Ethology, **74**, 133—145 (1987)

ISSN 0179-1613

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The Comparative Ethology of Courtship in Salamandrid Salamanders.
1. *Salamandra* and *Chioglossa*

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With 4 figures

Received: February 19, 1986
Accepted: May 2, 1986 (G. M. Burghardt)

Abstract

This paper describes for the first time spermatophore deposition and sperm transfer in the salamander genus *Chioglossa*. As in *Salamandra*, the *Chioglossa* male holds the female in ventral amplexus and deposits his spermatophore under the female's vent. The female drops down upon the spermatophore to accomplish sperm transfer. This mode of sperm transfer is unique to the salamandrid genera *Salamandra* and *Chioglossa* and is at least 26 million years old. These two genera also share a number of derived features of preliminary courtship.

Introduction

This report is the first in a series that has the aims of surveying the courtship behavior of the 16 extant salamandrid genera and making an evolutionary synthesis. The Salamandridae are of exceptional ethological interest because of the antiquity of the constituent genera and their diversification in modes of sperm transfer. The fossil record indicates that several of the modern genera were differentiated by the Eocene (~ 40 mya) and perhaps much earlier (ESTES 1981). Sperm transfer modes are evolutionarily conservative in salamanders (ARNOLD 1977). In proteids and in the most advanced families (ambystomatids, plethodontids, and salamandrids), the male deposits his spermatophore in front of the female and leads her over it. Some salamandrids use this mode, but in addition, three other modes are employed by different genera: deposition while the pair pivots about a fixed point, deposition under the female's vent, and direct transfer via cloacal apposition. A major goal of the present series is to deduce the

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transformations by which these behaviors were derived from one another. This first paper focuses on two closely related genera, *Salamandra* and *Chioglossa,* that deposit the spermatophore under the female's vent.

There are two species in the genus *Salamandra. Salamandra salamandra* ranges throughout Europe, east to Kurdistan and south to Morocco and Israel with striking geographic variation in coloration (EISELT 1957; THORN 1968). Its conspicuous color pattern is undoubtedly aposematic and warns predators of neurotoxic skin secretions. *S. salamandra* is a woodland species that retreats into damp underground shelters and is active on the surface during or after rainfall (JOLY 1968; DEGANI & MENDELSSOHN 1982). Most populations are ovoviviparous, with females giving birth to aquatic larvae, but in some montane populations females give birth to transformed (or nearly transformed) young (JOLY 1968; FACHBACH 1969). *Salamandra atra* is restricted to the Alps of central Europe and the mountains of Yugoslavia and Albania and characteristically inhabits alpine meadows (THORN 1968). The mating season lasts from May to August and, as in *S. salamandra,* courtship is terrestrial (HÄFELI 1971). Gestation lasts two or three years, depending on altitude, and the female gives birth to two metamorphs (HÄFELI 1971).

Chioglossa is a monotypic genus restricted to the mountains of Portugal and northwestern Spain. Adults are semi-aquatic to terrestrial and characteristically inhabit stream borders (GOUX 1957; BUSACK 1976). *Chioglossa lusitanica* is an elongate, agile species that may drop from rock crevices to escape in the stream below. Its behavior and habitat are reminiscent of the North American plethodontid *Eurycea longicauda.* Females lay their eggs underwater, attaching them to the undersides of rocks (GONÇALVES 1963).

In the past two decades three reports of *Salamandra* courtship have been published, each based on extensive observation and illustrated with photographs (HIMSTEDT 1965; JOLY 1966; HÄFELI 1971). These papers correct the numerous inaccuracies and misinterpretations that have plagued the literature on *Salamandra* sexual ethology. In contrast, courtship behavior in *Chioglossa* has been reported on only one previous occasion. THORN (1966) gave an excellent, detailed account of a 20-min courtship fragment, but unfortunately that fragment did not include spermatophore deposition or sperm transfer. The aim of the present paper is to report new observations on both genera and synthesize the existing information so that behavioral homologies can be detected and the phylogenetic relationships of *Chioglossa* and *Salamandra* to other salamandrids can be perceived.

Materials and Methods

Salamandra salamandra were obtained from three localities: Krefeld, Federal Republic of Germany (10 specimens); Rummelburger Forst, Unterharz, German Democratic Republic (three specimens); near Cardoso, Lucca Prov., Italy (13 specimens). No differences in courtship were noted between German and Italian specimens. The German specimens were obtained from correspondents and animal dealers in 1969. *Chioglossa lusitanica* (6 specimens) were collected near Salas, Oviedo Prov., Spain.

Salamandra salamandra were individually maintained in plastic shoe boxes (15 × 30 × 9 cm high) with a damp paper towel substrate at 15—20 °C on a natural (Chicago) photoperiod and fed earthworms (*Lumbricus terrestris*), crickets (*Acheta domestica*), fly larvae (*Sarcophaga bullata*) and moth larvae (*Galleria mellonella*). *Chioglossa lusitanica* were communally housed in a vivarium (90 × 30 × 40 cm) in which water flowed down a rough, slate wall with numerous retreats. A flat slate substrate (60 × 20 cm) at the base of the wall was the site of courtship activity. This platform rested over a water reservoir (10 cm deep) and in back of a water channel 4 cm wide and 30 cm long. The vivarium was maintained at 15—17 °C on a natural (Chicago) photoperiod. The *Chioglossa* were fed *Drosophila* (larvae and adults), annelids (*Enchytraeus albidus*) and *Galleria* larvae.

Sex of *Salamandra* was established by the conspicuous dimorphism in cloacal walls and relative body mass. Sex of *Chioglossa* was established by cloacal examination of anesthesized animals (males have cloacal papillae, females have cloacal folds). Individual identity of courting *Chioglossa* was established by individual differences in coloration pattern.

Salamandra salamandra courtship encounters were staged by placing a pair together in a clear plastic box, normally used for maintenance, or in a larger terrarium. Observations were made at night under dim light. *Chioglossa* courtship occurred spontaneously, always at night, and was observed under dim light or with an infra-red viewer (Find-R-Scope). Courtship sequences were recorded by still and cine photography (16 mm) and by time-lapse video.

Approximately 15 *Salamandra salamandra* courtships were observed, including 25 spermatophore depositions. *Chioglossa* courtship was observed on 7 evenings between 5 Sep. and 10 Oct. 1984, after the animals had been in captivity for 18 months. The courtship sequences lasted a total of 164 min. Four of the sequences included capture attempts; amplexus occurred in five sequences and spermatophore deposition in one sequence.

I. Ethogram

Actions performed by *Salamandra* are labeled S and actions performed by *Chioglossa* are labeled C.

Pursuit (S, C) — The male runs after a moving female, periodically pausing.

Nudging (S, C) — The male pushes against the female's body with his snout bent downward, rubbing his nares against her (Fig. 1 in HIMSTEDT 1965).

Dorsal clasping (amplexus) (S) — The male embraces the female's dorsum, holding with his forelimbs onto her neck, or her body (just behind her forelimbs) or anywhere along her trunk (Fig. 2 in JOLY 1966).

Chin-rubbing (S) — The male rhythmically swings his head back and forth with his head pressed downward, so that his chin rubs the female's dorsum. The action is commonly performed by *S. atra* during dorsal amplexus (Fig. 2 in HÄFELI 1971).

Ventral capture (S, C) — The male pushes his head under the female's body and crawls anteriorly under her body towards her forelimbs (Fig. 1 a—c and Fig. 3 in JOLY 1966; Fig. 1 in HÄFELI 1971). Just as his forelimbs are about to contact hers, he simultaneously raises both of his forelimbs, swings them upwards and forward (Fig. 1 d) and clasps both of the female's forelimbs from behind (Fig. 1 e). Occasionally, the *Salamandra* male turns posteriad after pushing under the female and captures the female's hindlimbs.

Ventral clasping (amplexus) (S, C) — The male's body lies under the female's body as he faces in the same direction and clasps the female. He holds his proximal forelimbs on top of her proximal forelimbs and presses his forefeet against the anterior surface of her distal forelimbs (Fig. 4 in HIMSTEDT 1965; Fig. 6 a in JOLY 1966). During ventral clasping the male performs the following actions:

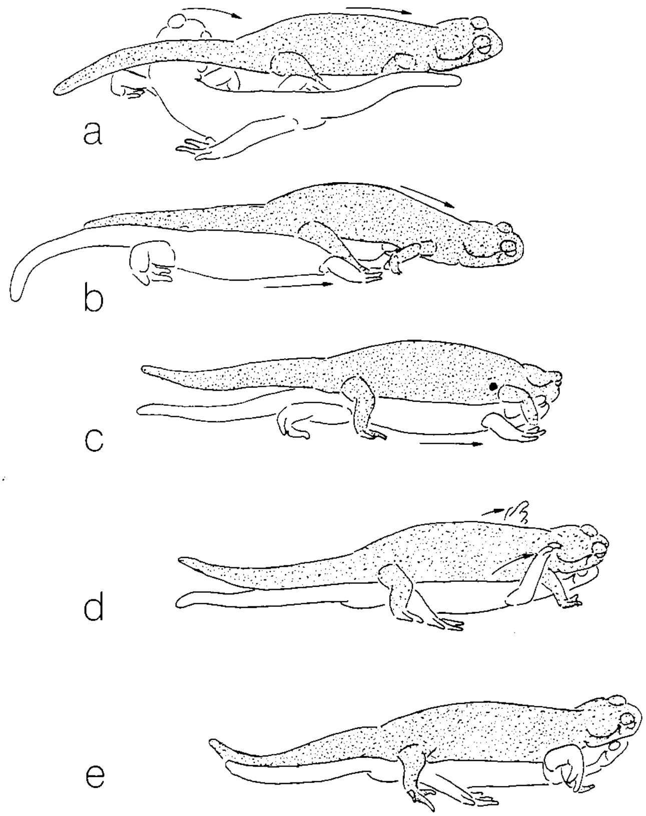

Fig. 1: Ventral capture in *Salamandra salamandra* (from a sequence of photographs). a) The male has shoved his head under the female's tail and is now turning his head towards the female (stippled) as she moves away from him. b) The male slides forward under the female as she continues to move forward. c) The male continues forward under the stationary female. d) The male rapidly swings both forelimbs upward. e) The male clasps the female's forelimbs with his forelimbs, holding her in ventral amplexus

Body-shifting (S, C) — The male slowly undulates his vertebral column while shifting his sacrum and tail from side to side and so rubs his entire dorsum on the female's venter. The sacral action is augmented by alternating extensions of the hindlimbs, which may either shift the male's body laterally or propel the pair forward. In addition, one hindlimb and then the other is raised and lowered in an alternating sequence, with the hindfeet slapping the substrate (Fig. 2a).

Shuddering (C) — The male rapidly turns his head and the anterior half of his body to one side and then back, sweeping through an arc of about 70°, and pulling the female along with him. The complete action lasts only about 0.1 s.

Twisting (C) — The amplectic pair revolves a few to several times about their long axis, eventually returning to the original male-under-female position, but with their tails intertwined.

Tail-undulation (S, C) — The male propagates slow waves of lateral undulation while holding his sacrum and vent stationary (Fig. 2b). His vent contacts the substrate and his tail is level. The waves move posteriad.

Head-swinging (S, C) — The male laterally swings his head back and forth, rubbing the dorsum of his head on the female's chin (Fig. 2c). The male raises his head at a 30—45° angle during head-swinging (Fig. 1 in THORN 1966). The tail-undulation may accompany head-swinging or the tail may be motionless.

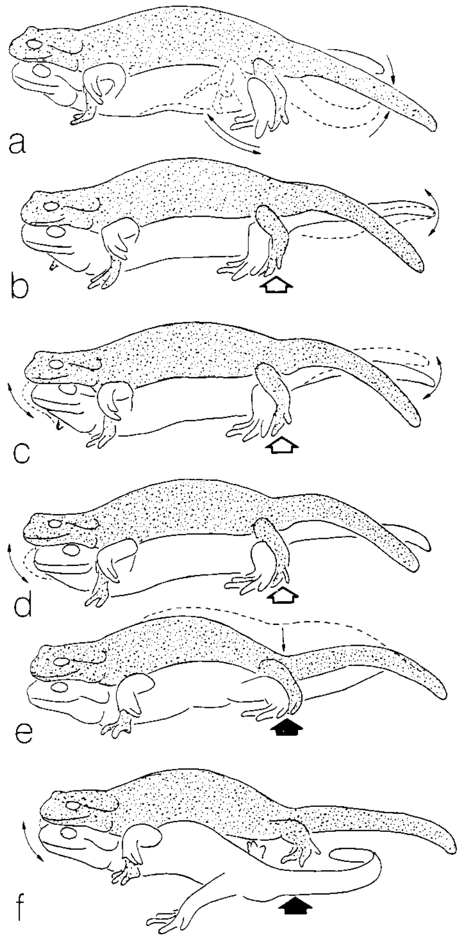

Fig. 2: Spermatophore deposition and sperm transfer in *Salamandra salamandra* (from a cine record of one continuous sequence lasting 128 s). a) The male holds the female (stippled) in ventral amplexus while body-shifting (0 s). b) The male begins spermatophore deposition while undulating his tail and holding his feet stationary (79 s). c) The male head-swings while continuing tail undulation (89 s). d) The male continues head-swinging but with tail stationary (110 s). e) The male has completed the first phase of sacral displacement. The female has dropped down towards the spermatophore (located above the solid arrowhead) (118 s). f) The male has completed the second phase of sacral displacement and performs head-swinging. The female rests with the spermatophore inside her cloaca (128 s)

Spermatophore deposition (S, C) — The spermatophore is deposited under the female's vent during ventral amplexus (Fig. 2). The male holds his hindlimbs stationary and presses his vent against the substrate (Fig. 3a—b). He undulates his tail and then begins head-swinging. At the onset of head-swinging, the lateral swings have a jerky appearance, for the male swings his head in one direction with two or more short strokes before reversing direction. As head-swinging proceeds, however, the strokes become continuous and the action becomes a smooth back-and-forth movement. The head-swings gradually increase in amplitude until finally the male swings his head through an arc of about 90°. He then ceases tail undulations while continuing head-swinging.

Sacral displacement (S, C) — In *Salamandra* this action usually follows spermatophore deposition, but in *Chioglossa* spermatophore deposition is not a prerequisite. The male moves his sacrum and tail laterally out from under the female's body while maintaining ventral clasping with his forelimbs. In both *Chioglossa* and *Salamandra,* the male pauses with his sacrum beside and almost in contact with the female's body (Figs. 2e and 3c). During this initial phase of sacral displacement the male ceases head-swinging. Next he pulls his sacrum and tail forward under the female's hindlimb and than flexes his sacrum laterally until it has swept a 45—90° arc from its original position under the female (Figs. 2f and 3d). The male holds this position with hindlimbs widely outstretched and immediately resumes head-swinging, all the while maintaining amplexus with his forelimbs (Fig. 7 in HIMSTEDT 1965; Fig. 6c in JOLY 1966).

II. Temporal Patterns

Salamandra salamandra: A sexually active male stands in an alert posture, with forelimbs extended and head raised (Fig. 1 in JOLY 1966). He rapidly pursues

Fig. 3: Spermatophore deposition and a failed sperm transfer attempt in *Salamandra salamandra.* a) Lateral view of a pair during spermatophore deposition (female above). The open arrowhead shows the position of the forming spermatophore. b) Dorsal view of a pair during spermatophore deposition. c) The male is just completing the first phase of sacral displacement. The spermatophore is visible just below the solid arrowhead. The female has fallen beside rather than on top of the spermatophore. d) The male has completed the second phase of sacral displacement. The female's vent still lies beside the spermatophore

a moving female. HIMSTEDT (1965) notes that pursuit is visually released, since the male will pursue various moving objects that approximate the size of a female. When the male reaches the female he nudges her, sometimes going partly astride her dorsum in the process (Fig. 1 in HIMSTEDT 1965). In some cases the male may clasp the female's dorsum with his forelimbs (JOLY 1966) while nudging her. Such dorsal clasping is relatively rare in *S. salamandra.* More often the male simply nudges the female while standing beside or astride her. Next the male attempts ventral capture.

Ventral capture attempts may be a prolonged affair if the female is nonreceptive. Such a female repeatedly flees when the male begins to crawl beneath her, aborting the capture and causing the male to revert to pursuit. Ventral capture is more likely to be successful when the female moves slowly or remains stationary. Once the male has engaged the female in ventral amplexus, he begins body-shifting.

Body-shifting is the most time-consuming activity in the amplectic sequence. Bouts of forward progress may alternate with stationary periods as the male continuously undulates and shifts beneath the female's body. JOLY (1966) notes that the female is an active participant during the body-shifting phase of amplexus, compensating with her hindlimbs for the male's shifting position. JOLY also found that very receptive females would head-swing in company with the male's head movements.

The onset of spermatophore deposition is marked by the cessation of body-shifting. Three distinct phases can be recognized. During the three phases of spermatophore deposition the female increasingly presses her vent against the male's tail base, so that the distal part of her tail arches slightly upwards (Fig. 5 in HIMSTEDT 1965). First, the male begins steady tail undulations, holding his vent stationary on the substrate; his head is motionless. In four cine records of spermatophore deposition the tail undulations occurred at an average rate of 1.01 undulations/s (± 0.20 S.D.). Second, he begins head-swinging while continuing tail undulations. Finally, he ceases tail undulation while continuing to swing his head. A sperm transfer attempt follows immediately. In the same sample of four spermatophore depositions, the rate of head-swinging gradually increased from 0.78 head-swings/s (± 0.19 S. D.) to a maximum rate of 1.41/s (± 0.23 S. D.) and then fell to 0.94/s (± 0.19 S.D.) just before sperm transfer.

Sperm transfer is accomplished during ventral clasping (Figs. 5—6 in HIMSTEDT 1965; Fig. 6 in JOLY 1966). During the first stage of sacral displacement, when the male lifts his vent off the spermatophore and moves his sacrum and tail to the side and so out from under the female, her vent drops partway towards the spermatophore. During the second stage, when the male draws his sacrum and tail forward under the female's femur without causing her to move her leg, the female may settle upon the spermatophore, inserting the entire structure in her cloaca. Sometimes the female drops down beside the spermatophore and may lift up and settle upon it, apparently orienting tactually to it. Remarkably, some spermatophores are missed entirely even though the female's vent is never more than 1 cm away.

While the female rests on the spermatophore, the male remains stationary with his sacrum at a 45—90° angle to the female's body. He commences head-swinging in this position (mean = 1.00 head-swings/s, S.D. = 0.15, N = 3 spermatophore depositions) and then ceases all head movement and holds his head tilted upward under the female's chin for a few to several minutes.

The male may now shift his sacrum back under the female and begin body shifting. Usually, however, the female twists free of the male and escapes or he releases her. In either case, the *Salamandra* male nearly always captures the female anew between successive spermatophore depositions. In my observations the male usually deposited three or four spermatophores in a courtship encounter.

Salamandra atra: The courtships of *S. atra* and *S. salamandra* are very similar both in behavioral elements and temporal patterning. The only difference that HÄFELI (1971) could detect, comparing his observations of *S. atra* with HIMSTEDT's (1965) account of *S. salamandra,* was in the frequency of occurrence, intensity and duration of dorsal clasping. The *S. atra* male invariably clasps the female's dorsum before sliding beneath her to begin ventral clasping. Chin-rubbing is more vigorous in *S. atra,* with the male clasping the female's neck and rhythmically rubbing his chin on the female's head with a pendulum-like, lateral movement of his head (Fig. 2 in HÄFELI 1971). Such chin-rubbing can persist for a half hour or more in *S. atra.* In contrast, although *S. salamandra* may employ all the same elements, chin-rubbing is not usually focused on the female's head as a throat-on-head rubbing action. Dorsal clasping is the exception rather than the rule in *S. salamandra,* and when it occurs it lasts only a few s.

HÄFELI (1971) mentions a second difference between the two species, implying that male *S. salamandra* use head-swinging only after spermatophore deposition. My observations show that the two species use head-swinging in the same three amplectic contexts: with body-shifting before spermatophore deposition, during spermatophore deposition and during sperm transfer attempts.

Chioglossa lusitanica: Courtship always occurred in the terrestrial portion of the vivarium. As in *Salamandra,* the sexually active male stands at an alert posture on extended forelimbs and rapidly pursues any moving salamander. Upon overtaking or reaching a female, the male nudges her briefly with his snout. The male was never observed to mount the female's dorsum. Instead, the male immediately attempted ventral capture. In two of the four capture attempts that were observed, the pursuing male moved towards the female's head, nudged her briefly and then shoved his head under her axilla. Ventral capture is identical to that in *Salamandra,* with the male pushing forward under the female's body, usually raising both arms just as he nears the female's head, but sometimes raising them in a more posterior position. When his up-raised forelimbs contact the female's forelimbs, he clamps them downward and holds the female in amplexus (Fig. 4).

Chioglossa and *Salamandra* share a number of amplectic elements and sequences. During the amplectic period that precedes spermatophore deposition, in both genera the male shifts his body and swings his upraised head under the female's chin. In *Chioglossa,* these actions are organized in bouts separated by

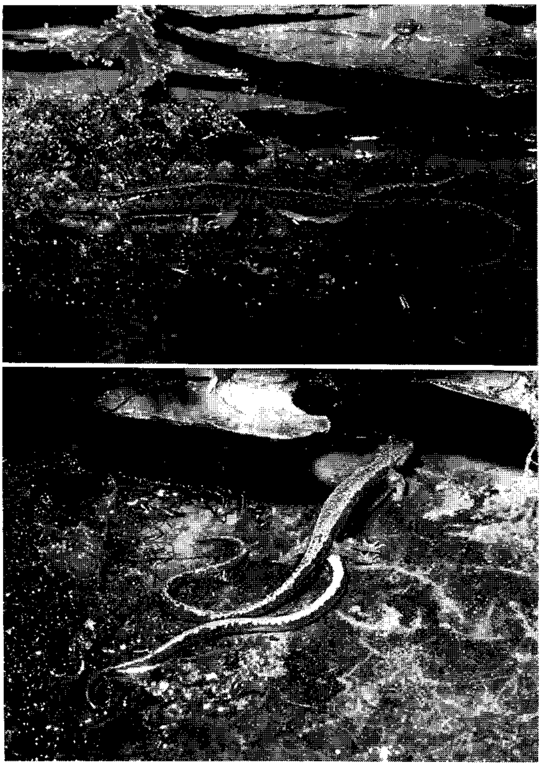

Fig. 4: Ventral amplexus in *Chioglossa lusitanica.* Above: the female lies on top of the male as he clasps her forelimbs with his forelimbs. The male is lifting his hind foot as he shifts his body laterally. Below: a dorsal view of the same amplectic pair. The male is largely hidden beneath the female, except for his tail

periods of inactivity. The male initiates a typical bout with head-swinging, adds body-shifting, then continues body-shifting with no head-swinging and finally lapses back into inactivity. In *Salamandra,* body-shifting tends to be an uninterrupted activity accompanied by periodic bouts of head-swinging.

Chioglossa show two activities during ventral clasping that are not present in *Salamandra.* Shuddering is a unique action in which the *Chioglossa* male makes vigorous lateral flexions. The action often initiates a bout of body-shifting. Secondly, the *Chioglossa* pair may rapidly rotate about their long axis for a few or several revolutions, eventually ending upright in the original ventral clasping position but with their tails twisted in a double helix. I could not decide whether twisting was caused by the female, in her attempts to escape the clasping male, or whether it was a male initiated activity. Twisting was of sporadic occurrence and was restricted only to one pair, whereas shuddering occurred periodically in all observations of amplexus that lasted 10 min or longer.

The spermatophore base of *Chioglossa* is a gradually tapered cone, about 5 mm tall and 2 mm in diameter at the base, and capped with a sperm mass less than 1 mm in diameter.The spermatophore resembles that of *Salamandra* (HIMSTEDT 1965; JOLY 1966) in shape but is smaller.

Chioglossa and *Salamandra* share all the same behavioral elements of spermatophore deposition and sperm transfer and differ only in the temporal organization of these behaviors. In both taxa, the male swings his head and undulates his tail during spermatophore deposition. In *Chioglossa,* however, the male commonly displaces his sacrum without first depositing a spermatophore. Thus the male may execute a number of sacral displacements before he begins true spermatophore delivery. In between sacral displacements, the male briefly reverts to body-shifting followed by a stationary bout of head-swinging and tail undulations. In the one spermatophore deposition sequence that was observed, the male performed 6 sacral displacements during a period of 28 min, but only the last two displacements were actual spermatophore deliveries. Thus the male *Chioglossa* apparently does not release the female between successive spermatophore depositions, as in *Salamandra.* Instead, the male shifts back under the female without interrupting amplexus and proceeds towards the next spermatophore deposition.

As in *Salamandra,* the *Chioglossa* male swings his upraised head under the female's chin after sacral displacement, when his sacrum is at a 45—60° angle to the female's sacrum.

Discussion

HENNIG (1966) has stressed the importance of derived characters in the inference of phylogenetic relationships. The sharing of derived characters (synapomorphies) is a sign of relationship, whereas the sharing of primitive characters does not provide phylogenetic information.

Chioglossa and *Salamandra* share three derived courtship characters that at present appear to be unique to these taxa. They may also be shared with the related genus *Mertensiella.* First, head-swinging during ventral amplexus and the temporal organization with tail-undulation appear to be synapomorphies. Likewise, deposition of a spermatophore on the substrate under the female's vent is unique to salamandrids and known only in *Chioglossa* and *Salamandra.* Finally, only *Chioglossa* and *Salamandra* retain both forelimbs in amplexus during and after the sacral displacement that follows spermatophore deposition. *Salamandra* and *Chioglossa* were osteologically differentiated by the upper Oligocene (ESTES 1981), so these three shared derived behaviors are at least 26 million years old. In contrast, ventral amplexus does not define *Chioglossa* and *Salamandra* as sister taxa, because this amplectic mode also occurs in *Pleurodeles* and *Tylototriton* (VON BEDRIAGA 1882; BOULENGER 1920; GALLIEN 1953; GYI 1969), as well as in *Mertensiella.*

The Caucasian and Middle Eastern genus *Mertensiella* is the closest relative to *Chioglossa* and *Salamandra* on anatomical grounds (ÖZETI & WAKE 1969; WAKE & ÖZETI 1969). *Mertensiella* shares with *Salamandra* the derived feature of ovoviviparity (MUSKHELISHVILI 1964). After an osteological analysis, ÖZETI (1967) proposed that *Mertensiella* be considered a subgenus of *Salamandra.* However, ÖZETI (1967) also found a number of skeletal features shared only by the two species, *Mertensiella caucasica* and *M. luschani.* In addition, the two species share an enigmatic, derived sexual dimorphism: the male possesses a protuberance, 1—2 mm tall, on the dorsum of his tail base. Despite the close relationship to *Salamandra,* there are grounds for viewing *Mertensiella* as a distinct genus (SANCHIZ & MŁYNARSKI 1979).

The courtship of *Mertensiella* is incompletely known, but the available records suggest a close affinity with *Salamandra* and *Chioglossa*. Only the preliminary courtship phases of *M. caucasica* have been observed. Spermatophore deposition and sperm transfer have not been recorded. CYRÉN (1911) briefly observed a pair in ventral amplexus under water. Courtship may be terrestrial as well as aquatic, since WOLTERSTORFF et al. (1936) found a male *M. caucasica* clasping a female in a collecting container with only damp moss. OBST & ROTTER (1962) observed aquatic courtship in a captive pair. They too observed ventral amplexus as well as a number of new elements: body-shifting (with the male rubbing his caudal protuberance sideways against the female's cloaca), male rubbing of the female's abdomen by head-swinging, and twisting of the pair about their long axes. The first two elements are present in both *Salamandra* and *Chioglossa*, the third is performed by *Chioglossa*.

In light of the result that both *Chioglossa* and *Salamandra* deposit the spermatophore under the female's cloaca, I can suggest a new role for the caudal protuberance of *Mertensiella* males. Possibly the protuberance is inserted in the female's cloaca during spermatophore deposition with the effect of stabilizing the female's position over the real spermatophore. From EISELT's (1966) excellent photograph of the caudal protuberance, we can note that it is in precisely the right position to align the male and female cloacae during spermatophore deposition. Furthermore, the caudal protuberance bears a remarkable resemblance to a *Salamandra* spermatophore. It is inclined anteriorly, is otherwise the correct shape (e.g., laterally compressed) and correct size, and it even possesses an apical knob which closely resembles the apical sperm mass of a *Salamandra* or *Chioglossa* spermatophore. Thus the caudal protuberance actually may be a false spermatophore that is withdrawn from the female's cloaca, as the male laterally displaces his sacrum and allows her to fall upon the real spermatophore. Observations of sperm transfer in *Mertensiella* easily could test these hypotheses.

The function of body-shifting in *Salamandra* and *Chioglossa* may be to lubricate the contact between the male's dorsum and the female's venter so that the female is not pulled to the side during sacral displacement, away from the spermatophore. In *S. salamandra* a whitish secretion is often visible between the bodies of the amplectant pair and a similar film was likewise visible in *Chioglossa* pairs during body-shifting. The supposition that the male produces a lubricating secretion could be tested in part by histological examination of males sacrificed during the act of body-shifting. SEVER & HOUCK (1985) successfully used this technique to determine which glands participated in forming the spermatophore of the plethodontid salamander *Desmognathus ochrophaeus*. A second possible source of fluid is suggested by JOLY (1966) who noted that *S. salamandra* females sometimes empty their bladders just before sacral displacement.

Acknowledgements

I am especially grateful to Lynne HOUCK for help with field work. Giorgio MANCINO graciously helped with logistics and field work in Italy, and Francisco DE BORJA SANCHIZ greatly facilitated field work in Spain. Robert THORN gave much useful advice on terrarium design and salamander care. Günther FREYTAG kindly helped me obtain specimens. I am indebted to Arnold KLUGE for encouragement during the early phases of the work. Lynne HOUCK, Frank MCKINNEY and an anonymous reviewer made helpful comments on the manuscript. Preparation of this manuscript was supported by NSF Grant BSR 85-08363.

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