

Postembryonic development of *Actinopus cf. insignis* and *Diplura paraguayensis* (Araneae, Mygalomorphae)

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Summary

The postembryonic development of two mygalomorph spiders, *Actinopus cf. insignis* (Actinopodidae) and *Diplura paraguayensis* (Dipluridae), is studied. The first postembryonic instar is intrachorionic, covered by the embryonic cuticle with egg teeth. In both species the second instar has a strongly bent body, integumentary spicules, few hairs on the tarsi, a pair of simple tarsal claws, and anterior and posterior spinnerets. The cheliceral fang of *A. cf. insignis* has a false pincer, while that of *D. paraguayensis* has only subapical denticles. The third instar *A. cf. insignis* retains six spinnerets (all of them with spigots); the anterior lateral spinnerets are lost in later stages. Three tarsal claws are present, and the paired claws are toothed. The paired claws of third instar *D. paraguayensis* have a single, sinuous row of teeth (adults have two rows); the inferior claw is toothed. The presence of six spinnerets, monoserially dentate paired claws, and pectinate inferior claws in early instars suggests that a reversal to these plesiomorphic states in a related taxon, *Micromygale*, could be due to neoteny and not to a *de novo* origin.

Introduction

Hitherto, various aspects of ontogeny are known for about 30 species of mygalomorph spiders. Some authors have studied embryonic development, others have studied stages after hatching or dispersal, but very few have studied the complete life cycle, from egg to adult. Given the scarcity of published information on this subject, even incomplete observations are interesting. With this in mind, we report here the results of a study of part of the postembryonic development of two species of Mygalomorphae.

Material and methods

Two females of *Actinopus cf. insignis* (Holmberg, 1881) and one of *Diplura paraguayensis* (Gerschman & Schiapelli, 1940) were collected with their egg sacs in the field. The eggs of one *Actinopus* did not develop; only one egg sac of each species was used in the present study. All the eggs from each sac were maintained and a certain number of specimens of successive instars were fixed. The methods for observing and describing the instars are those of previous papers (Galiano, 1967, 1972, 1973a, b, 1991). Temperature was 25–29°C; the eggs were maintained in the dark. The shedding of the embryonic cuticle is considered the first true moult. The instar covered by the embryonic cuticle with egg teeth is called

the first postembryonic instar, and subsequent instars are numbered successively. The abbreviations used can be found in Raven (1985). All the specimens examined are deposited in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”.

Results

Family Dipluridae

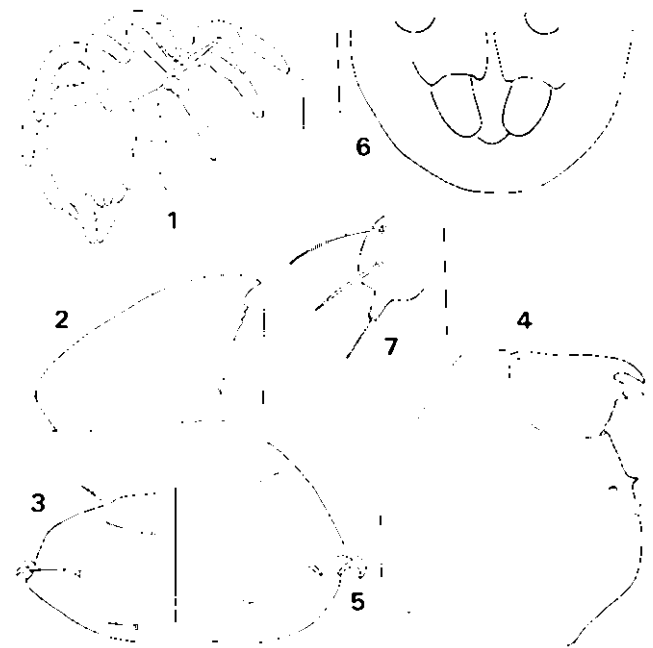
Diplura paraguayensis (Gerschman & Schiapelli, 1940) (Figs. 1–3)

Specimens and egg sac

One female from Isla San Martín, Parque Nacional Iguazú, Misiones province, Argentina, coll. P. Goloboff, October 1985. The egg sac was formed from 5 loose layers of white silk; the outer layer had detritus. The egg sac contained 134 eggs, with a diameter of 1.27–1.30 mm ($n=5$). Hatching: the covers of the egg (chorion and vitelline membrane) were broken and shed together with the embryonic cuticle. The first free instar is the second postembryonic instar.

Second postembryonic instar (Figs. 1–3) ($n=15$)

Body bent (Fig. 1), with legs segmented and extended laterally. Integument covered with spicules. Only six thick subapical setae on tarsi. No eyes. Basal segment of chelicerae wide; apical segment scarcely movable, slightly curved and tapering gradually at apex, with 1–3 small subapical ventral denticles (Fig. 2, showing a



Figs. 1–3: *Diplura paraguayensis*, second postembryonic instar. **1** Body; **2** Cheliceral fang, posterior view; **3** Tarsal claws, second leg.

Figs. 4–7: *Actinopus cf. insignis*. **4–6** Second postembryonic instar. **4** Chelicera, posterior view; **5** Tarsal claws, first leg; **6** Spinnerets and anal tubercle, ventral view. **7** Third postembryonic instar, left ALS. Scale lines=0.5 mm (1), 0.25 mm (6), 0.1 mm (2–5, 7).

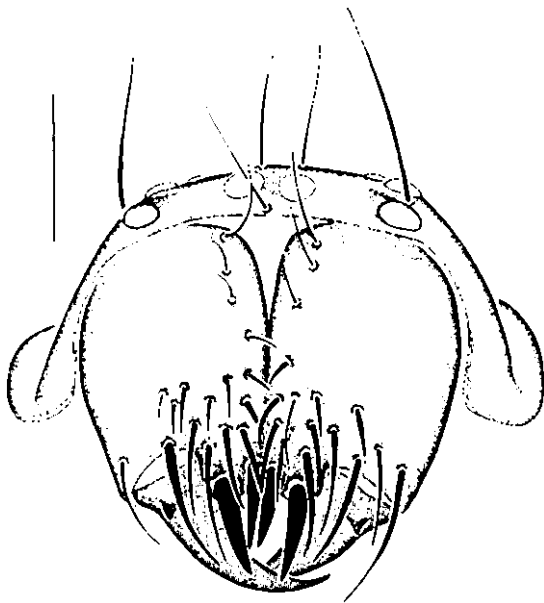


Fig. 8: *Actinopus* cf. *insignis*, third postembryonic instar, frontal view of cephalothorax. Scale line=0.25 mm.

specimen with 3 denticles). All leg tarsi with 2 claws (Fig. 3), palpal tarsi with single claw, apparently no third claw on any tarsus. Spinnerets (Fig. 1): a pair of conical appendages, widely separated, considered as ALS; PMS longer than ALS, PLS much longer, weakly divided into 3 segments. All spinnerets covered with spicules; no spigots present. In the course of the five days following hatching, the next instar (third) became visible through the integument. Some started moulting on the fourth day, but could not complete the process. They died the next day and were fixed.

Third postembryonic instar (observed inside the cuticle of the second) ($n=97$)

Integument with abundant long hairs, distributed over entire body. Chelicerae: fang normal, with opening for venom gland and tapered tip. Fang furrow with 6 well-developed teeth on promargin, and 3 smaller, more basal, on retromargin. Trichobothria: exact distribution could not be observed in specimens examined (mounted on slides); tibiae with 2 (in longitudinal row?), metatarsi with 2 in longitudinal row, and tarsi with 1. Tarsal claws: all legs with STC pectinate, teeth forming single, sinuous row (with basal teeth on external face and apical ones on internal); tooth rows more strongly sinuous on anterior legs; ITC present on all legs, with 2 long sharp teeth. Spinnerets: PLS and PMS with spigots. At this point of development of the third instar, it was not possible to see the ALS, but they could be present in the completely developed third instar. Small immatures from other localities do not have ALS.

Family Actinopodidae

Actinopus cf. *insignis* (Holmberg, 1881) (Figs. 4–12)

Specimens and egg sac

One female from Lima, Buenos Aires province, Argentina, coll. P. Goloboff, M. Ramírez and A.

Zanetic, November 1981. The egg-sac contained 135 eggs, spherical, yellow, with a diameter of 1.53–1.59 mm ($n=4$). The egg sac was opened on 4 December; hatching had already taken place, and that free instar is considered the second postembryonic instar.

Second postembryonic instar (Figs. 4–6) ($n=72$)

Body strongly bent, with legs extended laterally and with no visible segmentation. Integument initially lacks pigmentation, but at end of stage pigment of subsequent instar can be observed (by transparency) on anterior edge of cephalothorax and dorsal base of abdomen. Entire body covered by spicules, rather large in some areas (particularly anterior maxillary edge). Only 5–6 short thick setae at tarsal tips, 2 on subapical dorsum of chelicerae. No eyes. Chelicerae (Fig. 4) with basal segment protruding dorsally, apical segment articulated, with false pincer. Outer arm of false pincer larger, inner arm sometimes bifid and with short basal ramification. Basal segment of chelicerae with 2 teeth on promargin, and 1 tooth, low and blunt, on retromargin. No lyriform or tarsal organs visible (although conceivably overlooked). All tarsi with pair of small, simple tarsal claws (anterior one larger) (Fig. 5). ITC apparently absent. Palp with 1 simple claw. Spinnerets (Fig. 6): one pair of ALS monoarticulated and conical, and one pair of posterior spinnerets, bisegmented. Both pairs covered by spiculated integument, no other integumentary derivatives present. Basal segment of each posterior spinneret with internal dilatation, where integument is granulated (dilatation will become PMS in following instar).

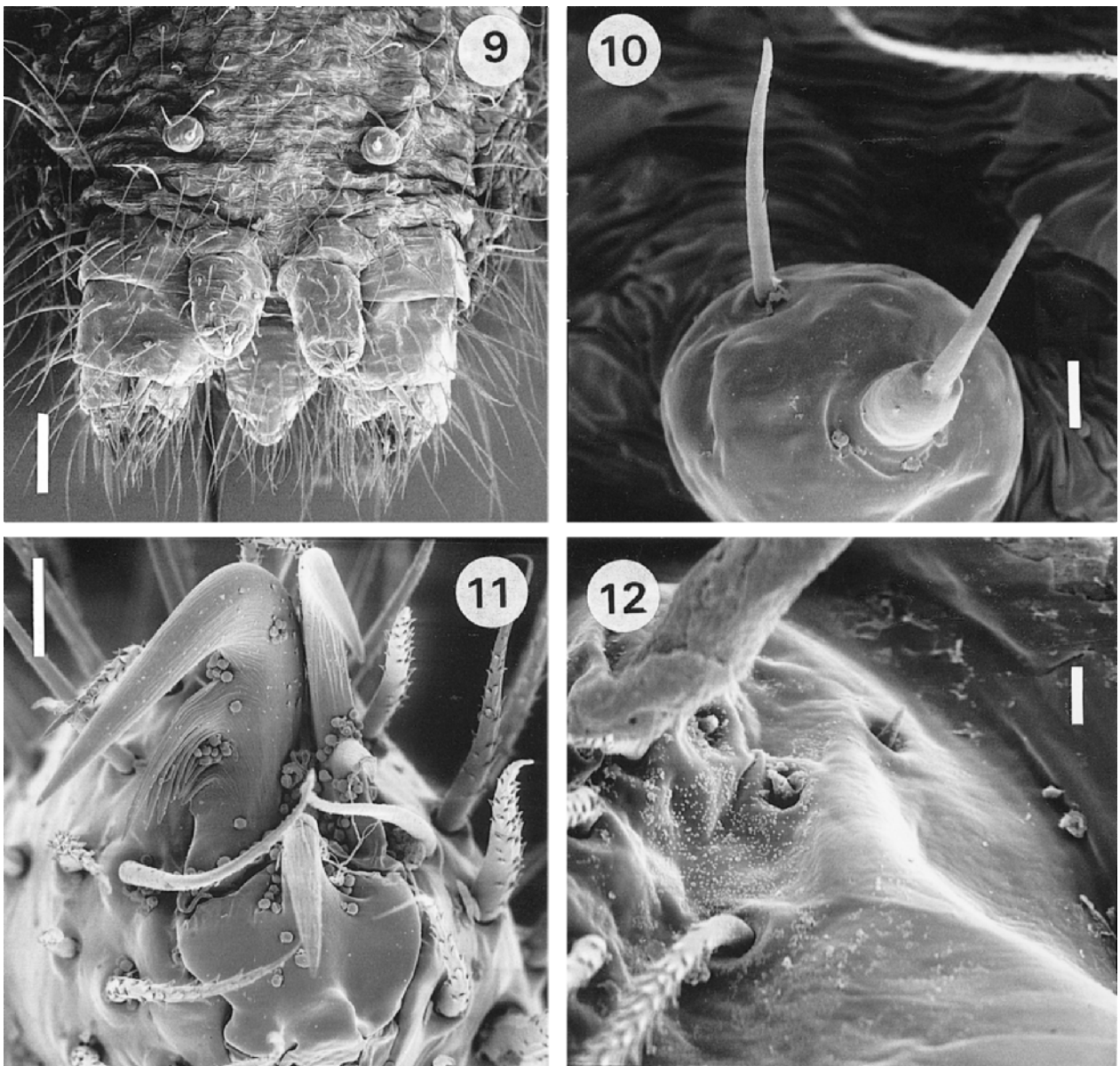
At a temperature of 25–29°C this stage lasted for about 24 days, when the second moult occurred. Apparently these conditions were not optimal, as in many specimens the abdomen started to shrink, probably because of consumption of the yolk reserves. Undeveloped eggs, from the other egg sac of the same species, were placed near the spiderlings, but no oophagy was observed [unlike in *Polybetes pythagoricus* (Holmberg) (Galiano, 1971) and *Loxosceles laeta* (Nicolet) (Galiano, 1967)].

Third postembryonic instar (Figs. 7–12) ($n=53$)

Cephalothorax and abdomen in same plane; legs contacting substrate. Initially with clumsy movements, but becoming more agile in subsequent days. Deposition of pigment continues through the stage. Cephalothorax (Fig. 8) wide, head very convex and elevated, fovea very wide and procurved, but rather shallow, with sigilloid tumescent extensions on sides. Eyes sessile, in two rows. A single long median hair on anterior margin of cephalothorax, 1 hair at side of LE and 2 behind MOQ. Sternum rounded, proportionally wider than in adults, with no sigilla; no suture between labium and sternum (adults have sigilloid impression behind labium). Chelicerae with single row of setae on dorsal anterior face; both margins of cheliceral furrow with 4 small teeth, apparently without denticles in furrow. Strong rastellum, as in Fig. 8. Short, thick, diagonal fang with a

basolateral tooth, acute tip and two longitudinal keels on outer surface. Maxillae subquadrate, with no cusps, with *c.* 15 short, thick, ensiform hairs along anterior dorsal face and some bifid hairs on dorsal face, similar to those described for some diplurids (Coyle, 1986; Goloboff, 1989) and migids (Goloboff & Platnick, 1987). Maxillary gland (Fig. 12) with “conic hairs” (as described by Goloboff, 1993: figs. 24, 25 for other mygalomorphs). Labium with 10 hairs similar to those on maxillae. Abdominal hairs long, erect, roughly forming transverse lines on middle of dorsum, longitudinal lines on sides. Each hair with a prominent base, placed on spot of brown pigment. Trichobothria: all legs with 2 on tibia (near mid-point, paired, anterior basal to posterior), 1 apical on metatarsus, and 1 medial on tarsus. Bothrium with sinuous basal plate. Lyriform and tarsal organs present. Chaetotaxy: Legs I and II, tibiae with retro-ventral setae only; metatarsi and tarsi with weak serial pro- and retro-ventral spines. Leg III, patella

with 2–3 short, strong, erect prolateral setae (on apical third), 4–5 longer spines forming crown along prolateral apex, 2–3 retrolateral apical; tibia with 3 dorsal basal spiniform setae plus 10 spines forming dorsal apical crown; metatarsus with laterodorsal spines; tarsus with apical ventral spines. Leg IV, patella with 10 spiniform prolaterodorsal setae; tibia unarmed; metatarsus with 0–1–1 prolaterodorsal; tarsus with apical ventral spines. STC: anterior tarsi with anterior claw larger, pectinate (Fig. 11; adults have single tooth), posterior claw with single tooth; posterior tarsi with anterior claw simple, posterior claw with small basal tooth. ITC present, simple, on all legs. Palpal claw with small basal tooth. Spinnerets (Fig. 9): ALS (Figs. 7, 10) conical, mono-articulate, with single spigot, and 2 hairs (one normal hair and one chemoreceptor). PMS monoarticulate, with 5 spigots. PLS triarticulate; basal segment with 1 apical spigot, middle with 2, apical with 13. All spigots with base and shaft fused (with no articulation); spigots of



Figs. 9–12: *Actinopus* cf. *insignis*, third postembryonic instar. **9** Spinnerets and anal tubercle, ventral view; **10** Right ALS (normal hair lost); **11** Tarsal claws, first leg; **12** Palpal coxa with maxillary gland and “conic hairs”. Scale lines=100 μ m (9), 10 μ m (10), 20 μ m (11), 5 μ m (12).

posterior spinnerets with long base and shaft, except one spigot on PMS with shorter base and shaft; single spigot on ALS with shorter, more globose base. Spinnerets with numerous lyriform organs similar to those of other mygalomorphs [described by Coyle (1984: fig. 13) for *Allothele* (Dipluridae), and illustrated by Goloboff (in press) for spinnerets and legs of several nemesiids].

At this stage the spiderlings can produce silk, but it is not known whether all spigots are functional.

Discussion

Comparison with development of other mygalomorphs

Spinnerets: Montgomery (1909) mentioned the presence of appendages on abdominal segments 4 and 5 in the embryo of *Euagrus* sp. (Dipluridae), corresponding to the anterior and posterior spinnerets. Holm (1954) made a similar observation in *Thelechoris striatipes* (Simon) (Dipluridae; then as *Ischnothele karschi* (Bös. & Lenz)), in which, during embryonic development, abdominal appendages are formed in the 4th segment and disappear before hatching. The appendages of the 5th segment are retained and divide after hatching, with the endopodite forming the PMS and the exopodite the PLS.

The first published record of mygalomorph spiders with ALS present in a post-hatching stage but disappearing later is for *Antrodiaetus unicolor* (Hentz), *A. pacificus* (Simon) and *A. stygius* Coyle (Antrodiaetidae) (Coyle, 1971). For *A. unicolor*, Tripp & Myser (1972) confirmed Coyle's observations, and Bond (1994) reported that each PLS of the second postembryonic instar (which he called "first free postembryonic stage") has a functional spigot, but the ALS have no spigots.

Both of the species studied here retain the ALS after hatching, and lose them in subsequent stages. All of the specimens under study died during the second or third instar, so it is not possible to know with certainty when the ALS are lost. Very small juveniles of *Diplura* and *Actinopus*, probably of the 4th or 5th instar, collected in webs or maternal burrows, lack ALS.

Actinopus and *Antrodiaetus* thus differ in that while the second instar of *Antrodiaetus* has ALS without spigots and PLS with one functional spigot (F. A. Coyle, pers. comm.; Bond, 1994), *Actinopus* at the same stage has no spigots on any spinneret. At the third instar, *Antrodiaetus* has lost the ALS, while *Actinopus* has ALS with one spigot, probably functional.

Diplura has, in the second instar, three pairs of spinnerets, ALS, PMS and PLS. Published data on other Dipluridae, e.g. *Euagrus* (Montgomery, 1909), *Thelechoris karschi* (Holm, 1954), and *Ischnothele siemensii* F. O. P.-Cambr. (Galiano, 1972), indicate that the anterior spinnerets are absent in the second postembryonic instar, i.e. they disappear before hatching.

Motility and relative position of cephalothorax and abdomen: In the previously examined species of Dipluridae (two species of Ischnothelinae), the instar after shedding of the embryonic cuticle has the body in a single plane, PLS and PMS with functional spigots, has

hairs, and is capable of relatively rapid movements. The equivalent instar of *Diplura* has the body bent at an angle, the integument has spicules, the spinnerets have no spigots, and the spiderlings cannot move by themselves. Paz (1993) studied *Linothele megatheloides* Paz & Raven, but his data allow no useful comparisons.

The second instar of *Actinopus* has the body bent and does not move, while the same instar of *Antrodiaetus* and *Aliatypus* (Coyle, 1971) has functional spigots. Although Coyle (1971: 279) does not mention whether the body is bent, he states that the spiderlings can move (albeit very slowly); consequently, second instar antrodiaetids must also have the body in a single plane.

Cheliceral fang: In the second postembryonic instar of *Actinopus*, the fang has a false pincer, similar to that described for atypids (*Atypus*; Canard, 1984; Schwendinger, 1990), antrodiaetids (*Antrodiaetus* and *Aliatypus*; Coyle, 1971), nemesiids (*Acanthogonatus* (= *Tryssothele*); Calderón, 1983; Calderón *et al.*, 1979, 1990; Iglesias *et al.*, 1987), and several theraphosids (*Grammostola*, *Acanthoscurria*, *Avicularia*, *Ceropelma*; Vachon, 1958; Galiano, 1969, 1972, 1973a, b; *Ischnocolus*; Schimkewitsch & Schimkewitsch, 1911). The third instar of all these genera, except *Grammostola*, has a normal fang.

The second instar of previously studied diplurids (ischnothelines) has a conical cheliceral fang, somewhat thicker than in the adult, but with no teeth or projections. The false pincer is also absent in ctenizids (*Cteniza moggridgei* O. P.-Cambr. and *Ummidia fragaria* (Dönitz); Buchli, 1970; Yoshikura, 1972) and the nemesiid *Nemesia caementaria* (Latr.) (Buchli, 1968). *Diplura* has the cheliceral fang conical, but with 1–3 small subapical ventral teeth. These teeth are reminiscent of the secondary projections of false pincers.

Phylogenetic implications

Some of the features observed in the early post-embryonic instars of *Actinopus* and *Diplura* are of particular phylogenetic interest. The first explicit hypothesis of mygalomorph phylogeny was proposed by Raven (1985), but several of Raven's conclusions have been challenged (using techniques of analysis developed after 1985) by Goloboff (1993). In Raven's (1985) cladogram the successive sister groups of the actinopodids are the migids, ctenizids, idiopids, and cyrtaucheniids, forming the group Rastelloidina; for these taxa, Goloboff's (1993) cladogram differed only in having ctenizids, idiopids, and migids plus actinopodids, as an unresolved trichotomy, and the Cyrtaucheniidae paraphyletic in terms of the other Rastelloidina. All the Rastelloidina (within which the actinopodids are deeply nested) are 4-spinnereted spiders, in which the ALS are absent. *Diplura* belongs in the Quadrithelina of Raven (1985; enlarged by Goloboff, 1993, to include also the Rastelloidina), a group characterised by the loss of the ALS. Although the second instar of *Antrodiaetus* (which has adults with four spinnerets) has ALS, the closest relatives of that genus (*Atypoides*, *Aliatypus* and the Atypidae) are typically 6-spinnereted spiders. In contrast,

the taxa hypothesised to be close relatives of *Diplura* and *Actinopus* are all 4-spinnereted (at least in the adults). It is therefore unexpected that in the early postembryonic instars, *Actinopus* and *Diplura* have ALS, in the third instar of *Actinopus* well-developed and apparently functional. This finding is not merely surprising, it also makes more plausible a controversial conclusion of Goloboff's (1993) analysis. In that analysis, the postulated sister group of the Rastelloidina, the Crassitarsae, was enlarged to include also the Microstigmatidae. Like the Rastelloidina, the Crassitarsae are typically 4-spinnereted spiders, but *Micromygal*, a microstigmatid genus nested deeply within the Crassitarsae, has six spinnerets — interpretable only as a regain. As Goloboff (1993) admitted, it seems unlikely that organs as complex as spinnerets could be lost and at a later time “re-evolve”; however, trees not requiring such a regain of spinnerets in *Micromygal* should have placed that taxon closer to the base of the mygalomorph cladogram, together with other (plesiomorphically) 6-spinnereted taxa, and most other characters except the spinnerets seemed to indicate that *Micromygal* belongs in the Crassitarsae. Raven (1985) and Griswold (1985) had suggested that *Micromygal* — the world's smallest mygalomorph — could be neotenic in several features. It is in this context that the presence of ALS in mygalomorphs with 4-spinnereted adults is particularly interesting. Although Goloboff (1993) accepted the dictate of the majority of the characters and the “regain” of spinnerets in *Micromygal* with reluctance, that reluctance may have had little justification. Whether the ALS are present may be not so much a matter of “re-evolving” but rather of the duration of their retention in ontogeny.

Other features of the early instars of *Actinopus* are less unexpected. Many of them simply indicate that the spiders in that stage are already well developed and share many of the characteristic features of the adults. The presence of an apical crown of strong, cusp-like spines on the third tibia has been proposed by Goloboff & Platnick (1987) as one of the synapomorphies of *Actinopus*, and the sinuous impression around the bothrial tricheme aperture as one of the synapomorphies of actinopodids. Other characters observed in the adults, and constituting synapomorphies at the genus or family level, are instead absent in the early instars. Tibia II with the retrolateral face covered with spines is synapomorphic for the genus (Goloboff & Platnick, 1987), but the early instars have only serial, retroventral weak setae (present also in adults). The elongate labium is one of the synapomorphies of the Actinopodidae (Simon, 1892; Raven, 1985), but in the juveniles it is subquadrate, as in the migids, ctenizids and idiopids. The maxillary gland lacks conic hairs in those Domiothelina examined for this character (Idiopidae and Actinopodidae), an absence which may be synapomorphic for the group (Goloboff, 1993), but these hairs are present in juveniles of *Actinopus* (as well as in more plesiomorphic Rastelloidina and the Crassitarsae). Although the cheliceral fang of the adults is somewhat keeled, the lateral keels appear more evident in the juveniles; the presence of

these keels in adult migids (one of the synapomorphies for the group; Simon, 1903; Raven, 1985) may be a neotenic feature [other possibly neotenic features of the Migidae are the reduction in number of spines on the third leg (Goloboff, 1991), the poorly developed sternal sigilla, and the reduction in number of dorsal setae on the chelicera; the last two are also observed in juvenile *Actinopus*].

Goloboff (1993) proposed that the family Dipluridae may constitute a paraphyletic assemblage, with diplurines (*Diplura*, *Trechona* and *Linothele*) more closely related to other bipectinate taxa (Rastelloidina plus Crassitarsae) than to the other “diplurids”. The differences in development may lend support to that hypothesis, as *Diplura* shares with other bipectinates a less developed second instar, perhaps a derived feature (as antrodiaetids and liphistiids seem to have motile second instars). Goloboff (1993) considered *Diplura* to have no false pincers, but if the structure now discovered can be considered a homologue of the false pincers, it could be additional evidence linking *Diplura* with other bipectinates rather than with other “diplurids”. Third instar *Diplura* have a single, sigmoid row of teeth on the STC, and several teeth on the ITC. Adults have 2 rows of teeth on the STC, and the ITC unarmed. The loss of the ITC teeth is supposed to be a synapomorphy defining a group containing *Diplura* (the Diplurinae, in Raven's hypothesis, or the Bipectina, in Goloboff's); in third instar *Diplura* that character appears in a more plesiomorphic state. The double row of teeth also defines the Bipectina; as Raven (1985) proposed, it seems most logical that the double row has arisen through the loss of the medial teeth joining the external (basal) and internal (apical) portions of the sigmoid row observed in many mygalomorphs. That transition, postulated by Raven (1985) for some cyrtauchenids, can actually be observed during the ontogeny of *Diplura*. The fact that early instars of *Diplura* have monoserially dentate STC and pectinate ITC also suggests two apparent reversals to plesiomorphic states in *Micromygal*, besides the number of spinnerets, which could be due to neoteny. According to Goloboff's (1993) cladogram, *Micromygal* belongs in a group characterised by having STC biserially dentate and ITC bare, but that genus has a single row of teeth on the STC and pectinate ITC. At least some taxa with biserially dentate STC and unarmed ITC in the adults, exhibit during the early instars conditions similar to those in adult *Micromygal*. The claw dentition and the presence of ALS suggest that Griswold (1985) and Raven (1985) were probably correct in postulating neoteny for *Micromygal*.

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References

- BOND, J. E. 1994: Seta-spigot homology and silk production in first instar *Antrodiaetus unicolor* (Araneae: Antrodiaetidae). *J. Arachnol.* **22**(1): 19–22.
- BUCHLI, H. H. R. 1968: Notes sur le mygale terricole *Cteniza moggridgei* (Pick. Cambr., 1874). *Revue Ecol. Biol. Sol.* **5**(1): 1–40.
- BUCHLI, H. H. R. 1970: Notes sur le cycle de reproduction, la ponte et le développement post-embryonnaire de *Nemesia caementaria* Latr. (Ctenizidae, Mygalomorphae). *Revue Ecol. Biol. Sol.* **7**(1): 95–143.
- CALDERON, R., PIZARRO, G., ROJAS, C. & SALINAS, J. 1979: Observaciones sobre la biología de *Tryssothele pissii* (Simon, 1888) (Araneae, Dipluridae) en el Parque Nacional La Campana. *An. Mus. Hist. nat. Valparaiso* **12**: 195–205.
- CALDERON, R. 1983: *Révision systématique des araignées mygalomorphes du Chili, suivie d'une étude sur le développement post-embryonnaire de Tryssothele pissii Simon, 1889 (Mygalomorphes: Dipluridae)*. 1–137. These Univ. Montpellier II.
- CALDERON, R., GARRIDO, M. & PINTO, C. 1990: Etapas del crecimiento de *Acanthogonatus franckii* Karsch, 1880 (Araneae: Nemesiidae). *Revta chil. Ent.* **18**: 19–24.
- CANARD, A. 1984: *Contribution a la connaissance du développement, de l'écologie et de l'écophysologie des aranéides de Landes Armoricaines*. 1–389. These Univ. Rennes I.
- COYLE, F. A. 1971: Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). *Bull. Mus. comp. Zool. Harv.* **141**(6): 269–402.
- COYLE, F. A. 1984: A revision of the African mygalomorph spider genus *Allothele* (Araneae, Dipluridae). *Am. Mus. Novit.* **2794**: 1–20.
- COYLE, F. A. 1986: *Chilehexops*, a new funnelweb mygalomorph spider genus from Chile (Araneae, Dipluridae). *Am. Mus. Novit.* **2860**: 1–10.
- GALIANO, M. E. 1967: Ciclo biológico y desarrollo de *Loxosceles laeta* (Nicolet, 1849) (Araneae, Scytodidae). *Acta zool. lilloana* **23**: 431–464.
- GALIANO, M. E. 1969: El desarrollo postembrionario larval de *Grammostola pulchripes* (Simon, 1891) (Araneae, Theraphosidae). *Physis B. Aires* **29**(78): 73–90.
- GALIANO, M. E. 1971: El desarrollo postembrionario larval en especies del género *Polybetes* Simon, 1897 (Araneae, Sparassidae). *Acta zool. lilloana* **28**: 211–226.
- GALIANO, M. E. 1972: El desarrollo postembrionario larval de *Ischnothele siemensi* Cambridge, 1896 (Araneae, Dipluridae). *Physis B. Aires* **31**(82): 169–177.
- GALIANO, M. E. 1973a: El desarrollo postembrionario larval en Theraphosidae (Araneae). *Physis B. Aires* (Sec. C) **32**(84): 37–45.
- GALIANO, M. E. 1973b: El desarrollo postembrionario larval de *Avicularia avicularia* (Linnaeus, 1758) (Araneae, Theraphosidae). *Physis B. Aires* (Sec. C) **32**(85): 315–327.
- GALIANO, M. E. 1991: Postembryonic development in ten species of neotropical Salticidae (Araneae). *Bull. Br. arachnol. Soc.* **8**(7): 209–218.
- GOLOBOFF, P. A. 1989: Una nueva especie de Dipluridae (Araneae): *Chilehexops misionensis*. *Revta Soc. ent. argent.* **45**: 77–83.
- GOLOBOFF, P. A. 1991: A new species of *Calathotarsus* (Araneae: Migidae) from Chile. *Jl N. Y. ent. Soc.* **99**(2): 267–273.
- GOLOBOFF, P. A. 1993: A reanalysis of mygalomorph spider families (Araneae). *Am. Mus. Novit.* **3056**: 1–32.
- GOLOBOFF, P. A. In press: A revision of the South American spiders of the family Nemesiidae (Araneae, Mygalomorphae). Part I: species from Peru, Chile, Argentina, and Uruguay. *Bull. Am. Mus. nat. Hist.*
- GOLOBOFF, P. A. & PLATNICK, N. I. 1987: A review of the Chilean spiders of the superfamily Migoidea (Araneae, Mygalomorphae). *Am. Mus. Novit.* **2888**: 1–15.
- GRISWOLD, C. E. 1985: A revision of the African spiders of the family Microstigmatidae (Araneae: Mygalomorphae). *Ann. Natal Mus.* **27**: 1–37.
- HOLM, A. 1954: Notes on the development of an orthognath spider, *Ischnothele karschi* Bös. & Lenz. *Zool. Bidr. Upps.* **30**: 199–221.
- IGLESIAS, P., CALDERON, R., PINTO, C., BONARIC, J.-C. & EMERIT, M. 1987: Caracterización del crecimiento de *Acanthogonatus franckii* Karsch, 1880 (Araneae, Nemesiidae). *Trav. Lab. Zool. Univ. Montpellier II*. 40 pp.
- MONTGOMERY, T. H. 1909: On the spinnerets, cribellum, colulus, tracheae and lung books of araneads. *Proc. Acad. nat. Sci. Philad.* **61**: 299–320.
- PAZ, N. 1993: Aspectos de la biología reproductiva de *Linothele megatheloides* (Araneae, Dipluridae). *J. Arachnol.* **21**(1): 40–49.
- RAVEN, R. J. 1985: The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bull. Am. Mus. nat. Hist.* **182**(1): 1–180.
- SCHIMKEWITSCH, L. & SCHIMKEWITSCH, W. 1911: Ein Beitrag zur Entwicklungsgeschichte der Tetraneumones. *Izv. Imp. Akad. Nauk.* (Ser. 6) **5**: 634–653, 685–705, 775–789.
- SCHWENDINGER, P. 1990: A synopsis of the genus *Atypus* (Araneae, Atypidae). *Zoologica Scr.* **19**(3): 353–366.
- SIMON, E. 1892: *Histoire naturelle des araignées* **1**(1): 1–256. Paris.
- SIMON, E. 1903: *Histoire naturelle des araignées* **2**(4): 669–1080. Paris.
- TRIPP, J. R. & MYSER, W. C. 1972: Descriptive embryology of the mygalomorph spider *Antrodiaetus unicolor*. *Ann. ent. Soc. Am.* **65**(6): 1310–1319.
- VACHON, M. 1958: Contribution a l'étude du développement post-embryonnaire des araignées. Deuxième note. Orthognathes. *Bull. Soc. zool. Fr.* **83**: 429–461.
- YOSHIKURA, M. 1972: Notes on the development of a trap-door spider, *Ummidia fragaria*. *Acta arachn. Tokyo* **24**(1): 29–39.