TRUNK SEGMENTATION PATTERNS IN REMIPEDIA

BY

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ABSTRACT

We examined segmentation patterns in 139 specimens of all currently known species of Remipedia. The trunks of remipedes are not always homonomous, i.e., with all their somites isomorphic in form. Some species exhibit somite heteromorphy, especially in regard to the anatomy of sternal bars. Furthermore, while the total numbers of trunk somites can be quite variable amongst Remipedia, there appears to be a lower limit of 16 somites in two species, *Godzilliognomus frondosus* Yager, 1989 and a new, undescribed taxon. Our data do not confirm that there is an upper limit of body sizes and/or the number of trunk somites in remipedes. Three stages of development have been recognized: juvenile, sub-adult, and adult. However, there are no reliable criteria to define any of these stages. Herein, we describe and define three true juvenile specimens of *Godzilliognomus frondosus*. At present no "larvae" are known, but it is not clear whether this is due to limitations of collecting tiny forms that may be living on or in bottom sediments, or whether remipedes develop epimorphically and hatch at a relatively advanced juvenile stage.

RÉSUMÉ

Nous avons examiné les modèles de segmentation chez 139 spécimens de toutes les espèces actuellement connues de Remipedia. Les troncs des rémipèdes ne sont pas toujours homonomes, c'est-à-dire, n'ont pas tous leurs somites de forme identique. Certaines espèces montrent une hétéromorphie des somites, en particulier par rapport à l'anatomie des barres sternales. De plus, alors que le nombre total des somites du tronc peut varier chez les Remipedia, il semble exister une limite inférieure de 16 somites chez deux espèces, *Godzilliognomus frondosus* Yager, 1989 et un nouveau taxon non encore décrit. Nos données ne confirment pas qu'il y ait une limite supérieure des tailles du corps et/ou du nombre des somites du tronc chez les rémipèdes. Trois stades de développement ont été reconnus : juvénile, sub-adulte, et adulte. Cependant, il n'y a pas de critère fiable pour définir chacun de ces stades. Nous décrivons ici et définissons trois spécimens juvéniles «vrais»

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de *Godzilliognomus frondosus*. Aujourd'hui, aucune «larve» n'est connue, mais nous ne savons pas si cela est dû aux limites du mode de récolte de ces formes minuscules qui peuvent vivre sur ou dans les sédiments du fond, ou si les rémipèdes ont un développement épimorphique et éclosent à un stade juvénile relativement avancé.

INTRODUCTION

In the last decades of the 20th century, many new higher taxa of crustaceans have been recognized. Few created as much excitement as the Remipedia Yager, 1981, which represented an entirely new class of arthropods. Among the diversity of both fossil and Recent crustacean body plans, Remipedia are distinguished by several unique features. The remipedes are hermaphroditic stygobionts that inhabit subterranean marine environments. Their head region is equipped with three pairs of strong, prehensile appendages typically followed by a long, homonomously segmented trunk.

Remarkably, virtually nothing is known about the modes of reproduction and development in Remipedia, which adds to the enigmatic status of these arthropods. Furthermore, we still know very little about remipede habits and habitats. To date, remipedes have been reported exclusively from anchialine cave systems in subtropical regions.

Schram et al. (1986) directed attention to the unique head anatomy of Remipedia, especially so since it was quickly recognized that features of the maxillules helped to distinguish the two families recognized in the living forms at that time. The subchelate array of limbs, combined with observations of predatory behavior in the field, established remipedes as carnivores. This anatomy, however, immediately led to some controversy. Carnivory traditionally is viewed as a derived, specialized mode of feeding. The distinctive head anatomy, however, was juxtaposed on a long, homonomously segmented trunk, which is often regarded as a primitive feature. Consequently, two perspectives on the evolution of the remipedes emerged. One side viewed remipedes as primitive (Schram, 1983) and, based on this assumption, suggested some new ideas about the origin of crustacean body plans and evolution of crustacean feeding types (Schram, 1986). Moreover, Emerson & Schram (1991) proposed that the group has a fossil record extending back to at least the Carboniferous. The other side believed that remipedes had to be derived and that their anatomy was the result of adapting to a very special, anchialine environment (Boxshall et al., 1992; and especially Wilson, 1992 therein). The controversy continues.

Surprisingly, however, the homonomously-segmented trunk, a presumably primitive region of the remipede body, has been largely ignored in comparative investigations. From the very beginning, the trunk limbs were described as serially repeated, similar pairs of limbs along the trunk. The trunk limbs on the first trunk

somite are often more slender than the subsequent appendages. The pairs of limbs near the body terminus are typically miniature in size or not fully developed. The limbs in between these two points are virtually identical, and even variations between species were felt to be restricted to different setal types and sizes, and slight variations in the distribution of these along the limb margins.

However, two aspects of the anatomy of these forms have indicated that the trunk is perhaps not so uniform as had been supposed. First, for a long time, the only break in the homonomous monotony of the trunk was thought to be the occurrence of the gonopores: female on the seventh trunk somite, and the male pores on the 14th somite (Itô & Schram, 1988). [In remipedes, the count of trunk limbs and somites begins with the first pair of biramous, paddle-like appendages, not with the so-called maxilliped.] The widely separated locations of the gonopores are a critical parameter, however, since this arrangement effectively constrains the lower limit of the number of trunk somites in adult remipedes. Among species, the number of trunk somites in adult specimens ranges from 15-16 (*Godzilliognomus frondosus* Yager, 1989) up to 42 (undescribed species of *Speleonectes* Yager, 1981 from the Yucatan Peninsula).

Second, more recently Koenemann et al. (2003) noted that the sternal bars of the trunk somites, which extend across the posterior edge of the sternites from the base of one of the trunk limbs to that of the other, occur in two forms among species: isomorphic and heteromorphic. This was the first time that anyone had recorded structural unconformities and irregularities along the length of the trunk.

Furthermore, the trunk of remipedes intrigues because for almost all species it cannot be characterized with a fixed number of somites, e.g., *Lasionectes entrichoma* Yager & Schram, 1986 has between 25 and 34 somites reported for its adult trunk. This phenomenon stands in strong contrast to what occurs in other homonomously segmented arthropods such as Chilopoda, in which trunk somite numbers are generally fixed for a species.

We are hindered in trying to understand the morphology and morphometry of the trunk in the remipedes due to the small quantity and quality of available information. Nevertheless, as we will show, much can be learned from an effective consideration of the available facts and careful examination of the specimens.

TRUNK HOMONOMY OR HETERONOMY?

It has been long known that not all trunk limbs in remipedes are exactly identical, e.g., Schram et al. (1986). In most remipede species, the first pair of trunk limbs is distinctly more slender and slightly smaller than those limbs that immediately follow. This reduction is not restricted to the first limb pair but

typically also includes the entire first trunk somite, which can be distinctly shorter and narrower than the following (second) somite. Depending on inter-specific variation, the first trunk somite can be more or less covered by the head shield. In one of the two described specimens of *Kaloketos pilosus* Koenemann, Iliffe & Yager, 2004, the first trunk somite is not only completely covered by the head shield, but also fused to the inner surface of the shield. It appears that remipedes exhibit a tendency towards integrating the first trunk somite into the cephalic tagma.

As one approaches the posterior of the trunk, the somites, sternal bars, and the limbs become smaller, and the most posterior of the trunk limbs are tiny, feeble appendages with greatly reduced setation.

Nevertheless, all of the trunk somites proper share a general form and each bears a pair of multi-segmented, highly setose, biramous paddles. Furthermore, in dorsal view, the remipede habitus conveys the general impression of similar trunk somites (fig. 1A). Hence, it has been a generally accepted mantra that remipedes have homonomous trunk somites.

However, Koenemann et al. (2003) explicitly noted that this assumption of homonymy was not strictly true. The large sternal plates certainly exhibit great similarity of form (fig. 2), but the sternal bars can be quite different depending on species. Isomorphic species have sternal bars (fig. 3A) that are typically sub-linear with parallel margins, i.e., really bar-like, and show little or no variation from anterior to posterior through the whole sequence. Heteromorphic sternal bars (figs. 1B, 3B, C) exhibit a variety of shapes, with either convex and concave margins, or flap-like pointed forms. Heteromorphy within species is characterized by an enlarged, flap-like sternal bar on the 14th trunk somite. This bar is distinctly larger than those anterior or posterior to somite 14. In addition, the sternal bars anterior to somite 14 are typically narrower than the posterior series, and have almost parallel margins. However, heteromorphy of sternal bars can also be observed across species. For example, the posterior series of sternal bars in *Lasionectes entrichoma* (fig. 3B) have concave margins, while *Speleonectes benjamini* Yager, 1987 (fig. 3C) and *Cryptocorynetes haptodiscus* Yager, 1987 have series with convex margins. Moreover, the modified sternal bars on trunk somite 14 vary in shape among heteromorphic species. For example, *L. entrichoma* displays an inflated strut with a concave margin (figs. 2, 3B), while in *S. benjamini* the bar on somite 14 has become altered into a sub-triangular flap (fig. 3C). Such modifications stand in strong contrast to the invariant series of an isomorph such as *Godzillius robustus* Schram, Yager & Emerson, 1986 (fig. 3A).

We wanted to find out whether there are inherent patterns of variation within heteromorphic series of sternal bars. The following six species of remipedes ex-
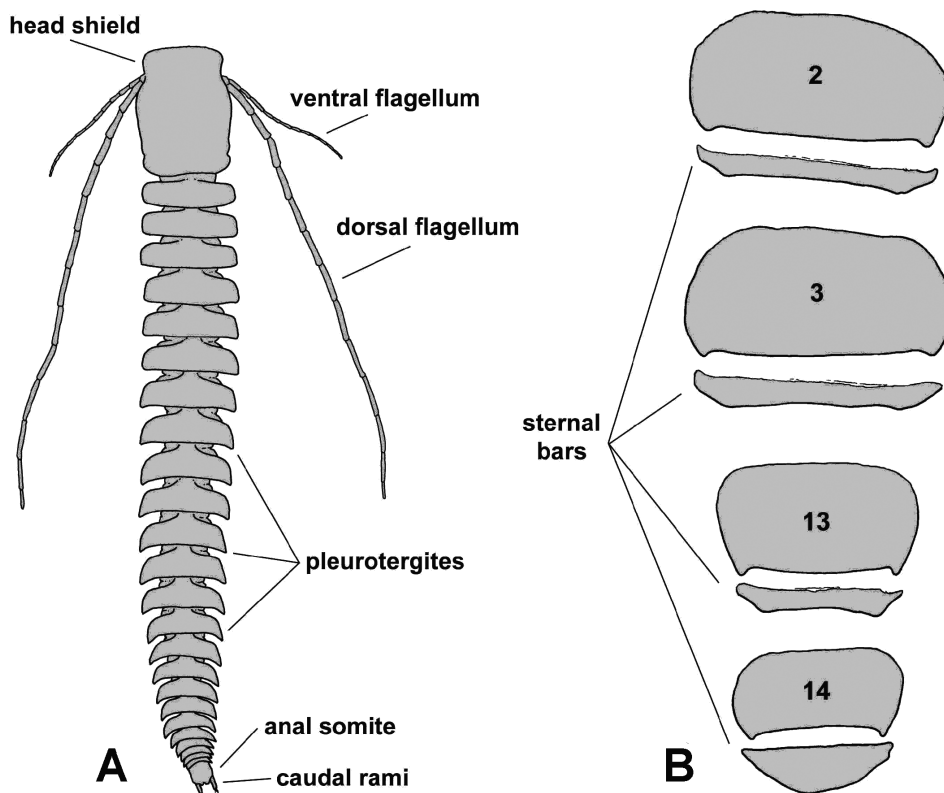
Fig. 1. The remipede crustacean, *Speleonectes parabenjamini* Koenemann, Iliffe & Van der Ham, 2003: A, head and trunk, dorsal view; B, sternites and sternal bars from ventral trunk; numbers represent individual trunk somites from anterior to posterior. [Modified after Koenemann et al., 2003.]

hibit heteromorphy: *Cryptocorynetes haptodiscus*, *Lasionectes entrichoma*, *L. exleyi* Yager & Humphreys, 1996, *Speleonectes benjamini*, *S. parabenjamini* Koenemann, Iliffe & van der Ham, 2003, and *S. lucayensis* Yager, 1981. All other currently known species of remipedes display isomorphy.

We measured the sternal bars in five of these species (we had only a single, partly dissected specimen of *S. parabenjamini* for study). For every adult specimen at hand we determined the maximum width (from left to right side of the trunk) and length (from proximal to distal margin) of individual sternal bars for each somite from the anterior to the posterior end of the trunk. In some taxa we examined, the sternal bars on the last two or three somites of the trunk were extremely small. Reliable measurements in these cases could not be taken and hence were omitted. For use in a diagrammatic comparison, we calculated the ratios of width by length for each individual sternal bar in all specimens and then calculated the mean ratios for each species (see Appendix A).
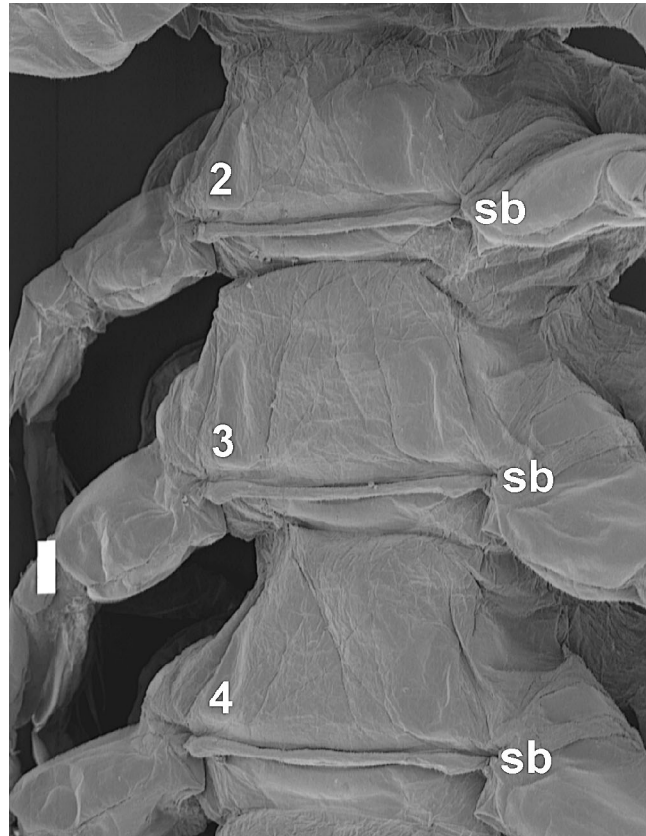
Fig. 2. SEM photo of the remipede crustacean, *Lasionectes entrichoma* Yager & Schram, 1986: ventral view of anterior trunk. Numbers indicate individual trunk somites; sb, sternal bar; scale bar, 100 μm.

As can be seen from the results in fig. 4, considerable variation in the width/ length ratios exists throughout the length of the trunk of the remipedes we studied. Plots of the ratios reveal that the sternal bars do **not** exhibit invariant slopes from anterior to posterior as one would expect in an isomorphic, truly homonomously segmented trunk such as in *G. robustus*. Rather, several consistent inflexion points and changes of slope on the curve characterize these plots. The first change of slope that can be noted in all five species occurs between somites 5 and 7. The most striking change is the mid-body inflexion associated with somite 14, the somite that bears the male gonopores. Here, a strong point of deflection occurs on a generally decreasing slope. In three species, this decreasing slope continues to a region between somites 24 and 25, after which slopes rise again. In *L. entrichoma*, this inflexion point begins at trunk somite 22. The two species with the largest numbers of trunk somites, *S. lucayensis* ($n = 2$) and *L. entrichoma* ($n = 9$), show inflexion points beyond somite 27.
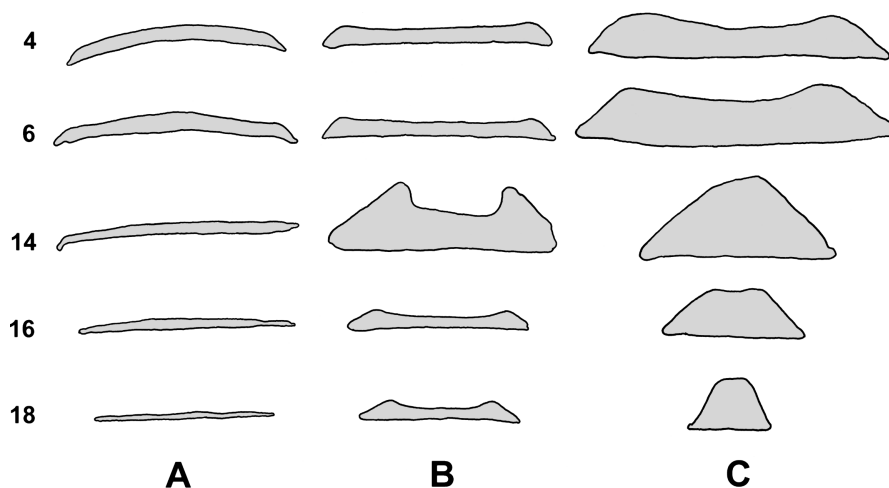
Fig. 3. Different types of sternal bars in three species of Remipedia: A, isomorphic sternal bars in *Godzillius robustus* Schram, Yager & Emerson, 1986; B, heteromorphic sternal bars in *Lasionectes entrichoma* Yager & Schram, 1986; C, heteromorphic sternal bars in *Speleonectes benjamini* Yager, 1987. Numbers indicate individual trunk somites.
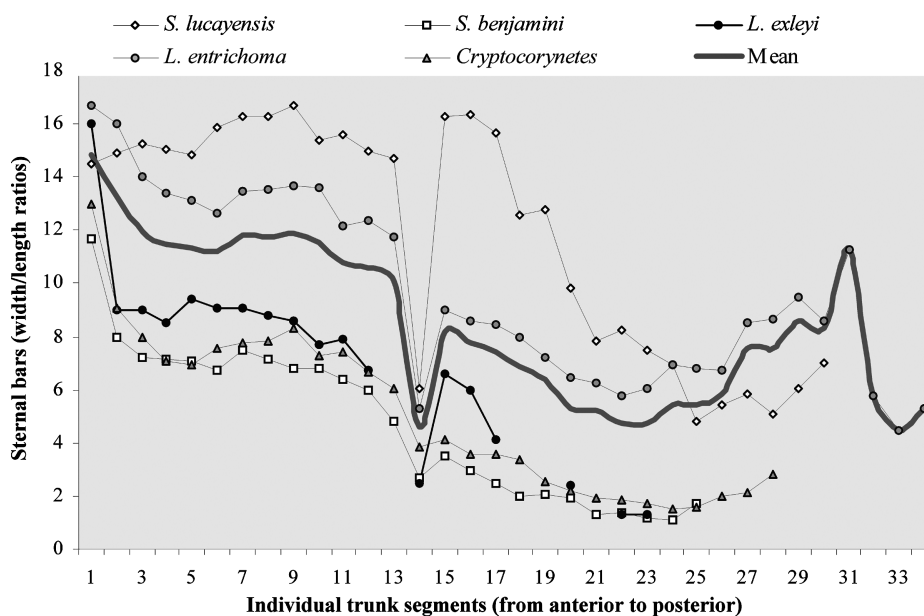
Fig. 4. Morphometric variation of sternal bars in five heteromorphic species of remipedes: *Cryptocorynetes haptodiscus* Yager, 1987; *Lasionectes entrichoma* Yager & Schram, 1986; *L. exleyi* Yager & Humphreys, 1996; *Speleonectes benjamini* Yager, 1987; *S. lucayensis* Yager, 1981. Please note that gaps in the series for the single specimen of *L. exleyi* are due to damaged somites. The bold gray curve represents the mean values for all heteromorphic remipedes investigated. See text for details.

Interestingly, two of these consistent inflexions correspond with the location of the gonopores: the female pores on trunk somite 7 and the male pores on somite 14. The functional or topographic significance of the heteromorphic morphologies is not evident. Since both shape and size of the sternal bars associated with the location of the male gonopores are strikingly different, one is tempted to spin off all sorts of copulatory explanations. For example, the distinctly modified bar on trunk somite 14 might be part of a 'lock and key' device, or a device to facilitate transfer of a spermatophore, or some other kind of morphological marker to facilitate copulation. The conceivable range of possible scenarios includes a 'head-to-tail' copulation with simultaneous mutual insemination, a 'head to gonopore' contact to pick up spermatophores for subsequent ex- or internal self-insemination with foreign sperm ('pseudo-self-insemination'), or simply a 'chest to chest' copulation (with trunk somite 7 of individual A connecting with trunk somite 14 of individual B).

However, any of these cases implies that the six heteromorphic species should have a higher reproductive success than the 10 isomorphic species currently known. One could come up with a variety of other functional scenarios, but without real observations of interactive behavior from the laboratory or field, it would be idle to speculate. In fact, genuinely nothing is known about the modes of reproduction and development in remipedes, i.e., we do not even know whether remipedes copulate at all, or whether they reproduce through external fertilization.

Nevertheless, it seems clear that we can no longer be comfortable with a generic disclaimer that the trunk of the remipedes is homonomous. The animals are much more complicated than that.

JUST HOW MANY TRUNK SOMITES ARE THERE?

Much of the available data concerning remipede trunk dimensions in the literature up to this point have been incomplete, and sometimes confusing and contradictory. This situation may in fact have contributed to a tendency among workers to largely ignore the incipient or obscure structural division within the trunk region. While the head of Remipedia consists of six somites (apparently with a tendency to integrate the first trunk somite into the cephalon), the literature only indicates a range of numbers for the total segmental make-up of the trunk. The number of trunk somites varies between species within a genus, but there is also considerable variation among individuals of a species.

Although intraspecific variation has been recorded in some places in the literature, it has seldom been clearly documented with detailed records, since often only information concerning the maximum number of trunk somites and the

largest body size have been provided. The literature generally distinguishes three categories of individuals: juveniles, sub-adults, and adults. However, it has never been clearly defined as to what constitutes membership in one of these categories, though some loose criteria seemed to prevail. Juveniles appeared to be those individuals of around 16 trunk somites and only a couple of mm in length. Adults, of course, were assumed to be reproductive and have variable somite numbers generally ranging from the high 20s into the low to middle 30s. Sub-adults, on the other hand, were regarded as individuals somewhere 'in between', generally with somite numbers in the low 20s.

We have compiled body lengths and trunk somite numbers for 139 specimens of all currently known species of Remipedia, including 16 described species, four undescribed taxa, and two unidentified very small specimens (Appendix B). In all specimens we examined, body lengths were measured from the anterior margin of the head shield to the posterior margin of the abdominal somite; the trunk somite numbers we recorded do not include the abdominal somite. In addition, we compiled trunk somite numbers and body lengths from the literature. However, since generally no information was given concerning how measurements and counts were carried out, we cannot exclude minor discrepancies between our own data and those compiled from the literature. For example, authors may have included caudal rami to measure body lengths, or counted the abdominal somite as an additional trunk somite. Nonetheless, we think that these possible discrepancies are negligible and fall within the normally distributed range of measuring inaccuracies.

Cryptocorynetes haptodiscus **Yager, 1987** was described on the basis of three adult and four sub-adult specimens. The largest of these specimens had a body length of 16.3 mm, and the maximum number of trunk somites observed was 32 [Yager (1987a) did not explicitly state whether both data records were obtained from the same specimen or from two different individuals]. In her table 1, featuring the largest known adults of 10 species of Remipedia, Yager (1994b) recorded 31 trunk somites for *C. haptodiscus* with a maximum body length of 18 mm. Finally, Yager & Carpenter (1999, table 1) entered for this species a range of 28-32 trunk somites corresponding with a range of body lengths from 9.7 to 17.6 mm.

We were able to measure two additional specimens of *Cryptocorynetes haptodiscus* (see Appendix B): one of 28 trunk somites at 11 mm (holotype, USNM 368231, acc. nr. 228198); and the other of 31 somites at 13 mm (collection Yager, BH 232). We also have at hand a single specimen of a new species of *Cryptocorynetes* with a 29-somite trunk of length 7.6 mm (collection of Iliffe/Koenemann).

Godzilliognomus frondosus **Yager, 1989** was described based on 2 specimens, the 7.3 mm holotype and a 7.8 mm paratype. Yager (1989) points out that
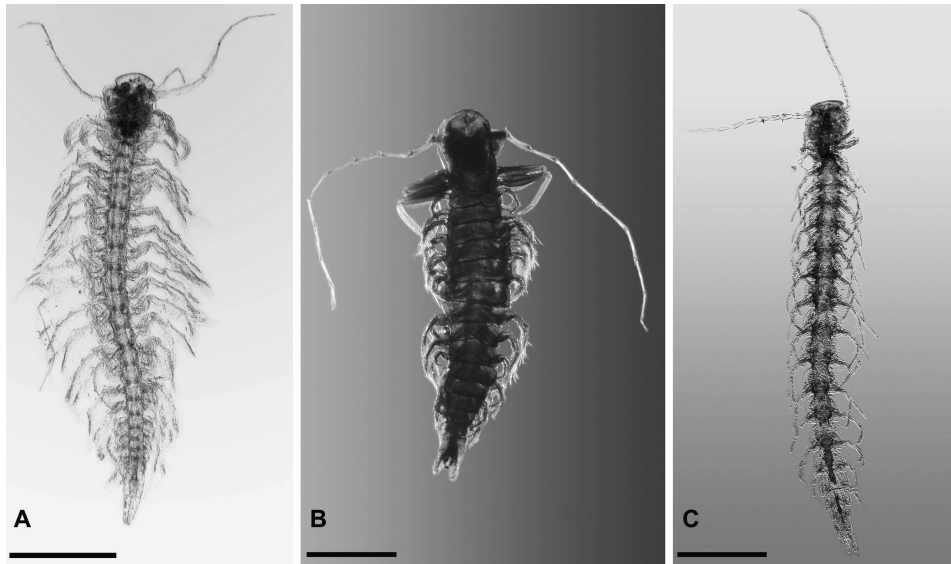
Fig. 5. Sub-adult and juvenile remipedes: A, unidentified sub-adult, 3.8 mm, from Dan's Cave, Abaco Island (SK 03); B, true juvenile of *Godzilliognomus frondosus* Yager, 1989, 4.0 mm, from Dan's Cave, Abaco Island (SK 02); C, sub-adult of a species near *Speleonectes epilimnius* Yager & Carpenter, 1999, 4.9 mm, from Old Freetown Cave, Grand Bahamas Island (SK 04). Scale bars = 1 mm.

G. frondosus is the "smallest species of remipede found to date" and that of 88 specimens collected, "all but six of the smallest individuals have 16 trunk somites, while the small ones have 15".

Seven additional specimens (all collections of Iliffe/Koenemann) we examined fall within the above ranges. However, two 15-somite individuals (3.0 and 3.6 mm, respectively) and one 16-somite specimen (4.0 mm) lacked limbs on the last (posterior) two trunk somites; the limbs on trunk somite 14 were either not detectable or present as small buds without any traces of (developed) gonopores (fig. 5B). Therefore, we consider these specimens as true juveniles. A 16-somite individual (4.7 mm long) lacks a set of limbs on the last trunk somite. Three of our specimens (4.9, 6.2, and 6.5 mm in length) appear to have a complete set of limbs. However, we do not know whether or not these specimens are sexually mature. Thus, *G. frondosus* is the only species of living Remipedia for which the developmental transition between the juvenile and (sub-)adult stages falls within a relatively concise number of trunk somites (14 to 16) and body size (4.0 to 9.3 mm). Since we do not know the developmental onset of sexual maturity, we consider the maximum recorded body size, 9.3 mm, as the sexually mature stage.

***Godzillius robustus* Schram, Yager & Emerson, 1986** was originally described based on two individuals: the holotype of 29 somites with a body 43.2 mm

long, and a shorter, smaller paratype. We have re-measured the paratype (SDNHM 2215) and noted a trunk of 28 somites and a body length of 35 mm. A third specimen is now available from the collection of Th. M. Iliffe (02-015) that possesses 27 trunk somites and is some 22.2 mm in length (Appendix B).

Kaloketos pilosus **Koenemann & Yager, 2004** is known from only two specimens: a 40-somite individual that is 26.5 mm long, and a specimen with 41 trunk somites and 29.0 mm body length.

Lasionectes entrichoma **Yager & Schram, 1986** has the most material available for study of any species of remipede. Schram et al. (1986, table 3) recorded from some 47 specimens of this species trunk somites ranging from 26 to 32 and body lengths from 11.8 to 31.5 mm. Yager (1994b) observed for this species 32 somites and a length of 33 mm as the maxima. Yager & Carpenter (1999) recorded a range of 16-32 trunk somites corresponding with a size ranging from 9.0 to 32.8 mm. We assume that the inconsistencies in maximum body length between Yager (1994b) and Yager & Carpenter (1999) may be due to rounding off and therefore use the more precise data of Yager & Carpenter for our comparison.

We have data for 48 specimens for this study that include many, but not all, of the specimens in Schram et al. (1986) plus additional material from recent field collections. Some 46 of these specimens range from 25 to 34 somites and extend from 10.7 to 32.8 mm in length. Two significantly smaller specimens (4.5 mm with 21 somites, and 9.0 mm with 16 somites) stand apart from the main cluster of larger specimens (fig. 6).

Lasionectes exleyi **Yager & Humphreys, 1996** had listed in its description one of the most complete specimen catalogs up to that time. The original sample contained one individual composed of 21 somites with a body length of 10.1 mm; and four individuals with 24 trunk somites and lengths of 10.3, 12.8, 14.2, and 14.5 mm, respectively.

Pleomothra apletocheles **Yager, 1989** was described based on 4 adults and 2 juveniles. Although Yager (1989) gives the maximum number of trunk somites (25) and the maximum body length (17.1 mm), it remains unclear whether both maxima were recorded for the same specimen. However, Yager (1994b) recorded these same numbers, i.e., 25 trunk somites and 17 mm length, for the largest known individual of *P. apletocheles*. Subsequently, Yager & Carpenter (1999) register a range of 16-25 somites for this species and a body size range of 5.2-17.1 mm. For our analysis, we assume that the maxima given by Yager (1989, 1994b) and Yager & Carpenter (1999) are based on the same individual, and that 17.1 mm (instead of 17 mm) is the accurate body length. We have been able to examine the holotype (USNM 235301), which has a trunk consisting of 24 somites and a body length of
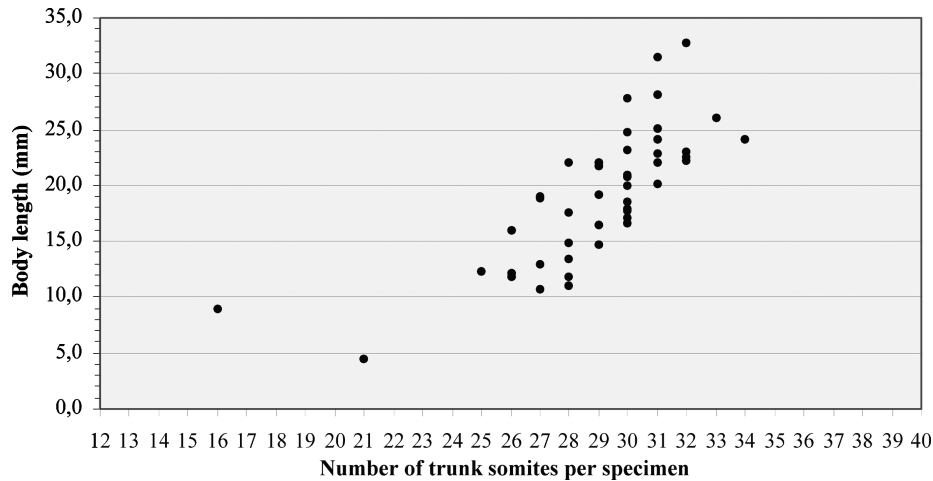
Fig. 6. Trunk somite numbers plotted against total body length for specimens of *Lasionectes entrichoma* Yager & Schram, 1986 ($n = 48$).

11.6 mm. Yager (1989) recorded a length of 12.3 mm for the holotype. We think that Yager may have included the length of the caudal rami with the total body length, which is the most likely explanation for this discrepancy of less than 1 mm. Either that, or there has been shrinkage of the specimen, which is possible. In addition, we can note here that a single specimen of a new species of *Pleomothra* we have at hand is 18.5 mm long with a 26-somite trunk.

Speleonectes benjamini **Yager, 1987** was described based on four adults, for which a maximum number of 27 trunk somites and a maximum body length of 16.8 mm were recorded. Yager (1987a) did not explicitly state whether these maxima were obtained from a single specimen or from several individuals. Yager (1994a, b) gave a maximum trunk length of 27 somites and a maximum size of 18 mm for the largest known adult of this species, and included minima for the "smallest juvenile or sub-adult": 20 trunk somites and 4.9 mm length (Yager, 1994a). Yager & Carpenter (1999) recorded for all described specimens of *S. benjamini* 20-27 trunk somites with a size range of 4.9-18.0 mm.

We re-examined the holotype and measured a body length of 14 mm. This is a 2.8 mm deviation from the length originally recorded by Yager (16.8 mm). Therefore, we used the mean value (15.4 mm) for our data. We also had access to additional material that included a 20-somite specimen of 8.2 mm and a 28-somite individual that is 20.0 mm in length.

Speleonectes epilimnius **Yager & Carpenter, 1999** was collected from caves on San Salvador Island, Bahamas. The original description is based on 8 specimens, of which the longest (18.3 mm) specimen possessed 21 trunk somites. The

body lengths of all 8 specimens ranged from 8.7 to 18.3 mm, while the range of trunk somites was limited to 20-21. This is a relatively wide size range (9.6 mm, some 52%) with one of the most restricted somite variations recorded up to that time.

We have an additional rather small specimen (fig. 5C) that appears to be a new species, morphologically close to *S. epilimnius*. This juvenile or sub-adult from Grand Bahama Island is 4.9 mm long and has 18 trunk somites.

Speleonectes gironensis **Yager, 1994** was recognized based on 14 specimens. The maxima for body length (14 mm) and trunk somite numbers (25) were observed in the holotype, while the smallest specimen (3.6 mm) had 19 trunk somites. These data also appeared again in Yager (1994b). However, Yager (1994a), as well as Yager & Carpenter (1999) further specified a trunk somite range from 19 to 25 somites and a body length lying between 3.6 and 14.0 mm. We assume the lowest somite number goes with the shortest body length (though this is not always true), but unfortunately no specific information is available on the distribution of trunk somites and body lengths in between maximum and minimum.

We had an opportunity to examine the holotype (USNM 259702) and confirm the data recorded by Yager (1994a). An additional specimen made available to us by J. Yager (CB 27) was 11.0 mm long and had 24 trunk somites.

Speleonectes lucayensis **Yager, 1981** was the first described species of the class Remipedia. The four specimens in the type series have 31-32 trunk somites, with a size range of 21.5-24.0 mm. Schram et al. (1986), who re-examined the four type specimens and one additional individual from the type locality, recorded 29-32 trunk somites and body lengths (based on 3 specimens) extending from 15 to 23.8 mm. Unpublished notes for the Schram et al. (1986) study provide the following additional data for these specimens: a 15 mm individual with 30 somites; an unmeasured individual with 30 somites; a 23.8 mm individual with 31 somites; and a 21.1 mm individual with 32 somites. Yager (1994a) provided a new minimum record for the smallest juvenile (4.0 mm with 16 trunk somites). The largest known adult (24 mm with 32 trunk somites) listed by Yager (1994b) and Yager & Carpenter (1999) is likely to represent one of the type specimens. Therefore, we did not include this record herein. Re-examination of available material by us uncovered a 12.0 mm individual with 21 trunk somites.

Speleonectes minnsi **Koenemann, Iliffe & Van der Ham, 2003** was based on a single, 18.0 mm specimen with 30 trunk somites.

Speleonectes ondinae **(Garcia-Valdecasas, 1985)** was collected from an anchialine lava tunnel on Lanzarote, Canary Islands. The original description was based on two specimens (19 and 22 somites long), of which only one could be

measured (15.5 mm). However, Schram et al. (1986) had six additional specimens ranging from 19-25 trunk somites and 8.3-16.1 mm in length. Yager & Carpenter (1999) basically listed the same minimum/maximum data, with the exception of the maximum body length (16.7 mm). We assume that the data by Schram et al. (1986) and Yager & Carpenter (1999) are based on the same specimens. We used the mean value (16.4 mm) of their disagreeing maximum body length for our data herein.

The restudy of *S. ondinae* by Schram et al. (1986) included unpublished notes that provided us with additional, detailed data on segmentation patterns: a 9.5 mm individual with 19 trunk somites, and four individuals (8.3, 10.7, 10.8, and 11.7 mm), each of which with 20 trunk somites.

Yager (1994b) entered the maximum length of this species as 17 mm with 25 somites, and recorded an additional 20-somite individual of length 10.1 mm (Yager, 1994a).

***Speleonectes parabenjamini* Koenemann, Iliffe & Van der Ham, 2003** is known from only two specimens. The 9 mm holotype has 22 somites; the paratype has 24 somites and measures 13 mm in length.

***Speleonectes tanumekes* Koenemann, Iliffe & Van der Ham, 2003** was described from a collection of 13 individuals. For three specimens specific somite numbers and body lengths were recorded (20 mm with 38 somites; 24 mm with 38 somites; 27 mm with 40 somites). Of the remaining 10 specimens, four had 39 somites and ranged from 19 to 25 mm, the others had 40 somites and did not exceed 26 mm.

***Speleonectes tulumensis* Yager, 1987b** was based on a collection of 21 adults, one sub-adult, and eight juveniles. In the original description, it was noted that the maximum number of trunk somites was 36 and the maximum body length 27.5 mm, but no data for smaller sizes were provided. Felgenhauer et al. (1992) confirmed that this species can "consist of as many as 36 segments". Yager (cf. Yager, 1994a, b; Yager & Carpenter, 1999) recorded 38 trunk somites and 30.2 mm as maxima for this species ("30 mm" in Yager, 1994b), and 17 somites as the minimum for the smallest known, 7.2 mm juvenile (Yager, 1994a; Yager & Carpenter, 1999). We examined a portion of the type series and confirmed the data given in the literature. In addition, we were able to record a relatively small (4 mm) paratype with 18 trunk somites.

***Speleonectes* sp. A** is an undescribed species from Yucatan, Mexico, that appears to be morphologically close to *S. tulumensis* (description in prep. by J. Yager). From material we have collected, it obviously has the most somites of any

known remipede, up to 42 somites, and it has a body length ranging from 20.6 to 40.8 mm (Appendix B).

New taxon M (S. Koenemann, in prep.) represents a new species, genus and family of Remipedia. Like *Godzilliognomus frondosus* it has a very short trunk that does not exceed 16 somites. Although this is a comparatively small species with a maximum body length of 13.1 mm, the smallest specimen (3.0 mm) seems to fall within the size range of juveniles of other species. The male gonopores on trunk somite 14 were not detectable in this specimen.

Finally, we have an **unidentified sub-adult specimen** 3.8 mm long with 22 trunk somites from Abaco Island that cannot be identified as one of the hitherto described species (fig. 5A).

DISCUSSION

To date, no remipedes have been collected with less than 15 trunk somites, and after almost 25 years of research we still do not know how the remipedes develop before the 15-somite stage. However, we can derive several conclusions from our data that offer new insights and address important points about basic remipede biology.

1. Among all the species of Remipedia investigated, the 48 specimens of *Lasionectes entrichoma* provided us with the largest sample size. The data plot in fig. 6 shows a cluster of larger specimens with trunk somites ranging from 25 to 34, while two single records of smaller specimens appear as outliers. We do not assume that this pattern of data records represents the normal distribution of individuals within a natural population. Instead, it more likely reflects a biased sample that is the result of various limitations related to collecting specimens in anchialine cave systems. In the vast majority of explored caves, remipedes, like most stygobionts, are very scarce. It is obviously easier to spot a single, larger individual than a small juvenile that is only a few mm in length. Moreover, juveniles may occupy less accessible micro-habitats, for example, cracks and crevices or bottom substrate.

Nevertheless, the data records of *Lasionectes entrichoma* show some interesting patterns. There is a distinct spread of body sizes in specimens with the same number of trunk somites. This spread seems to occur consistently in all somite categories. For example, specimens with 28, 30, 31, or 32 trunk somites exhibit size differences from 10.6 to 11.3 mm, which is approximately 1/3 of the total maximum body length. Similarly, of the two outliers, the shortest of all investigated specimens (4.5 mm) has 21 trunk somites, while the individual with the smallest number of trunk somites (16) is twice as long. The same trend of varying body

sizes can also be observed in other species, although we need larger sample sizes before we can draw unambiguous conclusions. One possible explanation for these size variations could be the fact that the specimens investigated in this study have been collected over a period of 20 years, and the sample might reflect long-term, perhaps periodical (or) climatic, fluctuations. In this scenario, molts during which trunk somites might be added could have occurred at much shorter intervals in generations with less limited resources (opposed to resource-limited generations that developed and grew at a lower rate). However, it is also conceivable that resources are distributed heterogeneously in a cave system and affect disjunct subpopulations of the same generation.

2. We have a distinct criterion to define a juvenile remipede. In three very small specimens of *Godzilliognomus frondosus* (3.0, 3.6, and 4.0 mm; see fig. 5B) and in a 3.0 mm specimen of the new taxon M, the limbs on trunk somite 14 (which bear the male gonopores) were either lacking or developed as small buds, and gonopores were not detectable. These individuals are obviously sexually immature and, therefore by definition, true juveniles.

One critical issue that is still quite unresolved concerns the mode of development in Remipedia. The many 'juveniles' described in the literature do not necessarily imply that these are the earliest developmental stages. Until now, true larvae seem to be lacking in the life cycle of remipedes, i.e., a nauplius, or intermediate stages between a nauplius and the 15-somite juveniles. Does this indicate that remipedes might just be epimorphic and hatch at the relatively advanced 15-somite stage? The smallest juveniles are in the range of 3 mm body length, and special efforts would need to be exerted to collect individuals smaller than that, especially if smaller also means shorter trunk somite numbers and thus not as readily visible to cave diving collectors.

However, numerous tows with plankton nets (93 μm mesh) in a variety of caves containing remipedes have yielded abundant collections of tiny copepods and ostracodes, but failed to turn up any smaller forms of remipedes. Remipedes inhabit lightless, fully marine salinity, low dissolved oxygen waters (generally less than 1 mg/l) of both limestone and volcanic (lava tube) caves. A suite of other stygobitic taxa including halocyprid ostracodes, epacteriscid and misophrioid copepods, thermosbaenaceans, cirolanid isopods, and shrimp are typically associated with remipedes (Iliffe, 2004). Some caves inhabited by remipedes are geologically recent, e.g., the Monte Corona lava tube on Lanzarote, Canary Islands, is believed to have formed about 4,000 to 5,000 years ago (Iliffe et al., 2000), while all currently known anchialine remipede habitats were dry and air-filled during Pleistocene glacial low sea stands occurring as recently at 18,000 years ago. Thus, it is highly likely that remipedes at one time inhabited yet undiscovered environments in older rocks and/or at greater depths and have only colonized their present

habitats when caves were newly formed or were flooded by raising post-glacial sea levels. Indeed, remipedes may still carry out significant parts of their life cycle, including early developmental stages, in currently inaccessible, deeper (below 100 m) cave or crevicular habitats.

3. We have no solid criteria to distinguish between true juveniles and true (= sexually mature) adults. In the literature, the terms 'juvenile', 'sub-adult', and 'adult' are used ad libitum, i.e., the largest specimens are regarded as adults, the smallest individuals as juveniles, and the vague size/somite range in between is occupied by sub-adults. In the reported data herein, a very small (3.6 mm) juvenile with 19 trunk somites was recorded for *Speleonectes gironensis*, although it is possible that this individual could be a sub-adult or even a sexually mature adult. [In fact, the same indefinable classifications have been used for almost all taxa by almost all authors.] We also cannot predict the onset of sexual maturity for the three truly juvenile specimens of *Godzilliognomus frondosus*: it may occur at the 15-somite or 16-somite stage, and, within the 16-somite stage, during an early or delayed developmental phase. Therefore, we cannot yet confidently distinguish between true juveniles and adults unless we know how remipedes develop and/or reproduce.

4. Similarly, the distinction between adults and sub-adults is loosely based on body sizes and the numbers of trunk somites. The term 'adult' implies that an individual is a fully grown and mature organism. However, our compilation of data does not reliably confirm an upper limit of body size and/or somite numbers for any of the species we investigated. The attribute 'fully grown' remains ambiguous. For example, the largest sample (*Lasionectes entrichoma*) contains a single specimen with 34 trunk somites, the maximum number recorded for that species. However, this specimen is 8.4 mm shorter than an individual with 32 trunk somites. This pattern appears similar to those seen in other species. Even the only two species for which we assume a fixed maximum number of 16 trunk somites, *Godzillognomus frondosus* and the new taxon M, do not exhibit a distinct upper limit of body sizes. It seems that in some samples of the larger species, an upper limit may have been reached, for example, 42 trunk somites and 41 mm in *Speleonectes* sp. A, from the Yucatan Peninsula. However, a sample size of $n = 7$ is too small to draw any reliable conclusion. We do obviously need much larger sample sizes to be confident about upper length and segmentation limits in adult remipedes. Therefore, until proven otherwise, we assume that the total somite number for adult remipedes for most species is not fixed but is rather variable.

This alleged fluidity of trunk somite numbers is unique among the arthropods, which typically have a fixed number of somites in the body by the adult stage. Deviations from that are rare, and certainly do not involve more than one or

two somites as is sometimes seen in myriapods (see Minelli, 2000, 2001). The only other exception within the Crustacea are the Notostraca, for which a varying number of post-maxillary somites has been recorded: 32-44 in *Triops* and 26-34 in *Lepidurus* (cf. Olesen, 2001). Our sample of *Lasionectes entrichoma* exhibited a spread of 4 somites in specimens above 25 mm. These spreads of somite numbers in remipedes seem rather high by most standards. Although we cannot say that all these animals were at a functional reproductive stage, we can say that these individuals bear fully developed gonopores and thus at least had the potential to reproduce.

It would appear that remipedes keep growing both in regard to absolute body size as well as to number of somites in the trunk once they reach the reproductive adult stage. This stands in contrast to what we know for other crustaceans that exhibit increases in body size correlating only with an increase in brood size or numbers of eggs produced (Hartnoll, 1985; Wenner et al., 1985) and not with increases in somite number. Thus, it is generally agreed that larger size is linked to longevity, and that both in turn are linked to fecundity, forming effectively a triad of selective adaptation. It is noteworthy in this regard that almost all crustaceans have uncoupled growth in size from increase in somite number (Botsford, 1985). Thus, in this respect, remipedes are not exceptional. However, while we know a great deal about the hormonal control of molting in crustaceans (Skinner et al., 1985), we lack any knowledge as to what controls the termination of somite formation. Some information indicates that such control is possibly programmed at a deeper genetic level (Hughs & Kaufmann, 2002; Schram & Koenemann, 2003). Clearly we have much to learn about the interaction of hormonal controls of growth and molting, and genetic constraints of body plans in crustaceans.

5. Plots of mean body lengths against the number of trunk somites of all available remipede data do seem to indicate that body length increased exponentially with increasing numbers of trunk somites (fig. 7). We also assume that the longer the trunk in remipedes, the greater is the variation of somite numbers in true adults, since sexual maturity may be reached at intermediate sizes in longer species. Perhaps there is selection in the remipedes to begin reproduction as soon as possible before the maximum size is achieved.

If all the raw data are pooled without regard to species (fig. 8), we can see that body size records occupy an almost continuous space, from the smallest number of trunk somites (14) to the largest (42). The largest spread of body size occurs in specimens with 29 trunk somites (including specimens of the largest remipede recorded at present, *Godzillius robustus*).
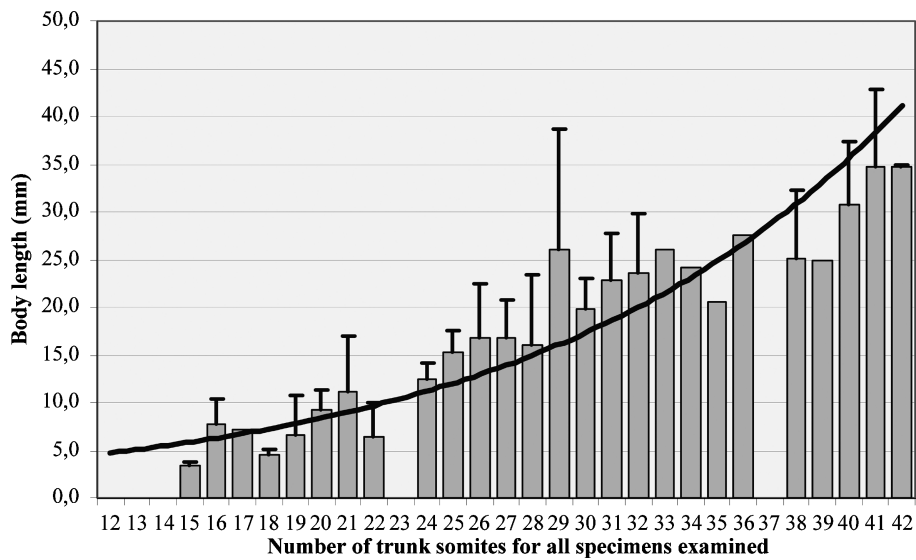
Fig. 7. Mean body lengths (gray bars) and standard deviations of all specimens investigated, plotted against the number of trunk somites ($n = 139$). The black solid curve represents a trend line.
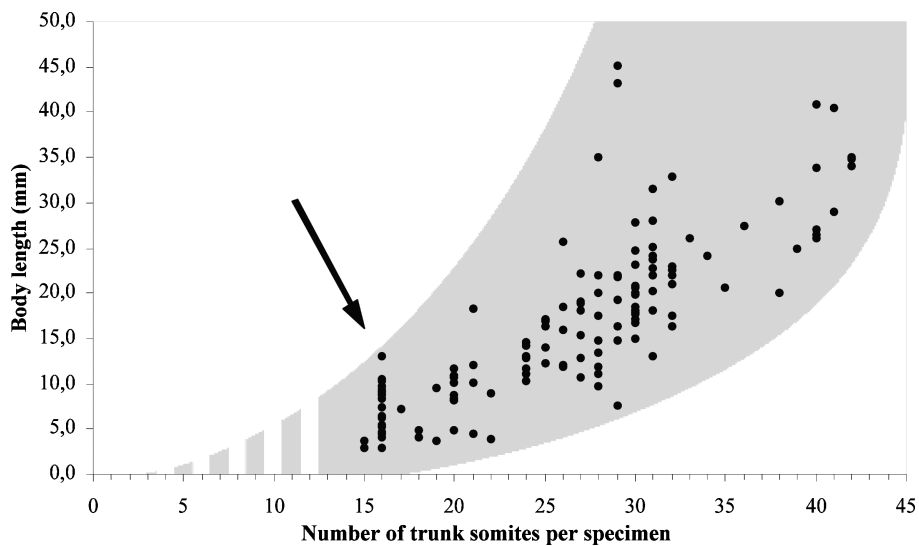
Fig. 8. Number of trunk somites plotted against total body lengths for all specimens of Remipedia investigated ($n = 139$). The black arrow points at a line of data points that belong to two species with 16 trunk somites, *Godzilliognomus frondosus* Yager, 1989 and the new taxon M. The gray shape indicates the predicted morpho-space within which different developmental stages of remipede crustaceans may occur.

CONCLUSIONS

Despite the ambiguity concerning trunk tagmosis, we have found that identifica-
tion of any individual as to species, no matter the size or the developmental stage,
is based on the complex set of features, almost always cephalic, that define that
taxon. It appears that very little alteration in details of mouth part anatomy or other
cephalic structures occur from the juvenile through to the adult condition.

Herein, we explored the variation in remipede trunk segmentation and body size
with a species by species survey (see Appendix B for details). The continuing lack
of any individuals with fewer than 15 trunk somites is uncontestable. One possible
reason for the lack of juveniles could be a collecting bias. Such individuals will be
less than 3 mm in size, and collecting such individuals will require some special
efforts. However, we also cannot rule out the alternative hypothesis that the animals
may actually hatch at a stage with 15 or 16 somites. Only concerted efforts to
collect data on ontogeny and development will answer this question, and this will
undoubtedly require some effort be made to achieve reproduction in the laboratory.

Clearly, the trunk region of Remipedia is of considerable interest. Careful con-
sideration of the available data uncovers patterns that indicate trunk heteromorphy
in some species of remipedes and raises several questions concerning alternative
possibilities in the development of these forms. It appears that a specific effort to
collect smaller and shorter individuals is called for. Of course, concerted efforts di-
rected at long-term maintenance of remipedes in the laboratory and breeding these
animals is a given. It is, nevertheless, obvious that the trunks of remipedes can no
longer be ignored.

ACKNOWLEDGEMENTS

APPENDIX A

Width/length ratios of sternal bars in five species. Mean values are given in bold font type. Abbre-
viations: TS, trunk somites; *L*, *Lasionectes*; *S*, *Speleonectes*; ZMA, Zoological Museum Amsterdam;
SDNHM, San Diego Natural History Museum; USNM, United States National Museum; BH, col-
lection J. Yager.

Coll. nr.	Species	TS1	TS2	TS3	TS4	TS5	TS6	TS7	TS8	TS9	TS10	TS11	TS12
SDNHM 2197	*L. entrichoma*	–	17.7	11.9	12.3	12.3	12.3	12.5	13.0	12.4	12.4	10.2	10.0
SDNHM 2194-1	*L. entrichoma*	11.6	11.8	10.4	9.5	11.0	10.5	11.4	10.4	8.9	8.7	8.6	8.2
SDNHM 2194-2	*L. entrichoma*	17.8	16.4	14.0	14.7	12.8	12.0	13.2	15.5	16.6	16.6	13.7	13.6
SDNHM 2198	*L. entrichoma*	–	15.0	15.3	14.4	13.4	13.8	14.0	12.7	13.1	13.6	11.2	12.2
SDNHM 2192	*L. entrichoma*	–	16.0	14.6	16.2	14.3	16.5	15.8	15.5	18.2	17.0	14.0	17.6
SDNHM 2191	*L. entrichoma*	–	17.3	17.3	14.6	14.0	15.6	16.7	16.0	16.4	14.2	14.6	14.0
SDNHM 2195-1	*L. entrichoma*	–	18.8	13.5	12.3	12.3	10.6	11.5	13.1	12.0	12.6	11.7	10.6
SDNHM 2195-2	*L. entrichoma*	14.8	14.1	12.4	10.9	12.0	11.3	12.2	11.8	11.5	12.7	11.9	11.4
SDNHM 2195-3	*L. entrichoma*	22.5	16.9	16.8	15.8	16.2	11.3	13.6	13.6	13.8	14.7	13.8	14.0
	L. entrichoma	**16.7**	**16.0**	**14.0**	**13.4**	**13.1**	**12.7**	**13.4**	**13.5**	**13.7**	**13.6**	**12.2**	**12.4**
BH 232	*Cryptocorynetes*	–	10.8	9.4	8.1	7.2	7.8	8.1	8.8	9.5	7.3	7.6	7.1
USNM 368231	*Cryptocorynetes*	13.0	7.3	6.5	6.1	6.7	7.3	7.4	6.8	7.1	7.2	7.3	6.2
	Cryptocorynetes	**13.0**	**9.1**	**8.0**	**7.1**	**7.0**	**7.6**	**7.8**	**7.8**	**8.3**	**7.3**	**7.5**	**6.7**
USNM 184343	*S. lucayensis*	17.0	17.0	17.1	16.9	17.7	18.3	18.6	19.0	19.3	16.6	18.6	18.6
SDNHM 2189	*S. lucayensis*	12.0	12.8	13.4	13.2	12.0	13.5	14.0	13.6	14.1	14.2	12.6	11.4
	S. lucayensis	**14.5**	**14.9**	**15.3**	**15.1**	**14.9**	**15.9**	**16.3**	**16.3**	**16.7**	**15.4**	**15.6**	**15.0**
BH 35	*S. benjamini*	10.2	7.7	7.2	7.1	7.6	7.0	7.6	7.0	7.1	6.3	7.0	7.0
USNM 228199	*S. benjamini*	13.2	8.8	7.5	7.2	7.1	7.2	7.7	7.6	7.2	7.6	6.8	5.9
ZMA CA8050	*S. benjamini*	–	7.5	6.9	7.2	6.6	5.9	7.2	6.9	6.2	6.6	5.3	5.0
	S. benjamini	**11.7**	**8.0**	**7.2**	**7.2**	**7.1**	**6.7**	**7.5**	**7.2**	**6.8**	**6.8**	**6.4**	**6.0**
USNM 274190	*L. exleyi*	16.0	9.0	9.0	8.5	9.4	9.1	9.1	8.8	8.6	7.7	7.9	6.7

Coll. nr.	Species	TS13	TS14	TS15	TS16	TS17	TS18	TS19	TS20	TS21	TS22	TS23
SDNHM 2197	*L. entrichoma*	10.4	5.2	9.0	9.6	8.2	8.7	8.2	5.8	6.5	6.7	6.7
SDNHM 2194-1	*L. entrichoma*	7.7	5.1	8.1	6.9	7.4	6.4	5.7	4.8	5.4	4.9	5.0
SDNHM 2194-2	*L. entrichoma*	11.8	4.9	8.2	7.0	6.8	6.9	5.6	6.1	5.4	5.0	5.7
SDNHM 2198	*L. entrichoma*	12.6	5.7	10.3	9.8	9.6	10.2	8.8	7.1	7.2	7.1	8.3
SDNHM 2192	*L. entrichoma*	14.7	5.5	10.1	8.1	8.2	8.2	8.4	6.4	6.6	5.4	6.5
SDNHM 2191	*L. entrichoma*	13.4	5.6	7.4	7.9	10.2	7.5	6.9	6.2	6.1	3.4	5.0
SDNHM 2195-1	*L. entrichoma*	11.7	5.6	9.5	9.1	8.6	7.1	5.4	6.0	6.1	5.9	5.8
SDNHM 2195-2	*L. entrichoma*	10.5	3.4	8.2	9.3	8.5	8.4	7.4	7.6	7.6	6.2	5.4
SDNHM 2195-3	*L. entrichoma*	13.2	6.6	9.9	9.6	8.7	8.4	8.7	7.9	5.6	7.2	5.9
	L. entrichoma	**11.8**	**5.3**	**9.0**	**8.6**	**8.5**	**8.0**	**7.2**	**6.4**	**6.3**	**5.8**	**6.0**
BH 232	*Cryptocorynetes*	6.3	4.0	4.2	3.5	3.9	3.6	2.5	2.3	1.9	1.8	1.6
USNM 368231	*Cryptocorynetes*	5.8	3.7	4.1	3.6	3.3	3.1	2.6	2.1	2.0	1.9	1.8
	Cryptocorynetes	**6.1**	**3.9**	**4.2**	**3.6**	**3.6**	**3.4**	**2.6**	**2.2**	**2.0**	**1.9**	**1.7**
USNM 184343	*S. lucayensis*	18.6	6.5	19.7	19.5	19.0	15.3	14.6	9.2	8.5	9.0	8.6
SDNHM 2189	*S. lucayensis*	10.8	5.6	12.9	13.2	12.3	9.9	10.9	10.4	7.1	7.5	6.4
	S. lucayensis	**14.7**	**6.1**	**16.3**	**16.4**	**15.7**	**12.6**	**12.8**	**9.8**	**7.8**	**8.3**	**7.5**
BH 35	*S. benjamini*	4.8	2.7	3.1	2.5	2.4	2.2	3.1	3.2	–	–	–
USNM 228199	*S. benjamini*	4.7	2.9	4.1	3.4	3.0	2.2	2.0	1.6	1.6	1.6	1.3
ZMA CA8050	*S. benjamini*	5.0	2.4	3.4	3.0	2.0	1.6	1.1	1.0	1.0	1.2	1.0
	S. benjamini	**4.8**	**2.7**	**3.5**	**3.0**	**2.5**	**2.0**	**2.1**	**1.9**	**1.3**	**1.4**	**1.2**
USNM 274190	*L. exleyi*	–	2.5	6.6	6.0	4.1	–	–	2.4	–	1.3	1.3

Coll. nr.	Species	TS24	TS25	TS26	TS27	TS28	TS29	TS30	TS31	TS32	TS33	TS34
SDNHM 2197	*L. entrichoma*	6.0	7.6	8.7	6.5	7.3	–	–	–	–	–	–
SDNHM 2194-1	*L. entrichoma*	5.0	4.3	4.3	4.6	5.4	7.7	13.7	–	–	–	–
SDNHM 2194-2	*L. entrichoma*	5.0	3.8	3.9	5.3	4.6	4.8	4.8	7.8	–	–	–
SDNHM 2198	*L. entrichoma*	10.0	12.3	10.7	14.9	18.8	12.7	10.1	14.8	5.8	4.5	5.3
SDNHM 2192	*L. entrichoma*	11.9	11.3	13.2	14.3	8.8	8.0	–	–	–	–	–
SDNHM 2191	*L. entrichoma*	6.0	4.5	4.9	5.2	6.7	–	–	–	–	–	–
SDNHM 2195-1	*L. entrichoma*	6.2	7.3	5.4	7.5	9.4	14.6	–	–	–	–	–
SDNHM 2195-2	*L. entrichoma*	7.5	5.0	5.0	10.4	10.4	–	–	–	–	–	–
SDNHM 2195-3	*L. entrichoma*	5.1	5.0	4.8	7.8	6.7	9.0	5.8	–	–	–	–
	L. entrichoma	**7.0**	**6.8**	**6.8**	**8.5**	**8.7**	**9.5**	**8.6**	**11.3**	**5.8**	**4.5**	**5.3**
BH 232	*Cryptocorynetes*	1.5	1.3	2.0	2.1	2.8	–	–	–	–	–	–
USNM 368231	*Cryptocorynetes*	1.5	1.9	2.0	–	–	–	–	–	–	–	–
	Cryptocorynetes	**1.5**	**1.6**	**2.0**	**2.1**	**2.8**	**–**	**–**	**–**	**–**	**–**	**–**
USNM 184343	*S. lucayensis*	8.0	4.3	5.7	8.0	6.0	5.8	7.0	–	–	–	–
SDNHM 2189	*S. lucayensis*	5.9	5.3	5.1	3.7	4.1	6.3	–	–	–	–	–
	S. lucayensis	**7.0**	**4.8**	**5.4**	**5.9**	**5.1**	**6.1**	**7.0**	**–**	**–**	**–**	**–**
BH 35	*S. benjamini*	–	–	–	–	–	–	–	–	–	–	–
USNM 228199	*S. benjamini*	1.1	1.7	–	–	–	–	–	–	–	–	–
ZMA CA8050	*S. benjamini*	1.1	–	–	–	–	–	–	–	–	–	–
	S. benjamini	**1.1**	**1.7**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
USNM 274190	*L. exleyi*	–	–	–	–	–	–	–	–	–	–	–

APPENDIX B

List with recorded body lengths and numbers of trunk somites (TS) for 139 specimens of Remipedia. Abbreviations: BH, CB, collection Yager; HT, holotype; JvdH, collection Van der Ham; notes Schram et al., unpublished notes of the Schram et al. (1986) study; n. sp., new species; *Speleonectes* cf. *epilimnius*, unidentified juvenile near *Speleonectes epilimnius*; SK, collection Koenemann; TI/SK, collection Iliffe/Koenemann; Y&C, Yager & Carpenter; other abbreviations as in Appendix A.

***Cryptocorynetes haptodiscus*:** Y&C 1999: 17.6 mm/32 TS; BH 232: 13.0 mm/31 TS; USNM 368231-228198: 11.0 mm/28 TS; Yager 1994b: 18.0 mm/31 TS; Yager 1987a: 16.3 mm/32 TS; Y&C 1999: 9.7 mm/28 TS.

***Cryptocorynetes* sp. A:** TI/SK: 7.6 mm/29 TS.

***Godzillius robustus*:** Y&C 1999: 45.1 mm/29 TS; SDNHM 2215: 35.0 mm/28 TS; USNM 216980 (HT): 43.2 mm/29 TS; TI 02-015: 22.2 mm/27 TS; Y&C 1999: 25.7 mm/26 TS.

***Godzilliognomus frondosus*:** Y&C 1999: 9.3 mm/16 TS; SK 01: 4.7 mm/16 TS; SK 01: 3.0 mm/15 TS; SK 02 (see figure B): 4.0 mm/16 TS; SK 02: 4.5 mm/16 TS; Y&C 1999: 3.7 mm/15 TS; SK 02: 3.6 mm/15 TS; TI/SK 02-022: 6.2 mm/16 TS; BH 234: 6.5 mm/16 TS.

***Kaloketos pilosus*:** ZMA. Rem. 204641 (HT): 29.0 mm/41 TS; collection Yager: 26.5 mm/40 TS.

***Lasionectes entrichoma*:** Y&C 1999: 9.0 mm/16 TS; Y&C 1999: 32.8 mm/32 TS; SDNHM 2191: 10.7 mm/27 TS; SDNHM 2191: 11.0 mm/28 TS; SDNHM 2191: 16.7 mm/30 TS; SDNHM 2191: 17.1 mm/30 TS; SDNHM 2191: 11.8 mm/28 TS; SDNHM 2192: 17.9 mm/30 TS; SDNHM 2193: 4.5 mm/21 TS; SDNHM 2194: 22.5 mm/32 TS; SDNHM 2194: 26.0 mm/33 TS; SDNHM 2194: 23.0 mm/32 TS; SDNHM 2194: 22.8 mm/31 TS; SDNHM 2195: 17.6 mm/28 TS; SDNHM 2195: 20.0 mm/30 TS; SDNHM 2195: 22.0 mm/29 TS; SDNHM 2195: 18.5 mm/30 TS; SDNHM 2196: 24.2 mm/34 TS; notes Schram et al. 1986, A: 20.2 mm/

31 TS; notes Schram et al. 1986, B: 12.9 mm/27 TS; notes Schram et al. 1986, D: 17.9 mm/ 30 TS; notes Schram et al. 1986, E: 19.2 mm/29 TS; notes Schram et al. 1986, F (HT): 31.5 mm/31 TS; notes Schram et al. 1986, G: 20.9 mm/30 TS; notes Schram et al. 1986, H: 27.8 mm/30 TS; notes Schram et al. 1986, I: 19.9 mm/30 TS; notes Schram et al. 1986, J: 17.7 mm/30 TS; notes Schram et al. 1986, 5: 13.5 mm/28 TS; notes Schram et al. 1986, 6: 16.4 mm/29 TS; notes Schram et al. 1986, 7: 22.2 mm/32 TS; notes Schram et al. 1986, K: 20.7 mm/30 TS; notes Schram et al. 1986, L: 22.0 mm/31 TS; notes Schram et al. 1986, O: 24.7 mm/30 TS; notes Schram et al. 1986, P: 25.1 mm/31 TS; notes Schram et al. 1986, Q: 23.1 mm/30 TS; notes Schram et al. 1986, R: 28.1 mm/31 TS; notes Schram et al. 1986, S: 24.1 mm/31 TS; SDNHM 2196: 21.8 mm/29 TS; TI/SK 03-019: 16.0 mm/26 TS; TI/SK 03-019: 19.0 mm/27 TS; TI/SK 03-019: 22.0 mm/28 TS; TI/SK 03-019: 17.6 mm/28 TS; TI/SK 03-019: 18.9 mm/27 TS; SDNHM 2197: 11.8 mm/26 TS; SDNHM 2197: 12.1 mm/26 TS; SDNHM 2197: 14.8 mm/28 TS; SDNHM 2198: 14.7 mm/29 TS; SDNHM 2198: 12.3 mm/ 25 TS.

Lasionectes exleyi: Holotype: 12.8 mm/24 TS; paratype: 10.1 mm/21 TS; paratype: 14.2 mm/24 TS; paratype: 14.5 mm/24 TS; USNM 274190-415110: 10.3 mm/24 TS.

Pleomothra apletocheles: USNM 235301 (HT): 11.6 mm/24 TS; Y&C 1999: 17.1 mm/25 TS; Y&C 1999: 5.2 mm/16 TS.

Pleomothra **sp. A**: TI/SK: 18.5 mm/26 TS.

Speleonectes benjamini: Y&C 1999: 4.9 mm/20 TS; Y&C 1999: 18.0 mm/27 TS; BH 35: 8.2 mm/ 20 TS; ZMA C.A. 8050: 20.0 mm/28 TS; USNM 228199-368231 (HT): 15.4 mm/27 TS.

Speleonectes epilimnius: Y&C 1999: 8.7 mm/20 TS; Y&C 1999: 18.3 mm/21 TS.

Speleonectes **cf.** *epilimnius*: SK 04 (see fig. C): 4.9 mm/18 TS.

Speleonectes gironensis: CB 27: 11.0 mm/24 TS; Yager 1994a: 14.0 mm/25 TS; Yager 1994a: 3.6 mm/19 TS.

Speleonectes lucayensis: SDNHM 2189: 15.0 mm/30 TS; SDNHM 2190: 12.0 mm/21 TS; USNM 184343 (HT): 22.0 mm/31 TS; notes Schram et al. 1986: 23.8 mm/31 TS; notes Schram et al. 1986: 21.1 mm/32 TS; Y&C 1999, Yager 1981: 4.0 mm/16 TS.

Speleonectes minnsi: Koenemann et al. 2003: 18.0 mm/30 TS.

Speleonectes **sp. A**: TI/SK YUC-04/1: 20.6 mm/35 TS; TI/SK YUC-04/2: 40.8 mm/40 TS; TI/SK YUC-04/3: 34.1 mm/42 TS; TI/SK YUC-04/4: 40.5 mm/41 TS; TI/SK YUC-04/5: 35.1 mm/42 TS; TI/SK YUC-04/6: 33.9 mm/40 TS; TI/SK YUC-04/7: 34.8 mm/42 TS.

Speleonectes ondinae: Notes Schram et al. 1986: 9.5 mm/19 TS; Yager 1994a: 10.1 mm/20 TS; notes Schram et al. 1986: 10.7 mm/20 TS; notes Schram et al. 1986: 10.8 mm/20 TS; notes Schram et al. 1986: 11.7 mm/20 TS; Yager 1994b: 17.0 mm/25 TS; Y&C 1999: 8.3 mm/20 TS; Y&C 1999, Yager 1994a: 16.4 mm/25 TS.

Speleonectes parabenjamini: Koenemann et al. 2003: 9.0 mm/22 TS; Koenemann et al. 2003: 13.0 mm/24 TS.

Speleonectes tanumekes: Koenemann et al. 2003: 27.0 mm/40 TS; Koenemann et al. 2003: 20.0 mm/ 38 TS; JvdH 12-01 A1-3: 25.0 mm/39 TS; JvdH 12-01 A1-3: 26.0 mm/40 TS.

Speleonectes tulumensis: Y&C 1999, Yager 1994a: 7.2 mm/17 TS; Yager 1987b: 27.5 mm/36 TS; Y&C 1999, Yager 1994a: 30.2 mm/38 TS; USNM paratype: 4.0 mm/18 TS.

Unidentified species: SK 03 (see fig. A): 3.8 mm/22 TS.

New taxon M: TI/SK: 8.4 mm/16 TS; TI/SK: 5.5 mm/16 TS; TI/SK: 8.8 mm/16 TS; TI/SK: 8.9 mm/16 TS; TI/SK: 3.0 mm/16 TS; TI/SK: 9.8 mm/16 TS; TI/SK: 7.4 mm/16 TS; TI/SK: 10.5 mm/16 TS; TI/SK: 9.2 mm/16 TS; TI/SK: 10.3 mm/16 TS; TI/SK: 10.4 mm/16 TS; TI/SK: 10.4 mm/16 TS; TI/SK: 13.1 mm/16 TS; JvdH: 9.3 mm/16 TS; JvdH: 9.0 mm/ 16 TS.

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