

## Life history variation in the gastropod genus *Lavigeria* (Thiaridae) of Lake Tanganyika

**Note: this text is an English translation of the paper Kingma, I. & Michel, E. 2000. Variation in reproductive strategies in the ovoviviparous genus *Lavigeria* (Gastropoda: Thiaridae) from Lake Tanganyika, East Africa. (in dutch). Corresp. Blad Ned. Malac. Ver. 312:15-24.**

The ancient lakes in the Rift valley of Eastern Africa (Victoria, Tanganyika & Malawi) are famous for their unique faunas. All three lakes have endemic species flocks. In Victoria and Malawi these flocks seem to be largely restricted to the cichlid fish. However in Tanganyika there are species flocks in numerous invertebrate taxa in addition to the cichlid fishes (Coulter 1991).

For example among the gastropods 80% of the species found in the lake are endemic. Most diversity is displayed in the family Thiaridae. The genus *Lavigeria* it is the most common thiarid genus and at the same time the most diverse (Michel 1995). It has an estimated species diversity of 20 or more endemic species (Michel & Todd, in prep). The often sympatric species show many shell morphological and genetic differences though they are phylogenetically closely related (Michel 1995, Michel in press, Michel & Todd in prep.).

In July and August 1999 we quantified reproductive strategies in 7 different *Lavigeria* species around Kigoma Bay (Tanzania). In this paper we discuss differences in brood and embryo sizes of the different species as the first in a series of reports on our findings.

We address three questions: 1) Are there differences in reproductive strategies among the species? These differences can manifest themselves at three different levels. a) differences in embryo size, b) differences in brood size and c) variation in the development of the brood. 2) Are there differences within a species that are site determined, i.e. do different populations differ in their reproductive strategies?

3) Is there is a trade-off between brood size and size of the embryo, both within and between species?

## Methods

### Sites

Most *Lavigeria* species have centers of species distribution varying between 0-20m depth. We collected by SCUBA and snorkeling at three sites.

We present analyses on differences in brood and embryo sizes among seven, frequently sympatric *Lavigeria* species collected from three sites. We chose sampling sites by their physical differences and geographic distance for two reasons. First because different species are found at dissimilar sites and second because we wanted to know if different conditions could influence different populations of one species. We collected from the following.

- 1) Hilltop Bay is part of Kigoma Bay; waste water and sediment runoff from Kigoma town makes the water here rich in nutrients, which results in a thick algal cover on the rocks. The bay stays shallow until it reaches the Kigoma bounding fault at its mouth. The substrates at the North and South end are a mixture of rocks and sand separated by a sandy beach. We collected in the shallow part at a depth from 1 to 5 meters.
- 2) 5 km South of Kigoma there is a small bay known as Jacobsen's Bay. Apart from farming there is little human influence in this pristine area. There are two small sandy beaches that divide the rocky shoreline. Gastropod species composition differed remarkably between rocky areas north and south of the divisions (Baraka, 1999). The algal cover is much thinner here and there is little accumulated sediment on the rocks. The steep sides of the bay consist of large boulders and rock surfaces. This is the only site where we were able to collect by SCUBA, enabling us to sample from the surface to 18 meters depth.
- 3) We were very fortunate in being able to collect at two sites in Gombe Stream National Park. This park, located about 50 km north of Kigoma, is one of the most

pristine areas around the lake. Here we collected specimens in a small shallow bay at the north end of the park in water less than 4 meters and at the south end of the park we collected from 2-6 meters depth. The substrate consisted of cobbles and rocks with a thin algal cover.

This study includes the follow seven species, from the indicated sample sites.

Open nomenclature is used for species whose taxonomy is currently under revision (Michel & Todd, in prep) and letters corresponding to a field guide for Tanganyikan gastropods (West et al, submitted).

*Lavigeria coronata* Bourguignat 1888

n=60

This species was believed to be extinct until a large population was discovered at the north side of Jacobsen's Bay in the summer of 1998. This is the largest *Lavigeria* species (adult female length: 25.02-35.01 mm) in lake Tanganyika with a heavily sculptured shells. The eggs are green. At Jacobsen's Bay we collected *L. coronata* from 2-18m. It shares its habitat with *L. grandis* and *L. nassa*.

*Lavigeria grandis* (Smith, 1881)

n=60

This species is present all round the lake showing a strong local variation (Michel & Hinkley, in prep). In the Kigoma area we collected it in Jacobsen's Bay and at the north end of Gombe Stream National Park. As its name implies this is a rather large species (adult female length in Kigoma: 22.8-31.20 mm) though individuals caught at Gombe are distinctly smaller (16.46-23.53 mm) also (Michel & Hinkley, in prep). The eggs of individuals in all populations are green. We found it occurring sympatrically with *L. coronata* and *L. nassa* in Jacobsen's Bay and with *L. nassa* and *L. new sp.B* at Gombe. At Jacobsen's we collected it at 1 to 10m, and at Gombe North at 2-4 meters.

*Lavigeria nassa* (Smith, 1881)

n=78

*L. nassa* is another lake-wide distributed species; we found it all our sampling sites. At our sites it's of intermediate size (adult female length 11.55-23.37mm). The eggs are green. At Gombe the juveniles are easily confused for *L. paucicostata* adults, but adults are easily distinguished by a dark brown horizontal band across the shell (Michel & Todd, in prep). It coexists with all other species. The only site where we found just a few individuals was at Jacobsen's Bay in the habitat of *L. coronata*. In the northern part of Jacobsen's Bay we found it more commonly, from 1-15 meters. At the other sites I found it at all collecting depths.

*Lavigeria new species M* (Michel & Todd, in prep)

n=45

This is one of the smaller species with a fine ribbed shell (adult female length 10.17-17.57 mm). Its dark chocolate color makes it quite distinctive, juveniles are a lot darker than those of other species as well. The eggs are green. In this study it was only found in the shallow water of Hilltop Bay occurring right at the surface to 4meters, sympatric with *L. nassa* and with *L. new sp. J* at the south end of the bay. It is absent from the sandy middle part of the bay.

*Lavigeria new species J* (Michel & Todd, in prep)

n=25

This species (adult female length 12.5-18.42 mm) is recognizable because of its distinctive ribbing pattern and conical shape. The embryos of this species are easily recognizable because they are yellow. It occurs sympatrically with *L. new sp. M* at the south end of Hilltop Bay, though it tended to cling to steep sided rocks with far less algal cover.

It did not occur at the surface only below 3 meters.

*Lavigeria paucicostata* (Smith, 1881)

n=28

The name “paucicostata” refers to the course ribs on the shell of this species (adult female length 11.66-17.66mm). Eggs are light yellow. At the south end of Gombe Stream National Park it is sympatric with *L. nassa*, which it resembles in immature stages.

*Lavigeria new species B* (Michel & Todd, in prep)

n=8

This is a brown, fine ribbed species (adult female length 13.22-16.32mm) with green eggs. It is sympatric with *L. grandis* and *L. nassa* at the north end of the Gombe Steam National Park, and does not occur in our sites around Kigoma.

### Disecting

We actively selected for the largest individuals because the focus of the study was on adult reproduction. A thickening of the shell aperture lip generally indicates maturity. However many females are fully reproductive before their aperture lips are completely thickened, therefore we collected a range of the larger individuals in a population with both thin and thick lips to sample across the onset of sexual maturity.

The shell of each individual was measured for five variables carefully broken so the body could be extracted intact.

We were not able to distinguish females from males by shell morphology, so both males and females had to be opened.

After opening we noted sex of the specimen and also if it had been parasitized by trematodes, as parasitization causes a female to stop producing offspring. Results on sex ratio and parasitization will be reported in a later paper.

The brood in a female *Lavigeria* is located in the mantle cavity in the palial oviduct.

If a female proved pregnant we cut open this organ and took out the brood with a brush to measure and count it. Counting was done using a dissecting scope on a petri dish lined with a 1mm grid. We separated embryos into five developmental stages (Figure 1) and measured the size of individuals at each stage.

Voucher specimens were kept of all species for future analysis (DNA and SEM).

## Analyses

We established the median and maximum brood and embryo size (at each developmental stage) for each species and all separate populations. We present these data graphically after analysis in Excel and Statistica.

Reproduction is strongly linked to age. Juveniles (by definition) don't reproduce and the onset of full reproductive output can be gradual, while senescence of the oldest individuals, similarly, can decrease reproductive output (Stearns, 1992). Thus very young or very old individuals may be expected to have smaller broods. Because of the tropical climate we don't have a good way of telling an individuals age. This makes it hard to tell if a small brood is caused by juvenility or senescence or if its just natural variation which is causing broods to be smaller than average. When plotting a distribution like this it ends up as a non-normal distribution with a mean that is drawn down by what appear to be outliers in the distribution. Therefore we chose the median instead of the mean as the center point in our statistical analysis.

## Results

### Median & Maximum brood size

Figure 2 shows median and maximum brood size by species. The species *L. nassa* and *L. coronata* have relatively large broods when compared to the other species. The medians of *L. new sp J*, *L. paucicostata* and *L. new sp B* are relatively close together. *L. new sp M* has the greatest difference between maximum and median brood size, with the maximum four times greater than the median. The species *L. coronata* and *L. nassa* also have maxima significantly larger than the median.

### Embryonic development

Figures 3a-g show the developmental trajectories of each species, plotting average embryo size by developmental stage. The error bars indicate the minimum and maximum embryo size in each stage. We combined 3a-g is combined in figure 3h, to facilitate cross species comparison. To this graph we added a sixth category: the hatching size of the

juvenile. When individuals were kept in tanks for several days they sometimes started releasing their offspring. These were always the largest sized stage V embryos. Embryos don't start growing larger until they pass the third developmental stage. This is when they start developing their shell. We found that the period of fastest growth is generally between the fourth and fifth stage, and from the fifth stage until the point of hatching. Two species differ from this generality. *L. nassa* reaches its maximum size when it reaches the fourth stage, while *L. coronata* doesn't grow much more after reaching early stage V.

As the embryos grow larger they start adding more whorls to their shell. This started in the fourth and continued in the fifth stage. While we made whorl counts throughout the study our final analysis revealed them to be inconsistent (*Reff.*).

#### Site differences

We had data on different populations for three species: *L. grandis* (1 distant and 2 close sites), *L. nassa* (3 distant sites) and *L. new sp. M* (2 close sites) Plots for embryonic development show no clear difference among sites within any of these species (Figures 4a-h). There are however differences in brood sizes (Figures 5a-c). The *L. grandis* individuals collected at Gombe have smaller broods than the ones from Hilltop. *L. nassa* doesn't show the same variation between these two sites; brood sizes are approximately the same in both locations. There is no difference in median brood size of *new sp. M* between the north and the south end of Hilltop Bay, although maxima differed markedly due to one extremely fecund individual.

#### Trade-Offs

To examine the relationship between the maximum size of the embryos and the maximum brood size we plotted these variables against each other (Figure 6a). A regression of all seven species shows an inverse relationship between the variables ( $r^2=$ , dotted line). As *L. grandis*, *L. coronata* and *L. new sp. B* have rather different shell shapes from the other four basically ovately conic species, removed them from the analysis and the relationship between brood size and embryo size for the four similar species becomes practically linear ( $r^2=$ , 4 species). *L. nassa* with its large brood has the smallest offspring

and *L. new sp. J* and *L. paucicostata* both have large offspring and small maximum brood sizes. We distinguish *L. grandis* and *L. coronata* with empty circles, as their size also allows them to have larger oviducts and therefore potentially more space for a brood. This means that they can have a relatively large brood while their embryos can be large as well. We note however that the line describing the relationship between their respective brood and embryo sizes is parallel to the regression for the other species. Thus these large species seem to follow a parallel allometry, but scaled up.

*L. new sp. B* also has a different shell shape which may affect reproductive output (discussed below). Although its offspring are intermediate in size it has the smallest maximum brood size of all species examined.

Figures 6b-h shows the relationship between brood size and maximum embryo size within each species. Within species there appears to be no trade off between brood size and embryo size. A noteworthy detail is the small amount of variation in maximum embryo size displayed by *L. nassa* and *L. coronata*.

## Discussion

The conclusions to our three main research questions are that there are differences in species reproductive strategies that are largely independent of site, but indicate a reproductive trade off. Specifically:

1) There are differences in brooding strategies between the *Lavigeria* species, both in final brood- and embryo sizes and in the allometry of the embryonic development. The seven species can be divided in two groups. One group consists of *L. nassa* and *L. coronata* which have relatively large broods but the maximum size of their offspring is quite small. The other five species have an opposite way of brooding, they have larger offspring but smaller broods. To explain this one should consider the energy investment by the female. The species with large offspring (*L. grandis*, *L. new sp. J* and *L. paucicostata*) invest more energy in each individual juvenile than the ones with small offspring. By producing small offspring the females of *L. coronata* and *L. nassa* can therefore produce more offspring with the same investment of energy. It is likely that

the developmental time of small offspring is also shorter, thus rate of reproduction is increased.

Similar differences are found when looking at the embryonic developmental strategies. Here again *L. nassa* and *L. coronata* appear to use a different strategy from the other species. Their eggs are relatively large, embryos start increasing in size quickly and reach their maximum size earlier in development than other species. These characteristics fit with the strategy of an opportunistic species. Species that can utilize a wide variety of habitats and that readily colonize new habitat often are able to produce offspring quickly. Preliminary research suggests that small *Lavigeria* offspring are more susceptible to predation by fish (Michel et.al., 1999). But large size of the brood may compensate (and feedback) for increased juvenile mortality.

In our data *L. nassa* follows the prediction of an opportunistic reproductive strategy. We found it at all our sampling sites in a wide variety of habitats. The only place where it seems to have decreased numbers (perhaps from competition) is at the south end of Jacobsen's Bay where it shares the habitat of *L. coronata*. Like *L. nassa*, *L. coronata* also has many, relatively small babies, but based on distribution can not be considered a habitat generalist as it is found in only one pristine site. Extensive surveys of the gastropod fauna have been conducted without finding live *L. coronata* specimens (Michel 1995). It appears to be a relict species with only one known population. Further ecological studies should test why these two species do not coexist well, and why *L. coronata* appears to be restricted in this way.

The other *Lavigeria* species seem to be more restricted as well, with either habitat restrictions, geographical restrictions or both. *L. grandis* is the only species with big babies found at several sites. But close inspection of the habitat in which it is found reveals that it only occurs on rocky surfaces in relatively clear water.

2) Within species site differences were found for one of the three species. *L. grandis* populations from Gombe and Jacobsen's Bay differ in morphology (Michel & Hinkley, in prep, Hinkley 1999) and brood size (this study). This suggests that the dispersal ability

of this species might be less than that of *L. nassa*, which does't show differences in brooding strategy between sites.

While we looked for differences in brood and embryo sizes in substrate separated samples of *L. new sp. M* we found none. We expect that the lack of differences may be because the north and south ends are quite close and the populations are linked by gene flow or because they don't differ enough in physical parameters to select for different reproductive strategies.

3) For many of the species examined there is an inverse relationship between the maximum size of broods and the maximum size of offspring. The larger size of *L. grandis* and *L. coronata* apparently does not change the allometry of this relationship, but just shifts it upwards to a different intercept, possibly due to the larger size of the mother.

However *L. new sp. B* appears to fall below the curve for the other *Lavigeria* species. This might be only a sampling phenomenon, as the sampling size was only  $n=7$ . There is however, another, more mechanistic explanation that should be tested. *L. new sp. B* has a narrow shell, thus for the same shell length (our proxy for size in this study) the female will have a smaller body size and thus decreased resources to invest in babies and less room in the mantle cavity to house a brood.

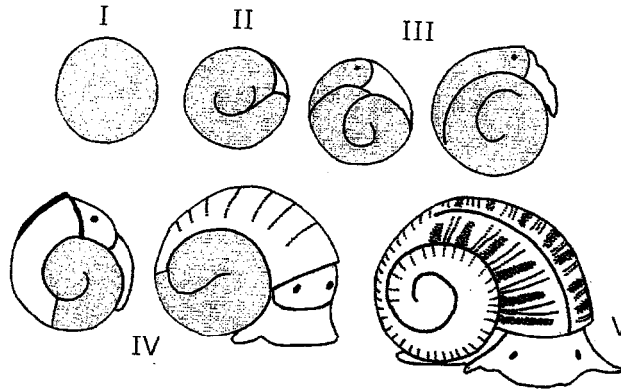
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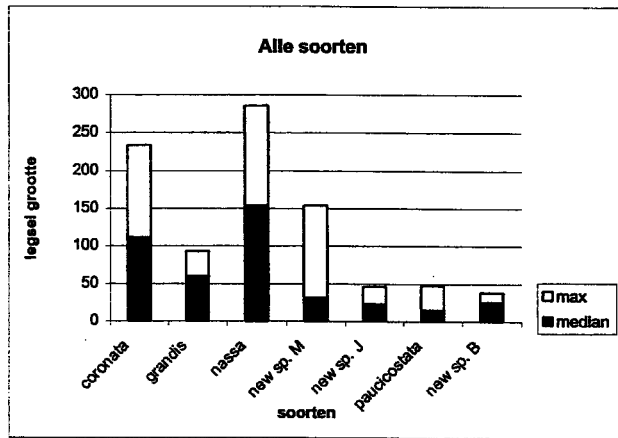
For help with sampling we thank K. Hinkley, N. Zorich and S. Baraka; and finally Drs. D. Cleary for enormous help with the analysis of the gathered data.

## Literature

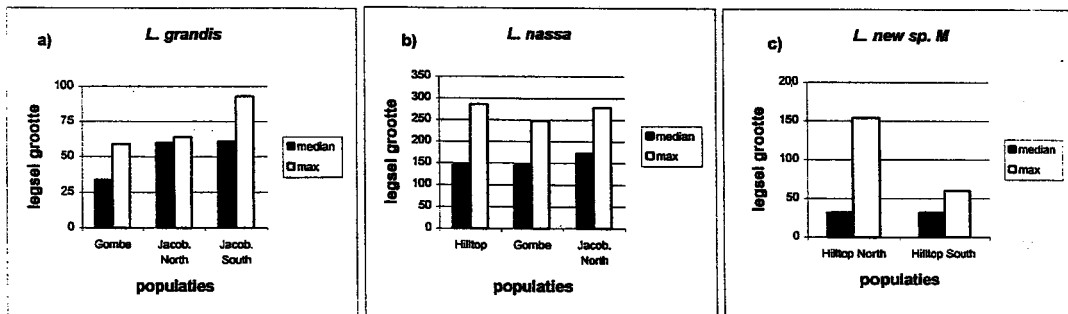
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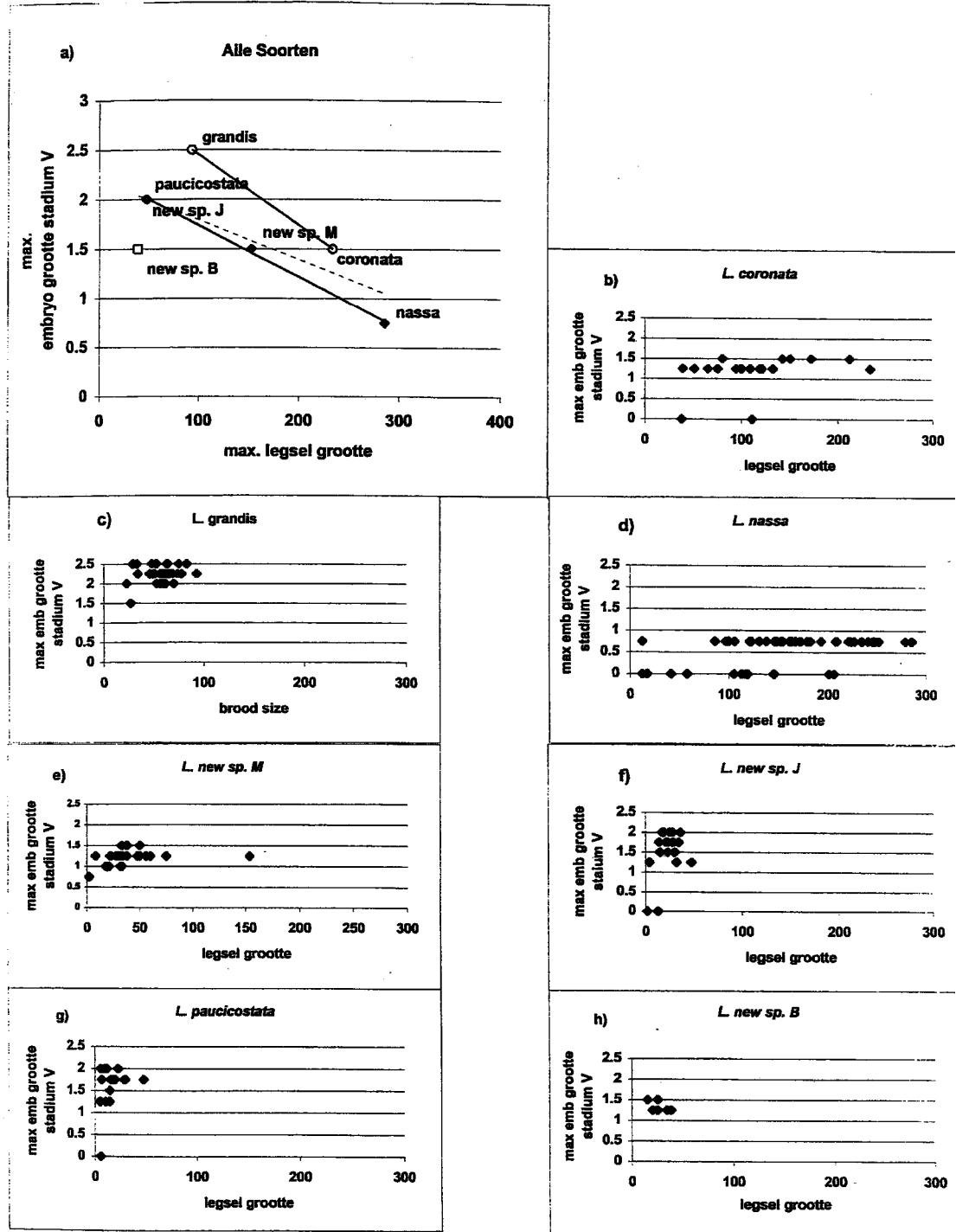
**Figuur 1**  
 Stadium I - Ei - rond hoopje ongedifferentieerde cellen, het gekleurde deel (dooier) wordt aangegeven als het grijs getinte deel.  
 Stadium II - Het embryo begint een herkenbare gescaliseerde vorm te krijgen, de kern van de protoconch is zichtbaar.  
 Stadium III - Het embryo ontwikkelt zich tot het punt waarop doorzichtige aanhangsel en ogen zichtbaar zijn.  
 Stadium IV - De schelp calcificeerd rond het bijna volledig gevormde embryo, de dooier is nog steeds zichtbaar in de schelp.  
 Stadium V - Volledig gevormd jong, er is geen dooier meer zichtbaar. Soms zijn in dit stadium ook de eerste teleconch windingen zichtbaar en begint de schelp verstevigingen te vertonen.



**Figuur 2** Histogram van de mediaan en het maximum van de legsel grootte per soort.

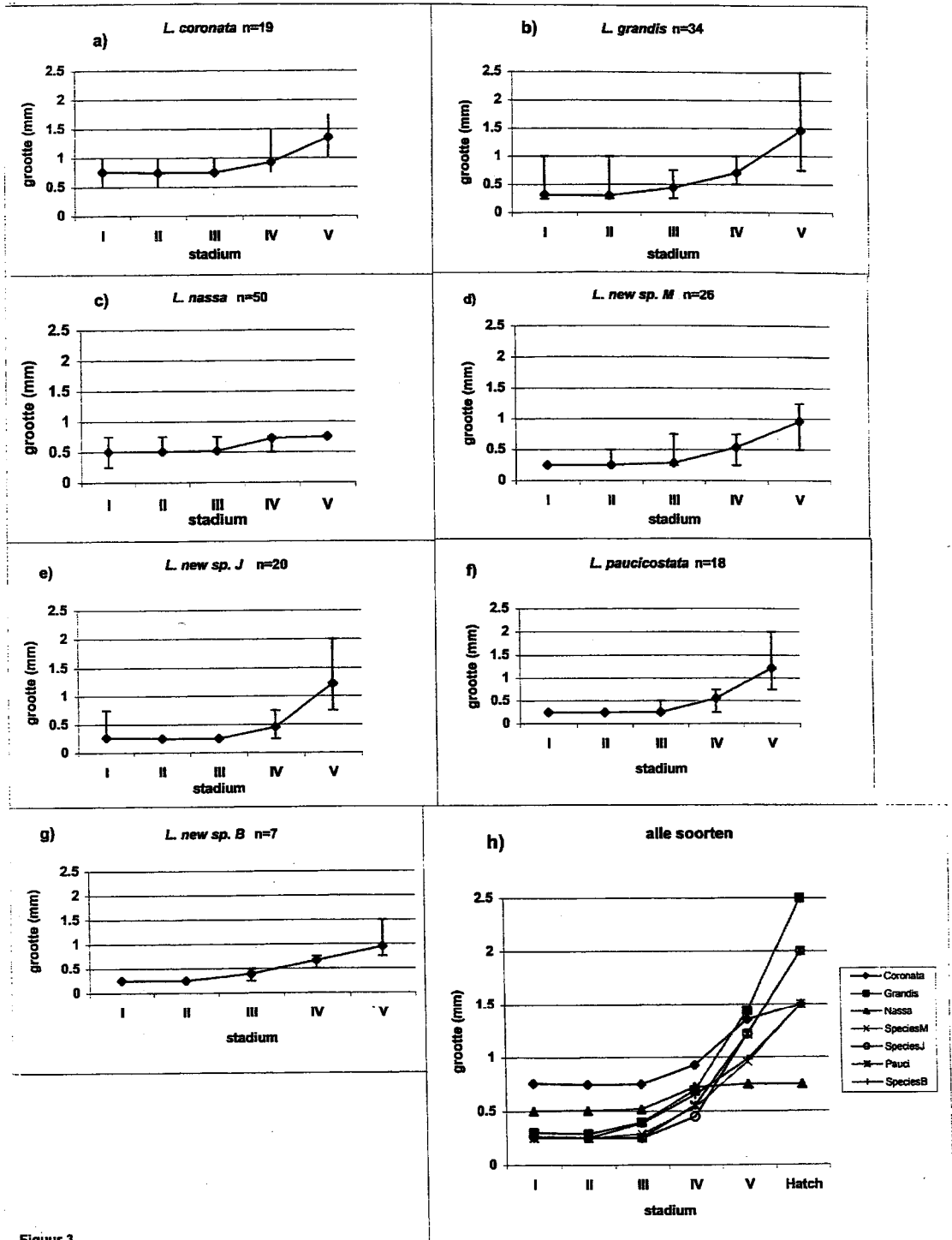


**Figuur 4**  
 Histogram van de mediaan en het maximum van de legsel grootte voor a) Voor 3 populaties van *L. grandis* (Gombe Stream National Park, de noordkant van Jacobsen's Bay en de zuidkant van Jacobsen's Bay, figuren 1-3);  
 b) voor *L. nassa* (Gombe Stream National Park, Hilltop Bay en de noordkant van Jacobsen's Bay, figuren 1-3);  
 c) voor *L. new sp. M* (noord en zuidkant van Hilltop Bay, figuren 1-2).



Figuur 5

a) Maximale legsel grootte uitgezet tegen de geboorte grootte van de nakomelingen van alle soorten. Regressie lijnen zijn getrokken voor alle punten en voor een selectie (besproken in de tekst: *L. paucicostata*, *L. new sp. J*, *L. new sp. M* en *L. nassa*). De lijn tussen *L. grandis* en *L. coronata* gebruikt maar twee punten en is derhalve geen regressie lijn b-h) maximale embryo grootte in het laatste ontwikkelings stadium uitgezet tegen de legsel grootte van ieder individueel legsel per soort. Als er geen embryos in stadium V werden aangetroffen word dat hier geïmponeerd als een 0.



Figuur 3

Gemiddelde embryo grootte (fout-balken geven minimum en maximum aan) voor elk ontwikkelings stadium per soort (a-g). 3h combineert de gegevens van 3a-g en er werd een extra categorie toegevoegd aan het eind die de grootte bij geboorte weergeeft.