over the pupa for a few seconds before they began the feeding process, which lasted about 30 minutes. Mitchell (1974) also observed the use of the adhesive organ in food capture in S. mohri; Sphalloplana pricei and Macrocotyla do not eat as well in culture as S. percoeca, and their use of the adhesive organ in food capture has not been observed, but it is probably employed in a similar manner. Since the adhesive organ of Kenkia rhynchida (Fig. 26) is very similar morphologically to that of S. pricei and Macrocotyla, its function is also probably similar, but only the examination of live specimens will substantiate this.

There are also some indications that the adhesive organ of Sphalloplana is used as a stimulus receptor. The rapid movement of the organ in S. percoeca just before lunging onto the Trichoptera pupa may have been to increase reception of stimuli. The stimuli in this case were probably chemical in nature since the prey was inactive. On several occasions I noticed S. pricei stop its forward motion, raise its head above the substrate and protrude the adhesive organ for several seconds. It is possible that the worm was intending to catch prey swimming through the water, but since there was no such suitable food in the culture dish, it seems more likely that it was using the organ

as a stimulus receptor.

I observed one other unusual use of the adhesive organ. On one occasion *S. pricei* was seen to use it as a weapon by rapidly striking it at the small paint brush I was using to remove it from the culture dish. On still another occasion I introduced live ostracods into a culture of *S. pricei*; the worms would not feed on them, but one was observed to strike rapidly at a nearby ostracod as an apparent defense movement. Although I know of no other records of the adhesive organ of planarians being used as a weapon, some species in other taxa are known to have similar structures with this function. One example is the pro-



Figs. 16-23. All figs., x 30.

16. Frontal section of S. percoeca from Sauta Cave, Jackson County, Alabama; adhesive organ protruded. 17. Sagittal section of S. percoeca from Sauta Cave, Jackson County, Alabama; adhesive organ protruded, 18. Sagittal section of S. percoeca from Clemons Cave, Jackson County, Kentucky; adhesive organ slightly protruded. 19. Frontal section of S. percoeca from John Rogers Cave, Jackson County, Kentucky; adhesive organ retracted. 20. Sagittal section of S. percoeca from Clemons Cave, Jackson County, Kentucky; adhesive organ retracted. 21. Sagittal section of S. mohri (paratype A of Mitchell's S. reddelli); adhesive organ retracted. 22. Sagittal section of Macrocotyla glandulosa from stream at Connor's Cave, Boone County, Missouri; adhesive organ retracted. 23. Sagittal section of S. pricei from Stokes Lane Spring, Nashville, Tennessee; adhesive organ retracted.

rnynchid alloeocoel *Prorhyncus applanatus*, which at the anterior end has a pharynx used as an organ of defense (Kepner and Taliafero, 1916).

It is obvious that the adhesive organ of cave planarians has a variety of uses. However, it is interesting to speculate why the organ should be developed to a higher degree in cave planarians than in most surface worms. It is probable that planarians might use the organ to grasp the substrate to avoid being washed out of the cave even though most planarians need the additional aid of the organ only during heavy precipitation when the water is not only very swift but also is loaded with silt so that grasping is made more difficult. Surface planarians, on the other hand, probably would not have so much difficulty holding on during these times because they can easily wrap around bits of algae. moss, or vascular plants common in surface streams but absent in caves. There would be strong natural selection pressures on cave planarians to develop methods of staving firmly attached to the substrate because those not doing so could be washed out of the cave and into surface streams where survival would be more difficult.

Predators.

There have been few observations regarding predation on caye planarians, but fishes, salamanders, and crayfishes appear to be the only potential predators since they are the only large, aquatic cohabitants with planarians. It is also noteworthy that I observed no fishes, salamanders, or crayfishes in pools of water containing cave planarians although they do occasionally occur in the same streams. No predation of cave fishes on planarians has been recorded. Only one observation of predation by salamanders is known: J. E. Cooper (personal communication) reported seeing the spring salamander Gyranophilous porphyriticus feeding on P. gracilis in Banners Corner Cave, Russell County, Virginia. The only observation regarding crayfish predation has been in the laboratory. One day I placed three P. gracilis in a culture dish with a cave crayfish, Orconectes pellucidus, and the next day the worms were gone. Some surface planarians are highly cannibalistic, but cannibalism has not been observed in cave planarians.

Parasites.

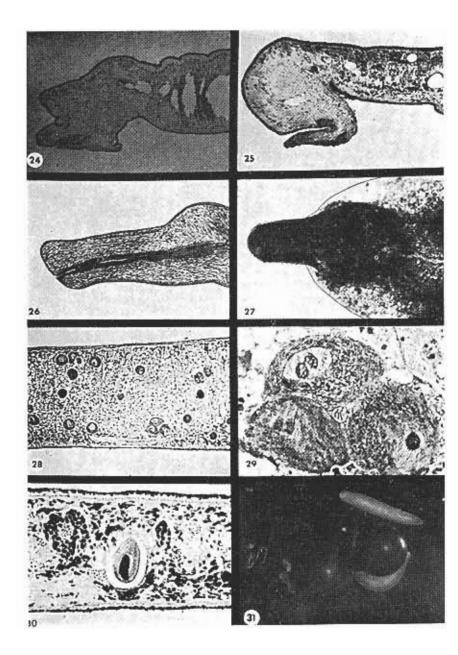
Kenk (1969) noted that all specimens of Planaria occulta (identified from a well in Virginia) he examined were heavily in-

fested with the holotrichous ciliate Sieboldiellina planariarum; these ciliates were found in the intestine, pharyngeal pouch, and copulatory bursa. In one of my specimens of S. percoeca from Hurt Cave, Wayne County, Kentucky, I found an unidentified large ciliate (Fig. 30) in the intestine but it did not appear similar to Sieboldiellina planariarum. Several specimens of S. percoeca from John Rogers Cave, Jackson County, Kentucky, were heavily infested by parasites in the mesenchyme (Figs. 28-29); and these closely resembled Holmquist's (1967) photographs of gregarines (Lankesteria or Monocystella) found in the surface planarian Dendrocoelopsis piriformis from Alaska.

Reproduction.

One of the major problems associated with planarian taxonomy is the fact that sexually mature specimens are usually needed to make positive identification. Fortunately, there is only one cave planarian, the troglophile *P. morgani*, that reproduces primarily asexually. During asexual reproduction the animals simply pull apart in the area posterior to the pharynx, so many specimens are small and they often have a short post-pharyngeal region. If these animals are fed well in the laboratory, they will often become sexually mature (Kenk, *in litt.*).

Other cave species examined have a fairly high percentage of mature specimens in most populations. The appearance of sexually mature specimens does not appear to be seasonal as in some surface species. Kenk (1969) stated that in Planaria occulta «the fact that sexually mature animals were collected in March, April, and November makes it probable that their sexual maturity is not of a seasonal nature». McRitchie (1959) indicated that in his collections of Spalloplana from Stokes Lane Spring in Nashville, Tennessee, «the animals have been abundant during the whole period from November until June except for a small decrease in number during December. During April and May, numerous specimens were found. I have found mature individuals of S. percoeca and S. pricei at all times of the year, although there appears to be a slightly greater incidence of mature specimens in winter. Some populations are significantly higher in the winter, but this is probably related to the fact that more suitable pools are available during the wet season. McRitchie (1959) found that «there is apparently no correlation between size and sexual maturity, although immature animals usually ranged in the smaller dimensions». In some respects I agree with this observation since a few individuals less than 6 mm long show signs of maturity and some larger



Figs. 24-31.

24. Sagittal section of *S. price*i from Stokes Lane Spring, Nashville, Tennessee; adhesive organ attached to substrate in early part of leech-like movement, x 30. 25. Sagittal section of *S. price*i from Stokes Lane Spring, Nashville, Tennessee; adhesive organ attached to substrate in late part of leech-like movement, x 30. 26. Sagittal section of *Kenkia rhynchida* adhesive organ retracted, after Hyman (1937b), x 30. 27. *S. price*i (whole mount cotype of Hyman's type series of *S. price*i from Refton Cave, Lancaster County, Pennsylvania); adhesive organ and surrounding tissue in form of snout, x 30. 28. Numerous gregarine parasites in mesenchyme of *S. percoeca* from John Rogers Cave, Jackson County, Kentucky, x 30. 29. Enlargement of Fig. 28, x 60. 30. Ciliated parasite in intestine of *S. percoeca* from Hurt Cave, Wayne County, Kentucky, x 30. 31, Young *S. price*i with broken cocoons (left) and unbroken cocoons (center) from Stokes Lane Spring, Nashville, Tennessee, x 15.

ones do not. However, there is undoubtedly a tendency for the largest worms to have the highest probability of maturity. The lack of maturity in some large individuals may be related to

parasitism or poor food availability.

There is some indication that once the species of Sphalloplana become mature, they will stay that way. I observed about 10 worms in a small pool in John Rogers Cave, Jackson County, Kentucky, over several consecutive months during which time the largest individuals staved mature and the smallest ones remained immature. No small juveniles were ever observed in this pool, nor did the smallest individuals appear to become larger: however, detailed notes on each specimen were not kept. I starved some mature individuals in the laboratory for several months, and at least some of these did not return to an immature state. However, in D. americana some individuals I observed became partly (and perhaps entirely) mature for a few weeks during early summer and then returned to the immature state during late summer. It is not known whether these changes are related to the irregular feeding schedule or whether they indicate a natural cycle.

No records have been published on the cocoons or young of the American kenkiid planarians, so my few observations on these stages of the life cycle are of some interest. On 26 May 1969 I found one cocoon in a culture containing only S. percoeca from Mammoth Cave; the cocoon was placed in a separate dish. It was spherical, about 1 mm in diameter, and not attached by a stalk as are cocoons of Dugesia. On 30 August 1969 I found two young worms about 2 mm long on the side of the culture dish above water level. One worm was dead, but the other lived about 9 days. The exact dates of cocoon deposition and hatching are not known since cultures were checked only about once a week, but I assume that development took about 3 months. Another cocoon of S. percoeca was collected in John Rogers Cave, Jackson County, Kentucky, on 7 March 1977. By 28 April 1977 three young had hatched. Each worm was about 5 mm long and continued to remain healthy for over a year even though I never fed them.

On 13 August 1969 I collected several spherical, unstalked cocoons about 1 mm in diameter from Stokes Lane Spring in Nashville, Tennessee, along with many large S. pricei. On 14 September 1969 four of these were broken accidentally while they were being photographed. About 5 to 10 young S. pricei were in each cocoon, but all these died in a few hours, presumably because they were not fully developed. On 27 October 1969 two of the unbroken cocoons were found to be broken open and about 20 young were in the culture dish (Fig. 31). By 10 November 1969 another cocoon yielded 17 young. Therefore, about

2^{1/2} to 3 months elapsed between the collection of the cocoons and the hatching of the young. Since the cocoons had probably been deposited several days before they were collected, 3 months again seems to be a reasonable estimate for development time. Kenk (1977) reported that a worm from his culture from this same locality deposited a cocoon in June that hatched in about 12 weeks and yielded nine young.

It is interesting that cocoons of the surface planarian Procotyla fluviatilis (not collected from caves) I have kept at cave temperature (about 13°C) hatched in 19 to 23 days and contained one to seven young. The few references to planarian development in the literature indicate that most surface planarians develop in less than a month, but the data are difficult to compare because of the various temperatures at which different investigators have maintained cultures. Kenk (1973) reported that three cocoons of D. americana maintained at 14°C hatched in about 6 weeks and vielded one, two, and three young. Gourbault (1969) compiled a table of most of the available information on this subject; the shortest development time listed for surface species is 10 to 20 days (for Dugesia tugubris) and the longest is 3 months (for Dendrocoleum album). However, the cavernicolous species mentioned by Gourbault develop in 2 to 6 months. Therefore, it is apparent that the development of cave planarians, generally takes considerably longer than for surface forms.

I collected unbroken but apparently sterile cocoons in Blowhole Cave, Pendleton County, West Virginia, and in the stream outside Connors Cave, Boone Couny, Missouri. None of these yielded any young. The spherical, unstalked cocoon collected near Connors Cave presumably came from *M. glandulosa*, because it is the only planarian known from that area that is capable of producing a cocoon this large (2 mm in diameter).

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RESUME

Des observations ont été faites sur la biologie de plusieurs espèces de planaires cavernicales (la plupart de la famille des Kenkiidae) récoltées vivantes dans plus de 50 grottes réparties dans 14 Etats. La plupart de ces espèces ont été maintenues en alevage au laboratoire, à la température de 12°C±3°C. Leur nourriture a été très variable, L'organe adhésif antérieur assure les fonctions suivantes: capture des proies, locomotion, défense contre les prédateurs et probablement chemoréception, mécanoréception, ainsi que cramponnement lorque l'animal est dans un fort courant. Les prédateurs sont probablement des poissons, des écrevisses et des salamandres. Des Sporozoaires et des Ciliés parasites ont parfois été trouvés. Les cocons se rencontrent en hiver, au printemps et en été; ils éclosent au bout de 3 mois environ et contiennent 2 à 17 jeunes.

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