

## A STERNOPHORID PSEUDOSCORPION (CHELONETHI) IN DOMINICAN AMBER, WITH REMARKS ON THE FAMILY

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**ABSTRACT.** The first known fossil of the pseudoscorpion family Sternophoridae is described from Dominican amber. The specimen, an adult female, is tentatively assigned to the extant species *Idiogaryops pumilus* (Hoff), known from Florida and Little Cayman Island. The incomplete state of the fossil is probably the result of scavenging while the animal was trapped on the surface of the resin. The cuticular parts have collapsed during fossilization and the golden appearance of the fossil is due to light being reflected from the surface of the cast, rather than from the cuticle itself. A thin layer of cerotegument is recorded in Sternophoridae. The morphology of the coxal area is reinterpreted. The so-called pseudosternum is delimited by the apparent internal borders of the coxae, which have moved laterally. A Y-shaped canal runs from the openings of the coxal glands to the oral cavity, carrying their secretions, together with those of the accessory glands of the coxae, to the oral cavity. The canal is covered by a series of overlapping tecta on coxae I–III and posteriorly on the palpcoxae. The coxae are fused medially from the posterior margin of coxa I to the anterior margin of coxa IV. The internal modifications of the median and posterior maxillary lyrifissures of pseudoscorpions are shown to be apodemes of trochanteral muscles of the palp. The suboral setae of the manducatory process of certain Sternophoridae are vestigial, suggesting that they may be undergoing a regression. The parallel between the morphology of the vestitural setae and that of setae *b* and *sb* of the chelicera is used to identify the missing seta of Sternophoridae as *sb*.

The Sternophoridae are a small, homogeneous family of pseudoscorpions, strongly adapted for life under the bark of trees. The twenty described species are currently placed in three genera: *Garyops* Banks 1909 from North and Central America and the Caribbean; *Idiogaryops* Hoff 1963 from Florida and the Caribbean; and *Aprosternophorus* Beier 1967 from eastern Africa, India, Nepal, Sri Lanka, Southeast Asia and Australasia (Harvey 1985).

Given their ecology and distribution, it is not unexpected to find a member of the Sternophoridae in Dominican amber, which is relatively young (15–20 My; Iturralde-Vinent & MacPhee 1996). Schawaller (1980a, 1980b, 1981a, 1981b) recorded six pseudoscorpion genera from this fauna, all of which are represented by extant species in the Caribbean region or Central America. What is, perhaps, surprising is that the fossil described here is morphologically indistinguishable from *Idiogaryops pumilus* (Hoff 1963), a Recent species known from Florida and Little Cayman Island (Harvey 1985). The assignment of fossils to extant species is almost always ques-

tionable, if only because fewer of their characters are visible. However, there is no reason, other than age, to suppose that the present fossil belongs to a different species. Pseudoscorpions are known to be an ancient group (Schawaller et al. 1991) and the wide distribution and morphological homogeneity of Sternophoridae (Chamberlin 1932; Harvey 1985) suggest conservative rates of evolution within the family. Recent material of the three sternophorid genera has also been examined for comparative purposes and some of the results are given at the end of this paper.

### *Idiogaryops pumilus* (Hoff) (Figs. 1, 2)

*Garyops depressa* (not Banks): Banks 1909: 305–306; Hounscome 1980: 85 (in part: misidentifications).

*Garyops pumila* Hoff 1963: 7–10, figs. 5–6.

*Idiogaryops pumilus* (Hoff): Harvey 1985: 165–166, figs. 32, 38, 40, 46–50, map 2.

? *Idiogaryops* sp. Harvey 1985: 166–167, figs. 33, 40.

**Material examined.**—1 ♀, amber fossil (Miocene?) from Dominican Republic (exact provenance unknown). Deposited in the Nat-

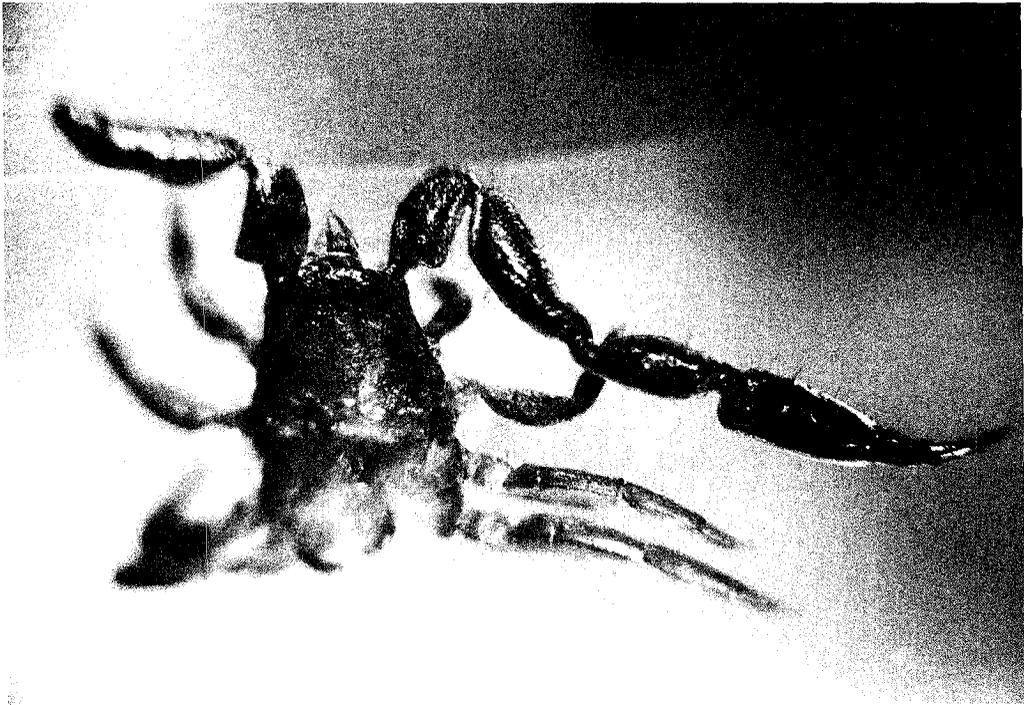


Figure 1.—*Idiogaryops pumilus* (Hoff), female, dorsal view of amber fossil (image of left palp distorted by oblique edge of block).

ural History Museum, London (Dept. of Palaeontology; registration number JA 43). Presented by R. Rontaler, 5 December 1996. The amber piece is clear, golden-yellow and has been ground and polished parallel to the dorsal plane of the specimen to facilitate accurate observations.

**Description of fossil.**—Palps and anterior part of carapace deep reddish-brown; legs and posterior region of carapace yellowish-brown (probably darkened by process of fossilization). Vestitural setae of dorsal surfaces with blunt tips. Cuticular parts smooth, apart from granulation on lateral surfaces of palps. Most parts of body covered by a thin, clear layer of cerotegument, which seems to have expanded into the resin.

Carapace strongly flattened, with a moderate, lateral constriction at level of leg I; posterior part weakly sclerotized; surface with irregular transverse lines in anterior half; posterior margin lost. Eyes absent. Setae small and sparse. Pleural membrane finely plicate (portion visible on right side). Opisthosoma missing, only represented by cerotegument of ventral surface and a few detached setae.

Chelicerae with 4 setae on hand, *b* blunt, other setae acuminate. Spinneret difficult to see clearly, but apparently long and with three rami.

Palps as shown in Fig. 2. Femur and patella fairly robust; lateral surfaces with strong granulation, dorsal and ventral surfaces smooth. Femur with a long tactile seta, proximad of middle. Chela with granulation at base of hand; hand broader than deep, with sides subparallel in dorsal view and parallel in lateral view. Fixed finger with 7 trichobothria (*isb* absent). Movable finger with three trichobothria; *st* about one-third of distance from *b* to *t*. Fixed finger with 4 and movable finger with 6 thickened (presumably spatulate) setae on paraxial face. Distal teeth retrorse, proximal teeth reduced.

Coxae with 'pseudosternum' typical of family. Legs short and robust; arolia fan-shaped, shorter than the claws, which are robust. Setae (including 'tactile setae') typical. Joint between femur and patella of all legs vertical (slightly oblique dorsally) and immobile.

Measurements (in mm; ratios in parenthe-

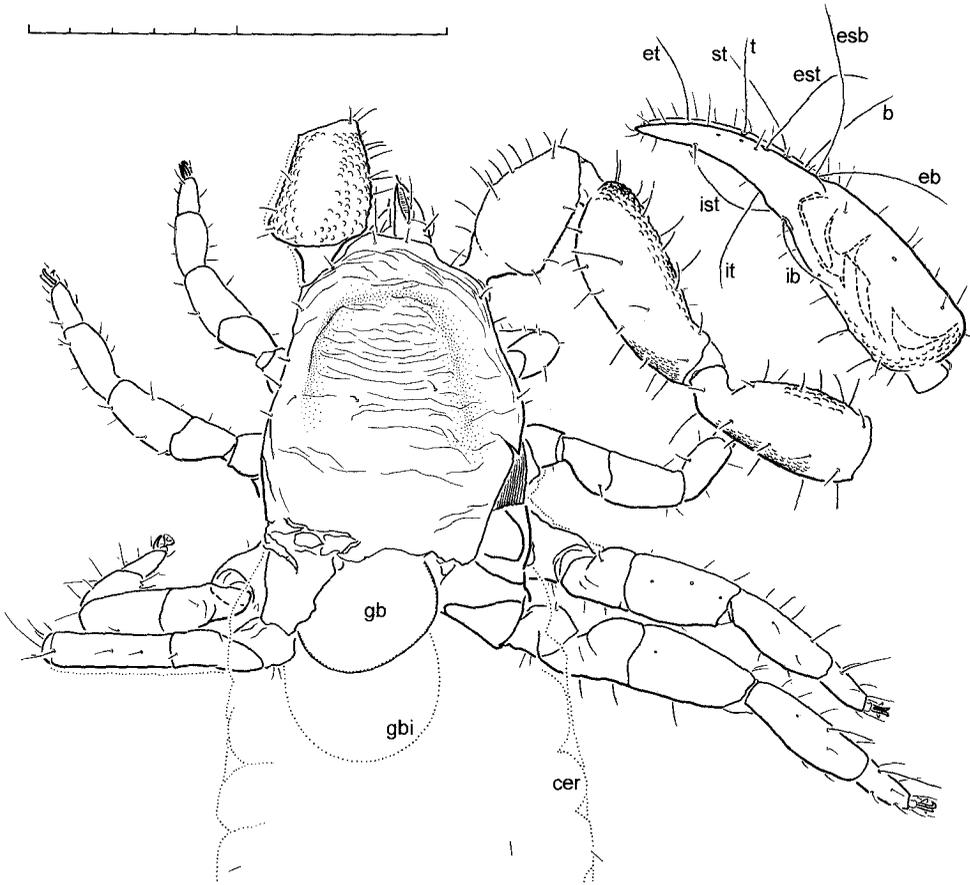


Figure 2.—*Idiogaryops pumilus* (Hoff), female, dorsal view of fossil cast. Left palp omitted, apart from trochanter. Right chela shown separate from rest of palp simply for reasons of format (see Fig. 1 for true position). Cerotegument indicated by dotted lines (only shown in part). Cracking of cuticle only indicated on hand of chela. Granulation of palps only shown in part. Abbreviations: *cer* = cerotegument; *gb* = gas bubble; *gbi* = imprint of bubble in cerotegument. Scale line = 1 mm.

ses): Carapace (estimated)  $0.84 \times 0.61$  (1.4). Right palp: trochanter  $0.41 \times 0.20$  (2.05), 'heel'  $0.29$  (1.48); femur  $0.59 \times 0.20$  (2.95); patella  $0.46 \times 0.20$  (2.31); chela (including pedicel)  $0.95 \times 0.23$  (4.10) length without pedicel  $0.93$  (4.04); hand length (with pedicel)  $0.54$  (2.34), without pedicel  $0.51$  (2.21), depth  $0.18$ ; movable finger  $0.47$  (0.97 length of hand without pedicel). Leg IV: femur  $0.24 \times 0.19$  (1.3), patella  $0.31 \times 0.19$  (1.6); femoropatella length  $0.51$  (2.7).

**Remarks.**—The fossil is almost indistinguishable from the descriptions of *I. pumilus* given by Hoff (1963) and Harvey (1985). The measurements of the palpal segments fall slightly below those given for Recent *I. pumilus* (e.g., femur length  $0.62$ – $0.72$ , patella

length  $0.52$ – $0.61$ , chela length without pedicel  $0.95$ – $1.07$ ), but these differences are judged to be insignificant; the measurements of Recent specimens are based on only five females from Florida and are unlikely to represent the true range of variation in this species. It is also possible that the specimen has undergone some compression during fossilization (see remarks under Taphonomy).

Harvey (1985) briefly described and figured a male paratype of *I. pumilus* that differed from the male holotype in having a greatly reduced dorsal apodeme of the genitalia. Harvey concluded that the paratype belonged to a new species, but did not name it due to the lack of sufficient material. In the absence of any further information, it seems more rea-

sonable to regard the small apodeme of the paratype as either an abnormality or part of the normal range of variation in *I. pumilus*. However, if Harvey's interpretation is correct, it would not be possible to assign the fossil described here to either *I. pumilus* or the unnamed species.

### TAPHONOMY

At first sight, the remains of the pseudoscorpion seem to be in very good condition. When examined more closely, however, it becomes clear that the cuticle has collapsed in many parts, resulting in extensive cracking (this is only indicated for the hand of the chela in Fig. 2). Hence, what is really seen is the cast left in the resin before the specimen collapsed. Because they were embedded in the resin, the hairs of the setae and trichobothria remained in their original positions, giving the cast a very lifelike appearance. The collapse of the cuticle explains the shiny golden appearance seen in reflected light, which is also characteristic of other Dominican amber fossils. Where the cuticle is no longer in contact with the amber, the light is reflected from the surface of the cast, but where it is still in contact with the amber, it is seen as a drab patch. Fortunately, the cuticle only collapsed after the resin had hardened, leaving a faithful representation of the external surfaces. The resin was able to diffuse through the cerotegument before hardening and seems to have caused it to expand.

The incomplete nature of the fossil was initially rather puzzling. The loss of part of the left palp, the opisthosoma and part of the carapace almost certainly occurred after the animal had become trapped on the surface of the resin. This can be deduced from the fact that the outline of the ventral surfaces has been preserved in the form of the cerotegument and a few detached hairs. There are no signs of decay, and the specimen cannot be an exuvium because, in addition to being adult, remains of the internal tissues can be seen. The only plausible explanation is that the exposed parts were scavenged shortly after the pseudoscorpion became stuck in the resin. The scavenger—perhaps an insect—must have been relatively large: it bit through the left palp at the base of the patella and tore the opisthosoma from the prosoma, leaving the cerotegument stuck in the resin.

The absence of debris suggests that the specimen was only briefly exposed before being covered by a second flow of resin. The removal of the body left a concavity in the surface of the first flow, which trapped an air bubble (Fig. 3: *gb*) just behind the carapace. At this point, the specimen was upside-down in the resin: the pressure of the bubble created a large bulge in the layer of cerotegument above it (Fig. 3: *gbi*). Before the resin solidified, it was turned over, such that the remains of the pseudoscorpion were dorsal side up relative to gravity. The bubble slowly rose away from the cerotegument and came to rest just below the torn margin of the carapace. From the size of the impression left in the cerotegument, it can be seen that the bubble decreased in volume. This could be due to diffusion, contraction of the resin or compression, either alone or in combination.

Because the cuticle cracked, rather than simply disintegrating, it was probably subjected to a significant pressure after being buried. If so, the cast now observed must be smaller than the living animal. Grimaldi et al. (1994) discussed differences in the size of cuticular parts of insects and their casts in amber, but concluded that "Since it is unlikely that the cuticular surface would shrink, even during dehydration, it is more likely that the cast surface represents expansion of the amber, probably due to polymerization of the original resin." There is indeed a large difference in size for the specimens they illustrate, without any obvious damage to the cuticle, but the assumption that cuticle cannot shrink during fossilization is questionable. If, as Grimaldi et al. suggest, an expansion of the amber has occurred, the original cuticle ought to show a finer, less distorted preservation of detail than the cast. From their scanning electron micrographs (e.g., figs. 26, 27), it appears that the opposite is the case, indicating that the cuticle has shrunk. Baroni Urbani (1980) interpreted the damage seen in certain ant specimens in Dominican amber as due to shrinkage and collapse of the cuticle, probably as a result of heating (D. Schlee *in* Baroni Urbani 1980).

The possibility of changes in size during fossilization has not been considered in previous studies of amber pseudoscorpions. Although the differences are probably small, it is evident that caution is needed when comparing morphometric data for fossil and Re-

cent specimens. In identifying the present fossil as *I. pumilus*, I have assumed that its dimensions have decreased slightly. If it could be shown that a significant increase in size was involved, this identification would be incorrect.

### MORPHOLOGICAL NOTES

The following notes are mainly based on two adults (1♂1♀) of an undescribed *Afrosterphorus* species—closely related to *A. hirsti* (Chamberlin 1932)—from Australia (Northern Territory, The Bark Hut, Arnhem Highway, under bark of *Eucalyptus* sp. 18 June 1984, M. Kotzman; MH 611.07-08; deposited in MNHN). Additional observations were made on type material of *Garyops sini* (Chamberlin 1923) and *Afrosterphorus cylindrimanus* (Beier 1951) housed in MNHN, and on specimens of *G. depressus* (1♀, Dominican Republic, Pedernales Prov., 10 km N. Cabo Rojo, beating thorn scrub, 22 August 1988, M.I. Ivie, T.K. Philips & K.A. Johnson; WM 7186) and *I. paludis* (Chamberlin 1932) (1♂2♀, U.S. Virgin Islands, St. John, Great Lameshur Bay, East shore, under bark, 14 June 1980, W.B. Muchmore; WM 5705).

**Cerotegument.**—A layer of cerotegument is present in Sternophoridae, but it is easily overlooked because it is thin and closely appressed to the surface of the epicuticle. It is most evident when it becomes damaged and detached, as can be seen in Harvey's (1985: fig. 7) scanning electron micrograph of the coxal region of *A. hirsti*. In transmitted light, the cerotegument is transparent and shows a very fine, irregular granulation. Harvey (1992) regarded the presence of cerotegument ("pseudoderm") as a synapomorphy of the Garypidae and Larcidae (Garypoidea), but it is more widespread, occurring sporadically in at least the Cheliferoidea (e.g., Mahnert 1985) and Feaelloidea (pers. obs.).

**Coxal tecta.**—The presence of a 'pseudosternum' has traditionally been considered one of the most characteristic features of the Sternophoridae. Chamberlin (1923, 1931) defined it as a secondary space between the coxae, resulting from a "partial mesal membranization of coxae I to IV." Harvey (1985) failed to find any indication of a membrane in *A. hirsti*, using scanning electron microscopy, and therefore interpreted the pseudosternum as a desclerotization of the coxae, rather than

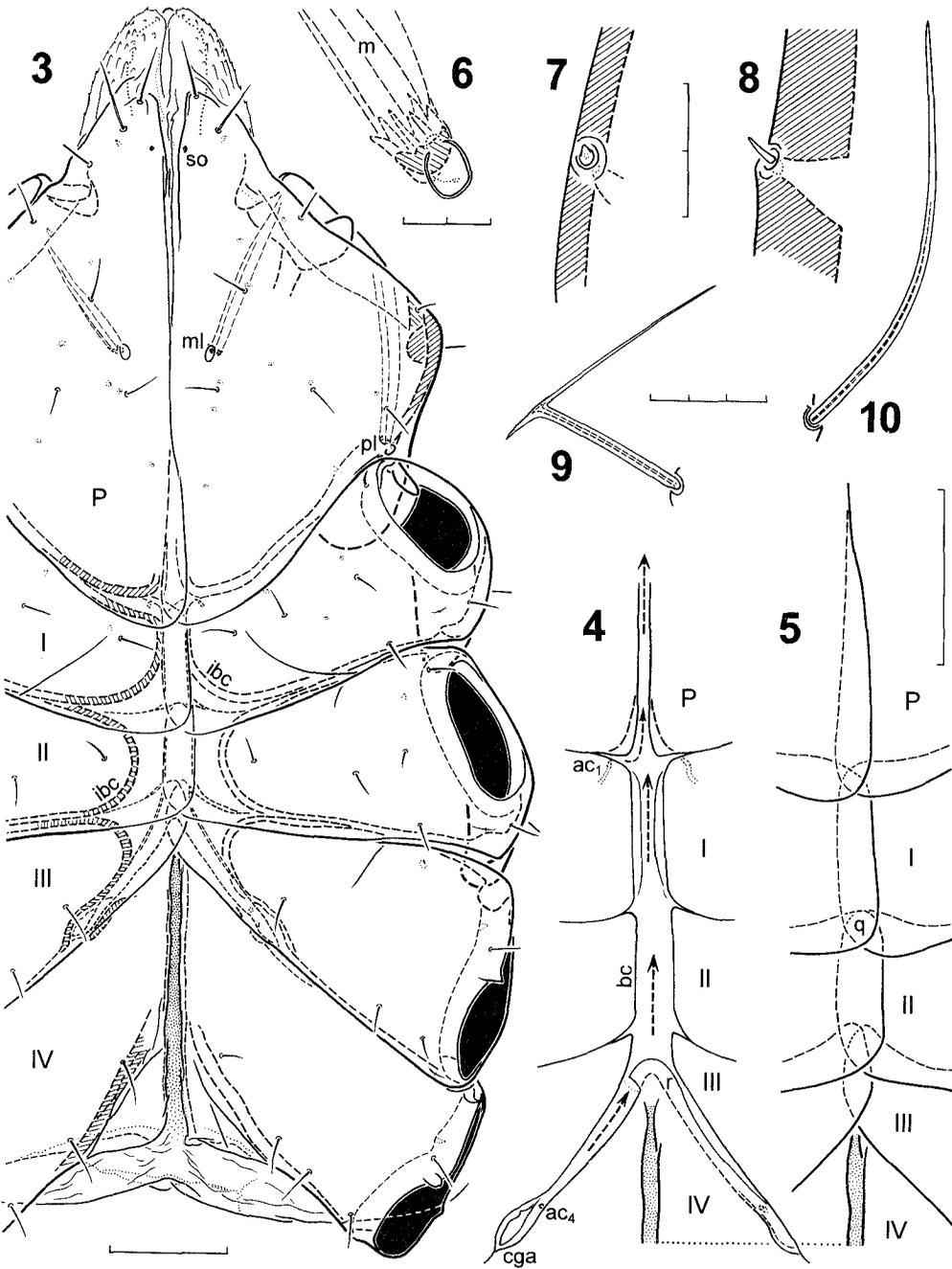
a membranization. The difference between these interpretations may seem slight, but it reflects an apparent incongruity between the observations made using light and scanning electron microscopy. When Hoff's light micrographs (1963: figs. 1, 5) are compared with Harvey's scanning electron micrograph (1985: fig. 7), the difference is striking. The explanation lies in the presence of a previously overlooked series of plate-like expansions of the paraxial walls of the coxae, which are here termed the *coxal tecta*.

The tecta are present on coxae I–III and the posterior part of the palp coxae. Their extreme thinness (about 2 μm where they meet) means that they are almost transparent and difficult to observe in ordinary preparations. They are best seen in specimens cleared in lactic acid. The following description is mainly based on the material of *A. aff. hirsti*, but the general form seems to be the same in other sternophorids.

The tecta of each side extend past the midline, which means that they overlap. In the specimen shown in Fig. 3, the tecta of the right coxae pass beneath those of the left coxae. In addition to this transverse overlapping, the tecta overlap longitudinally, with the tectum of one coxa lying beneath that of the following coxa. The combination of these two types of overlapping results in three points at which four tecta are superimposed. The second of these points has been marked *q* on Fig. 5. At this point (looking ventrally), the external tectum is that of right coxa I, below which is the tectum of the right coxa I, followed by that of right coxa II and finally the tectum of left coxa II, which is nearest to the body. This can be represented more concisely by the sequence right I/left I/right II/left II, going from ventral to dorsal. Naturally, it is the posterolateral margins of tecta I and the anterolateral margins of tecta II that are involved at *q*.

The space between the coxae is therefore completely covered anteriorly of coxa IV and would not normally be visible with scanning electron microscopy. In reflected light, the tecta give the 'pseudosternum' a slightly iridescent appearance, caused by diffraction effects.

When a sternophorid is examined in transmitted light, two sets of apparent borders are evident. The first and most obvious of these are the internal walls of the coxae (to which the leg muscles are attached). These borders



Figures 3-10.—Coxal region and cheliceral setae of Sternophoridae. 3-7, *Afrosternophorus* aff. *hirsti*, female (MH 611.08). 3, Coxae, ventral view; 4, Coxal canal (most of posterior rim removed from right coxa IV; arrows indicate inferred flow of secretions); 5, Overlapping of coxal tecta; 6, Right median maxillary lyrifissure, with apodeme (hatched) and muscle; 7, Left suboral seta. 8-10, *Garyops depressus*, female (WM 7186); 8, Left suboral seta; 9, Abnormal seta *es* of left chelicera; 10, Normal seta *es* of right chelicera. Abbreviations: I-IV = coxae I-IV;  $ac_1$ ,  $ac_4$  = ducts of accessory glands; *bc* = border of canal; *cga* = atrium of coxal gland; *ibc* = internal border of coxa; *m* = muscle; *ml* = median maxillary lyrifissure; *P* = coxa of palp; *pl* = posterior maxillary lyrifissure; *q* = point at which four tecta overlap; *r* = posterior rim of coxal canal; *so* = suboral seta. Scale divisions: 0.1 mm (Figs. 3-5); 0.01 mm (Figs. 6-10).

delimit the 'pseudosternum' and are the only parts that have moved antiaxially. The cuticle between them (the pseudosternum) is neither membranous nor desclerotized—it is simply thinner than that of the rest of the coxa. Closer to the midline lies the second series of apparent borders (*bc*), which represent the edge of a curve seen in tangent. These curves correspond to a furrow between the coxae or, more exactly, a canal. It is only once the nature of this canal is understood that the function of the tecta becomes clearer.

**Coxal canal.**—The coxal glands of most arachnids are associated with canals or ducts that carry their secretions towards the oral region. Pseudoscorpions are no exception, but the course followed the secretions of their glands has received little attention. This may be due to the obscurity of the opening on the posterior margin of coxa III, which is covered by the posterior margin of coxa IV. Heurtault (1973) even concluded that the coxal gland lacked an external opening and was solely endocrine, based on histological studies of *Neobisium caporiaccoi* Heurtault 1966.

Hammen (1986: fig. 4B; 1989: fig. 115B) illustrated a tiny 'orifice' associated with the intercoxal tubercle of *Chthonius tenuis* L. Koch 1873. He interpreted the intercoxal tubercle as a vestigial sternapophysis and noted that sternapophyses are often associated with the 'taenidia' (canals) of coxal glands. Unfortunately, the nature of this 'orifice' is unclear. It is certainly not the opening of the coxal gland (which is larger and situated further along coxa III) and I have not been able to find anything similar in *Chthonius*. Nevertheless, Hammen's implication that the secretions of the coxal glands flow between the coxae is correct. This becomes evident when other families are considered, many of which show a well defined canal, running from the openings of the coxal glands to the oral region.

The Sternophoridae are one of the most convenient groups in which to study the course of the coxal canal. This is because the flattening of the coxae reduces the three dimensional nature of the canal, simplifying the observations and their interpretation. Although this flattening also involves some unusual modifications, the basic form is similar to that found in other families and can therefore serve as an example.

Each coxal gland of Sternophoridae opens

into a large cavity in the posterior margin of coxa III (Fig. 4: *cga*). This cavity, here termed the coxal gland atrium, also contains the openings of smaller gland ducts (one in *A. aff. hirsti*, two in *A. cylindrimanus*), which are assumed to belong to the anterior accessory glands (*ac*<sub>4</sub>) (acinous glands of coxa IV; Heurtault 1973). The secretions of the accessory and coxal glands flow into the two branches of the canal between coxae III and IV (Fig. 4). The fluid continues along the unpaired median canal, which receives the secretions of another pair of accessory glands (presumably *ac*<sub>1</sub>) at the anteromedian corners of coxa I. The presence of small branches of the canal between coxae I/II and II/III, suggests that secretions from the accessory glands of coxae II and III (not observed) may also flow into the canal. The combined secretions then flow into the oral cavity, which marks the end of the canal.

The course of the coxal canal is shown in Fig. 4. The drawing has been simplified by omitting the tecta, the bases of which correspond to the apparent lateral borders of the canal (*bc*) in ventral view. The posterior branches of the canal are bordered by an extended rim (or minitectum), which runs continuously along the anterior borders of coxae IV (Fig. 4: *r*). The fact that the rim crosses the midline without interruption is significant for two reasons. Firstly, it shows that the canal is closed posteriorly, removing any possibility of fluid flowing backwards along the space between coxae IV. Secondly, it shows that the anteromedian borders of coxae IV are fused. In fact, the canal is sclerotized for much of its length, which means that the other leg coxae are fused. This can be inferred from the porosity of the canal, which extends to the base of coxae I. Pore canals are typical of the sclerotized parts of pseudoscorpions and are never found on the membranes. This fusion is probably partial in the case of coxae I, which seem to have retained faint traces of their original borders. It appears that the floor of the canal was formed by a simultaneous sclerotization of the original intercoxal membrane and incorporation of the original coxal margins. The paraxial borders of coxae IV are free for most of their length, being separated by an ordinary intercoxal membrane (shown stippled in Fig. 4).

As yet, the presence of fluids in the canal

has only been directly observed in the chernetid *Lamprochernes savignyi* (Simon 1881). Because the coxae are still relatively mobile in this species, the movement of fluid can be observed if a live specimen is trapped beneath a coverslip. As the animal struggles to free itself, the coxae move apart medially, revealing the fluid in the coxal canal. The fluid is clear and inconspicuous in transmitted light, but its presence is evident from the meniscus that moves back and forth as the coxae open and close.

There can be little doubt that the secretions of the coxal glands follow the same course in all pseudoscorpions, even when there are no obvious modifications of the coxal margins (as Chthonioidea and most Neobisioidea). Indirect evidence for this is provided by the similarity of the positions of the glands and the presence of modifications facilitating the flow between coxae I and the palpcoxae. It is already known that 'washing fluid' moves from and to the oral region along intercoxal space in the Chthonioidea and Neobisiidae (Weygoldt 1966, 1969; Judson 1990). Indeed, the assumption that this fluid is produced by oral glands now seems questionable: it could equally be produced by the coxal glands.

Returning to the coxal tecta, it is evident that they serve to cover the canal, closing it off from the exterior. While it is possible that they form part of the canal (meaning that they are in contact with the secretions), their primary function is probably one of protection. Because Sternophoridae live in confined spaces, it is presumably important to prevent the fluid from coming into contact with the substrate or the canal from being blocked by debris. Similar tecta are also present in *Apocheiridium* Chamberlin 1924, another strongly flattened genus, adapted to living in tight bark-crevices. The covering of the canal varies in other groups, ranging from a simple rim to a membranous extension.

The coxal canal of pseudoscorpions provides a remarkable parallel to the podocephalic canal of actinotrichid mites. Although they occupy different positions (the podocephalic canal runs laterally, above the anterior coxae), each receives the secretions of the coxal glands and accessory (non-nephridial) glands. The podocephalic canal also shows the same tendency to become covered by tecta

and may even become completely internal in some Prostigmata (Grandjean 1938).

**Maxillary lyrifissures.**—Chamberlin (1931) noted that the median and posterior maxillary lyrifissures of certain Cheliferoidae show specialized internal processes, from which he inferred that they had evolved into a different sensory structure from the normal lyriform organs. Although not mentioned in his text, Chamberlin (1931: fig. 20F) also figured an internal process of the median manducatory lyrifissure in *Garyops sini*. Similar modifications can also be found in Cheiridioidea, Garypoidea and Neobisioidea, though their development is more variable and less well marked in the latter group.

These internal structures are in fact apodemes. The median manducatory lyrifissure is attached to one of the flexor muscles of the trochanter and the lateral lyrifissure is attached to an extensor muscle (Figs. 3, 6). The apodeme itself is a continuation of the plate of cuticle bounded by the lyrifissure and is attached to the muscles via short tendons. As the muscles contract, the plate will be pulled inwards. Chamberlin's interpretation is probably correct, in the sense that the lyrifissure must be detecting contractions of the attached muscle, rather than stresses across the cuticle.

It should be noted that an analogous curving has occurred in the dorsal femoral lyrifissure of Chernetidae, Cheliferidae and Atemnidae (Harvey 1992). However, there is no indication of an apodeme associated with these lyrifissures.

**Suboral seta.**—Judson (1985) briefly discussed the presence of a modified 'sensory seta' at the mesal border of the manducatory process in pseudoscorpions. Because the term 'sensory seta' is almost meaningless, it is here replaced by *suboral seta*.

The suboral setae of Sternophoridae are particularly interesting because they show the most reduced form yet known. The suboral setae of *Garyops depressus* are small, but otherwise unremarkable (Fig. 8). In contrast, those of *Idiogaryops paludis* and the *Aprosternophorus* species examined have the hair shortened to the point where its height scarcely exceeds its breadth (e.g., Fig. 7). At low magnifications, it appears as a mere dot in the middle of its areole (Fig. 6) and could easily be mistaken for the base of a broken hair.

However, the seta has retained its lumen and tapers to a point.

These reductions confirm that there is an evolutionary trend towards a decrease in the size of the suboral seta. In view of the extreme reduction seen in sternophorids, it is possible that this regression can lead to the complete loss of the suboral seta. This might explain the curious absence of suboral setae in the Pseudogarypidae, whose sister group—the Feaellidae—have short suboral setae.

**Cheliceral setae.**—There is an interesting parallel between the form of the vestitural setae and certain setae on the cheliceral hand in pseudoscorpions. When the dorsal vestitural setae are modified in a particular way, the proximal setae of the chelicerae tend to have the same morphology, although it may be less marked. This parallel differentiation is most clearly seen in the Panctenodactyli, partly because they often have strongly modified vestitural setae and partly because of the small number of fundamental setae (five or less). Excluding cases of secondary multiplication (neotrichy), it is setae *b* and *sb* that follow the form of the vestitural setae, whereas setae *is* and *ls* remain simple and acuminate. Seta *es* is sometimes modified like *b* and *sb*, but is more often simple, perhaps due to its lower position (ventral vestitural setae also tend to be simple).

Harvey (1985) noted that seta *b* (= *bs*) of Sternophoridae differs from the other cheliceral setae in being blunt. This unusual form is found in the dorsal vestitural setae of all Sternophoridae. Assuming that the rule of parallel differentiation holds in this family, it provides a simple way of deciding which of the original five setae has been lost from the cheliceral hand. According to Chamberlin (1931) and Harvey (1985), it is *ls* that has been lost, whereas Hoff (1963) interpreted the missing seta as *sb*. Excluding *es* (the identity of which is not in question), if *ls* were missing, one would expect two of the remaining setae (*b* and *sb*) to be blunt. The fact that only one blunt seta (*b*) is present indicates that the missing seta is *sb*, thus confirming Hoff's view.

The female of *G. depressus* examined here shows an unusual abnormality of seta *es* on the left chelicera. The seta is roughly T-shaped, except that one of the arms is much longer than the other (Fig. 9). The lumen of

the seta is enlarged at the node, but does not extend much further (*cf.* Figs. 9 and 10), which means that the hair is thinner than usual beyond this point. The fact that the bifurcation occurred so far from the base suggests that the anomaly was caused by mechanical deformation during ecdysis, rather than by a doubling of the hair.

**Trichobothriotaxy.**—Harvey (1985) showed that previous reports of sternophorids with a full complement of eight trichobothria on the fixed finger of the chela were due to errors of observation. Schawaller (1991) later illustrated a female of *Afrosterophorus cylindrimanus* (Beier) [possibly *A. dawydoffi* (Beier 1951), according to Schawaller (1994)] as having four trichobothria in the internal series of the fixed finger. However, the extra, distal trichobothrium in the internal series was drawn by mistake (W. Schawaller *in litt.*). The loss of trichobothrium *isb* therefore remains a synapomorphy of the Sternophoridae.

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