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**EVOLUTION OF THE GENUS STOMION (COLEOPTERA:TENEBRIONIDAE) IN
THE GALÁPAGOS ISLANDS**

By Terrie L. Finston, B.Sc.

**A Thesis Submitted To
The Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of
Master of Science
Department of Biology**

Carleton University

Ottawa, Ontario

May 11, 1993

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Evolution of the genus Stomion (Coleoptera:Tenebrionidae) in
the Galápagos Islands

submitted by Terrie L. Finston, B.Sc. Hons.
in partial fulfilment of the requirements for
the degree of Master of Science

Thesis Supervisor

Chair, Department of Biology

Carleton University

28 May, 1993

Abstract

This study involved ecological, morphological, and genetic examination of an endemic species swarm of flightless tenebrionid beetles in the Galápagos Islands in order to understand the patterns and processes of insular radiation events.

Ecological data suggest that Stomion is a feeding and habitat generalist. Thus, unlike Darwin's Finches, there is no evidence to suggest that radiation in this genus is due to feeding or behavioral adaptations.

Twelve taxa were identified using standard taxonomic and morphometric methods. Morphological similarity is high among species, and there is some evidence for two main body shapes.

Genetic similarity is also high among species of Stomion. Estimated divergence times among species are three million years or less. This falls within the commonly accepted age of the Galápagos Islands. However, one species appears to have diverged much earlier. This supports the hypothesis that nearby submerged sea mounts may have once been available for colonization.

Acknowledgements

It seems appropriate to begin this saga of evolution in the Galápagos with a tip of the hat to the man who made the islands a mecca to all enthusiasts of natural history. Charles Darwin was the first naturalist to notice and collect Galápagos tenebrionids; only serendipity (and perhaps size) kept the beetles from becoming as famous as Darwin's Finches. I just wish Chuck had labelled his beetle collections with site information.

A warm thanks goes to my advisor, Stewart B. Peck, who, fortunately, did notice that the beetles offer an equally interesting evolutionary tale. Stewart's affection for los encantadas, and other interesting (and coincidentally?? warm) places and never-ending curiosity about the natural world was refreshing and inspiring. He taught me, among other things, that there are always more questions.

Thanks to Dr. George Carmody and Dr. Suzanne Warwick, the other members of my committee who provided guidance throughout this project, and who did their fair share of reading previous drafts of this thesis.

Thanks to the entomology folks who provided both technical support and conversation: Karen, Tessa and Joyce; perhaps the next graduate student will be a coffee drinker. Thanks especially to Nancy House for slogging through the first draft of the first chapter of the first thesis I've

ever tried to write. Dr. John Heraty also contributed his two cents worth (although it was more like \$20.00) on an early draft of Chapter 2. Thanks to Lew for showing me around a scanning electron microscope. I would probably still be printing this, if not for the help of Jussi Helava.

My time in the Galápagos was made all the more pleasant by the field assistance and comraderie I received from members of "El Grupo Peck": Joyce Cook, Moraima Inca, Bernard Landry, Ricardo Palma, Richard Perry (an honorary member), Eduardo Villema, and of course SBP. Thanks to the other wonderful people at the Charles Darwin Research Station in Puerto Ayora, especially Sandra Abadrabo who shared my delight in collecting things small, dark and six-legged. It didn't hurt that tenebrionid habitat is also prime beach real estate. The Charles Larwin Research Station kindly provided meteorological data for use in Chapter 1. The trip would not have been the same without the crew of the Saturno- the three Luchos kept us well fed and on course (most of the time), and should I mention the moonlight serenades?

Thanks to all my friends at the Hebert Zoo, who kept in touch across the iles to ask how chings were going, and to the zookeeper himself, who never asked how things were going (that's o.k; one gets tired of THAT QUESTION, especially near the end).

And most importantly, there aren't words enough to

thank my husband Richard Perry, who was too busy taking care of me to notice (or just too considerate to mention it) that my head has been somewhere else for the last two years. Perhaps now we'll have a life together again; I think there are a few movies we need to catch up on.

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General Introduction

The Galápagos Islands have long been recognized as "living laboratories" of evolution. The biological processes of dispersal, colonization, genetic differentiation, and speciation may be explored in the context of a wealth of geological, climatological, and other information which is known about this archipelago.

The Galápagos islands straddle the equator, and lie 960 km west of the coast of Ecuador. There are about 30 named islands, and many more small rocks and islets (Figure 1). The islands have been available for biological colonization for about 3 million years (Jackson, 1991). The islands are of volcanic origin and have never had a mainland connection (Jackson, 1991). The first volcanic mounds appeared above the ocean surface above a hot-spot below the Nazca sea-floor plate on which the archipelago sits. The oldest dated rocks come from the islands of Española and San Cristóbal in the south-eastern corner of the archipelago, (Cox, 1983). The youngest rocks are those found on Isabela and Fernandina, the western-most islands.

Most of the central and southern islands are positioned on a shallow volcanic submarine platform known as the Galápagos platform, which lies about 400 metres below sea level (Thornton, 1971). The northern group of islands are separated by a drop in the platform to depths of 2000 metres. The central islands may have been joined during the

Pleistocene if sea levels dropped by 150 metres (Jackson, 1991).

The Galápagos has a disharmonic, unbalanced fauna (Thornton, 1971). Reptiles are over-represented, while mammals and amphibians are under-represented. This can be explained in terms of the oceanic isolation of the archipelago, and the differing dispersal abilities of various organisms. Much of the flora and fauna of the Galápagos arrived via long-distance dispersal methods: in the air through flight, or as aerial plankton; or by sea-rafting. Some inhabitants have been brought by human introduction, perhaps beginning in 1535. What happens to island organisms after their arrival has been the focus of much research ever since Darwin. Islands provide small-scale model systems in which we can study the dynamics of isolation, differentiation and speciation.

Darwin's Finches provide a text-book example of adaptive radiation under the influence of selection and isolation. (Lack, 1968, Grant, 1981). Selection in the islands may be acting in response to two sets of parameters. First, the islands themselves differ from one another in physical characteristics such as size, height, age, and climatological factors. The different island environments provide a variety of physical conditions in which adaptation and selection can act. Second, each island may be biologically differentiated and consist of up to six

discrete vegetation zones (Wiggins and Porter, 1971). These zones may provide microhabitats in which selection can act.

The vegetation zones arise due to a precipitation gradient which is affected by island elevation and wind direction (Figure 2). Not all islands are composed of all six vegetation zones. Those with lower elevations, such as Baltra and Santa Fé, have only two zones: the littoral and arid. Six zones are found on the high elevation islands such as Santa Cruz and Isabela. The first is the littoral zone, a narrow strip which rises only a few metres above sea level. The flora and fauna are heavily influenced by the ability to tolerate salt. The littoral zone is followed by the arid zone which may rise to 120 m on the south side of islands, and up to 300 m on the north side, which is often in the rainshadow of the islands' mountains. The arid zone vegetation is composed of drought tolerant plants such as small shrubs, trees, and herbs, and the cactus genera Opuntia Mill. and Jasminocereus Britt. and Rose. The third vegetation zone is the transition zone, which is composed of many evergreen species, as well as both xerophytic and mesophytic plants from the zones below and above. It is a large zone, located generally from 80 m to 200 m in elevation. The limits of this zone also vary in elevation between the north and south sides of an island. Following the transition zone is the Scalesia (Arn.) zone. It begins at about 180 m and may rise as high as 550 m. It is

is characterized by the presence of the composite Scalesia and a thick understory. The next zone is the Miconia zone. It begins generally around 400 m, and begins the trend of decreased rainfall with increased elevation. The last zone is the fern-sedge zone. Generally, it begins around 525-550 m in elevation, and rises to the tops of the mountains. It lies above the layer of clouds which cover the high elevations of the islands, and thus experiences drizzle more often than rain.

Radiation in some organisms is thought to have occurred as a result of adaptation to the conditions of these various zones; the bulimulid land snails are one such example (Coppoio, 1984).

Isolation is also a key factor in speciation processes on islands. Geographic speciation may occur when dispersal events are rare, thus reducing the diluting effect of gene flow from outside sources. Isolation in the Galápagos occurs on three levels. First, the islands themselves are isolated from the South American coast, the nearest major landmass, 960 km to the east. Second, the islands are isolated from one another by sometimes large water gaps, both in distance and in depth. Currents may affect the dispersal ability between islands. The equatorial current flows from east to west, which probably increases the likelihood of dispersal in this direction, but limits the amount of dispersal in the opposite direction. There may also be isolating barriers on

individual islands. Geological disturbances such as newly formed lava fields may have an isolating effect in restricting gene flow between populations.

Up to now, much research on adaptation and speciation has focused on the more conspicuous members of the fauna: the giant tortoises, iguanas, and Darwin's finches. Recent work suggests that equally interesting evolutionary problems may be found among the invertebrates (Peck and Kukalova-Peck, 1990).

In particular, three genera of flightless tenebrionid beetles contain 37 described species, with widespread distributions in the archipelago. Collectively, these three beetle genera represent the greatest known assemblage of endemic insect species in these islands. However, like the finches and tortoise races, individual species are restricted to one or a few nearby islands (Van Dyke, 1953).

Questions arise about the mode of speciation in these beetles. Is speciation in the tenebrionids a result of adaptation to and selection in the varied environments that each island offers? Or did differentiation arise as a result of simple allopatric isolation? Adaptive radiation has been invoked to explain the morphological differences observed in the tortoises and Darwin's Finches (Jackson, 1991; Grant, 1981), but is this a viable explanation for beetle evolution in the islands?

This study focused on the genus Stomion, an endemic

genus containing nine described species. Evolution in the group is examined through population, ecological, morphological and genetic trends. Populations are investigated to answer questions about population sizes and individual dispersal abilities in order to estimate the potential for gene flow. Ecological data can be used to identify adaptive trends among species. Morphometric and phenetic examination of the species are used to test hypotheses about species status and to resolve sister-species relationships. Lastly, genetic data is used as an independent test of ideas about population sizes, gene flow, and species relationships. All of these data can be examined in the context of the well-studied geological history of the archipelago to present a reconstruction of the biogeographic history and evolution in the genus Stomion.

General Methods

Field work in the Galápagos took place from early March until mid-July of 1992. Beetles were collected from 20 of the islands and islets of the archipelago. Those sites which contained Stomion and their abbreviations are listed in Table 1.

Most collecting was done at dusk when the beetles came out to scavenge. Occasionally, beetles were found during daylight hours, under leaf litter, or buried in the sand.

Beetles were placed in plastic jars with mesh screen covers and transported to the Charles Darwin Research Station where they were kept alive in cultures containing wood shavings. The animals were fed oatmeal and small pieces of apple while in captivity. The beetles were fed once a week, and any dead specimens were removed and preserved in a 70% ethanol-acetic acid solution.

Prior to our return to Canada, live beetles were frozen on dry ice for transport. The animals were placed in an ultra-cold freezer (-80°C) awaiting electrophoretic analysis.

Ethanol preserved specimens were pin-mounted for morphological examination. Some specimens were left in ethanol solution for later dissection and examination of internal structures. Two individuals of each morphotype were cleaned in a soap solution in a sonicating bath, and mounted on points for scanning electron microscopy.

Chapter One: Ecology and Population Dynamics of Stomion and other Galápagos Tenebrionids

General Introduction

Tenebrionid beetles, commonly known as darkling beetles, are often conspicuous and abundant members of surface dwelling communities in arid and semi-arid environments (Crawford, 1990). While the life history of tenebrionids on the Galápagos Islands remains under-studied, they may share life history characteristics with other better known desert tenebrionids. Tenebrionid species occur sympatrically in deserts all over the world (Thomas, 1983). The usually black, flightless, ground dwelling adults are most active at night, but some species are also observed scavenging at dusk and dawn, or on overcast days (Doyen and Tschinkel, 1974). Both adults and larvae can be long-lived, and the number of instars can be high, reaching 10 in some species (Allsop, 1980). Larval lifespans may be as long as one year (Doyen and Tschinkel, 1974), and in the laboratory, adult lifespans can reach two years (Aalbu, 1995). Others are known to have three year life-cycles (Allsop, 1980). In some arid species, the larval period is relatively short, and the adults are long-lived; oviposition occurs only during the rainy season, and larvae develop quickly, as an adaptation to ephemeral conditions (Watt, 1974). The adults and larvae are omnivorous detritivores, eating mainly leaf

litter and fruits of desert plants, although they have been observed to feed on fecal matter and carrion (Thomas, 1979, 1983).

This is the first study of beetle ecology in the Galápagos Islands, and with the exception of the carpenter bees (Linsley, et al, 1966), fire ants (Lubin, 1984), and pollinating insects (Linsley, 1966), insect ecology has been overlooked in this archipelago. In order to fully understand radiation within the tenebrionids in the Galápagos, it is necessary to study beetle assemblages for evidence of micro- or macrohabitat division, interspecific competition, and the structure of populations; that is, their size (total number of individuals making up a population), density (the number of individuals per unit area), substrate and food preferences, dispersal abilities, etc.

There are a number of ecological factors which may affect tenebrionid beetle populations both on short and long-term time scales. Extreme climatic conditions such as drought or abnormal temperatures may affect reproductive rates and juvenile recruitment rates, as well as mortality rates in adults (Ahearn, 1971). Local density and relative species richness may be affected by substrate type and vegetation composition. Beetle activity on any given day may be affected by temperature, relative humidity, moon phase, recent rainfall, or amount of cloud cover (Thomas, 1979).

Several estimates of community structure, distribution,

and dispersal ability have been determined for populations of tenebrionid beetles (see Thomas, 1979; Doyen and Tschinkel, 1974; Thomas and Sleeper, 1977; Whicker and Tracy, 1987). Communities consisting of several different tenebrionid species and genera are not uncommon. At the Central Plains Experimental Range in Colorado, twenty-eight different tenebrionid species were found, eight belonging to a single genus (Whicker and Tracy, 1987). Other studies have been concerned with behaviour and interaction of beetle communities. One such study provided evidence that interspecific competition was not a contributing factor to the composition of communities of adult tenebrionids (Wise, 1981). Another study suggested that species diversity was not correlated to vegetational heterogeneity in desert tenebrionids, and that niche separation was not a factor in local assemblages of beetles (Thomas, 1983). However, preferences for food resources among 13 species of tenebrionids in a desert-steppe community was found to act in niche partitioning (Rogers, et al, 1988). Substrate type may also aid in spatial and ecological separation (Doyen and Tschinkel, 1974).

In order to better understand the population dynamics of the genus Stomion and two co-occurring genera of tenebrionid beetles in the Galápagos Islands, a three-part ecological study was carried out. Population characteristics such as relative species abundance, habitat associations,

population sizes and vagility will aid in understanding the ecological factors which may have led to radiation within these three genera of tenebrionids. The sections of the tripartate study are as follows: (1) weekly 100 metre transect collections, (2) a mark and recapture study, and (3) an analysis of site ecological data for Stomion.

The transect study was conducted to examine interspecific abundances of the three genera of tenebrionids found at a single site. Weekly examination of the beetle community can provide information about the effects of immediate climatic conditions on beetle activity. Because the study bisected the transition from the warm/wet to the cool/dry season (Jackson, 1991), seasonal trends in abundance were also examined.

The mark and recapture study was conducted to estimate population sizes, densities, and vagilities for species of each of the three genera found at a site. Population sizes and the dispersal abilities of species will affect certain genetic dynamics, such as gene flow and genetic drift. These factors are important in understanding how gene flow is interrupted and genetic isolation occurs. In addition, by using four separate grids in areas with slightly different vegetation composition and abundance, information about habitat associations for the species studied could be collected.

Interspecific competition in local communities is

suspected to play a role in the composition of those communities (Wise, 1981). Examining the frequency in which the three genera of flightless tenebrionids occur together at sites may help in understanding the role of competition in the composition of their communities. In addition, associations between species or genera and the dominant vegetation or substrate type at each site may help in understanding macro- or microhabitat division among these genera. Adaptation to local environments has probably played a large role in the radiation of Darwins finches (Grant, 1981), but whether this has been a contributing factor to speciation in the darkling beetles of the Galápagos Islands is unknown.

I. Transect Study

Methods

A 100 m transect was marked along a one metre wide foot trail leading away from Bahia de Tortuga, Isla Santa Cruz. This crossed the littoral and arid zones. The substrate changed from a fine white sand to volcanic rock approximately twenty metres from the start of the transect. Trips to the site were made every 5 or 6 days and continued for eight weeks. Censusing began on 8 May, 1992 and was completed on 7 July. Baits of 5 gm of dry oatmeal at 2 m

intervals were laid out at 6:00 in the evening, and beetle counting commenced at 7:30 p.m. The beetles are night active and emerge from their hiding places by 6:30 p.m. The transect was inspected once, beginning at the site closest to the beach, and ending at 100 m. The number of individuals at each bait site of each of the three genera of tenebrionids were recorded. A bait site is defined as the area surrounding the bait, delimited by the edges of the trail, and extending 1 m in front and behind the bait. Each bait site covered approximately 2 m². To insure consistency in the area of each site, animals outside the trail were not included in the count. During the first two weeks, some animals were removed for species identification; on subsequent weeks, the animals were counted, but not removed. Species richness and the total number of all species collected were tabulated for each week.

In order to examine the effects of local climatic conditions on species abundance and activity, weather data collected at the Charles Darwin Research Station was used for analysis. The research station lies approximately 2 km from the study site at Tortuga Bay, and is thus representative of the climatic conditions at the study site. Data included in this analysis were temperature and humidity at 6:00 p.m., total precipitation, number of hours of sunlight, and minimum and maximum temperatures for the day in which the census was made. In addition, the total

precipitation for the seven day period preceding the census was used. Pearson correlations and their corresponding probabilities were calculated between these ecological data, and weekly species richness (number of different species found in the evening's collection) and individual species abundances using the CORR module in SYSTAT (Wilkinson, 1988). The relative abundances of each species were tabulated weekly in the form of ratios.

Results

Four species of tenebrionids belonging to three genera were found at the study site. They are Ammophorus bifoveatus Waterhouse, Blapstinus lugubris Boheman, B. spatulus Van Dyke, and Stomion laevigatum Waterhouse. The number of individuals encountered of each species varied considerably; they ranged from 25 S. laevigatum to 108 Blapstinus lugubris, 451 B. spatulus, and 615 A. bifoveatus for a total of 1199 beetles. The total number of individuals counted each evening ranged from 2-208, and the number of species observed ranged from one to four. Table 2 shows the total number of individuals collected for each species over the study period. The total number of all species reached a plateau by the 6th week and remained nearly constant for the remainder of the study. Individual trends varied, however. Ammophorus bifoveatus and Blapstinus spatulus showed a general increase in abundance over the study period, while

Stomion laevigatum and B. lugubris numbers remained relatively stable. These data are plotted for each species for the duration of the study (Figure 3).

Correlation of species abundance and richness with seven environmental conditions often showed significant but negative correlations (Table 3). For example, the number of individuals of B. spatulus and A. bifoveatus are negatively correlated with maximum daily temperature, temperature at 18:00 hours, the days' precipitation, hours of sunlight during the day, and the total precipitation for the week preceding the census. In contrast, the number of different species observed in a census was shown to be positively correlated with percent relative humidity. The days' minimum temperature showed no effect on species' abundance or diversity. The numbers of S. laevigatum and B. lugubris were not correlated with any measured environmental conditions.

II. Mark and Recapture Study

Methods

The location for this portion of the investigation was also Bahia de Tortuga on Santa Cruz Island. The sandy littoral zone was selected for the field site.

Four separate quadrats, each consisting of 25 traps were arranged. The traps were placed 2 m apart in a 5 by 5

configuration so that each grid covered a 64 m² quadrat. Each quadrat was separated from any other quadrat by a minimum distance of 16 m (Figure 4). The traps consisted of small, unbaited cylindrical plastic containers with a diameter of 10 cm and a depth of 6 cm. Each trap was equipped with a cover which was used to close the traps and a wire screen which was used when the traps were open to discourage predation by birds and lizards.

The vegetation was not homogeneous over the entire study area. The quadrats differed both in plant species present and in the proportion of ground covered by vegetation. The plant composition in order of abundance for each quadrat is as follows, with the estimated percent of ground cover noted in brackets: I. Scaevola plumieri, Ipomoea pes-caprae, Sesuvium portulacastrum, Heliotropium sp., some grasses (80%); II. Scaevola plumieri, Ipomoea pes-caprae, Sesuvium portulacastrum, Prosopis juliflora (90%); III. Scaevola plumieri, Sesuvium portulacastrum, Ipomoea pes-caprae, Heliotropium sp. (60%); IV. Heliotropium sp., Tiquilia darwinii, Cryptocarpus pyriformis, Prosopis juliflora (15%).

The traps were opened for a twelve hour period, from dusk to dawn, at five day intervals from June 15th to July 8th, 1992. Individuals caught in the traps were recorded by quadrat and trap number, and marked with a dot of white Liquid Paper® typing correction fluid in the corner of the

elytra which corresponded to the quadrat in which it was caught. For example, a beetle captured in quadrat 1 was marked with a dot in the lower right corner of the elytra. The beetle was then released into nearby vegetation. Thus, recaptured individuals could be identified with respect to their original quadrat of capture. Estimates of population size (N) and density per hectare were calculated for the quadrats in which there were appreciable recaptures using the formulae described by Thomas and Sleeper (1977):

$$N = \frac{M}{1 - (\frac{M}{t})}; s^2 = \frac{M^2 t (t-r)}{r^3}$$

where M= number of individuals marked; r= number of individuals recaptured, and t= total number of captures. Density is calculated by dividing N by the unit area in hectares.

Population distributions were examined with respect to vegetation composition in order to understand the habitat associations of the genera. In addition, the vagility of each species was examined by totaling the number of individuals which were recaptured in the same quadrat in which they were marked. Those species which have small ranges would be expected to be recaptured more often in the same quadrat in which they were originally marked, and those species which are more vagile would be expected to be recaptured in different quadrats.

Distribution of the captured animals within the quadrat was analyzed to add additional evidence to vagility patterns. If the animals have a very large range, they might be expected to be caught more frequently in traps at the perimeter of the grid. If, on the other hand, their range is small, they may be captured more often in the internal traps of the grid. The total catches per trap were plotted for each grid to look for distribution trends. Summary statistics were calculated for each grid: mean number of catches per trap, standard deviation, and dispersion index. The dispersion index (DI) was calculated for each grid as:

$$DI = \frac{\text{variance}}{\text{mean}} \times \text{degrees of freedom}$$

(Fowler and Cohen, 1990). If the beetle catches are randomly dispersed throughout the grid area, we would expect the variance to be similar to the mean (Fowler and Cohen, 1990). If the beetles are contagiously dispersed, or clumped, we would expect the variance to be greater than the mean. The data were then tested against Poisson (random) predictions, or negative binomial (clumped) predictions. A chi-square test was used to test goodness of fit between the observed distribution among traps and the distribution predicted by the models.

Results

Four species belonging to the three genera were captured, marked, and released. They were Ammophorus bifoveatus Waterhouse, Blapstinus lugubris Bohemann, B. spatulus Van Dyke, and Stomion laevigatum Waterhouse. The total number of captured individuals were 37 A. bifoveatus, 119 B. spatulus, 1 B. lugubris, and 171 S. laevigatum (Table 4). Of the 328 beetles captured, marked, and released, there were only four recaptures. The first recapture occurred on the second week of the study. Blapstinus spatulus was recaptured 3 times; twice in quadrat I during weeks 3 and 4, and once in week 2 in quadrat II. A single individual of A. bifoveatus was recaptured in quadrat II during week 5. All four recaptured individuals were collected in their original quadrat of capture. None of the collections resulted in recapture rates high enough to meaningfully estimate population size or density for any of the species.

The number of captures per quadrat was somewhat proportional to the amount of vegetation cover. The greatest number of captures came from quadrats I and II, which were estimated to be 80% and 90% vegetated. The fewest number of captures came from quadrats III and IV, which were 60% and 15% vegetated, respectively. Ammophorus and Blapstinus were rare in the less vegetated quadrats. No Ammophorus were captured in quadrat III and Stomion was more than four times more abundant than Blapstinus. In quadrat IV, Stomion was

twenty-seven times more abundant than Blapstinus and fourteen times more abundant than Ammophorus (Table 4).

The number of beetles and the frequency of that number occurring in traps was tabulated (Table 5). The mean number of beetles per trap, standard deviation, and dispersion index was also calculated for each quadrat. The distribution of beetles among the traps suggest that beetles are abundant in some areas of a quadrat but are in low numbers in other areas. The dispersion index (DI) tests of the distribution of beetle catches in the four quadrats showed that only one of the four (quadrat IV) fit a random distribution model; the other three (quadrats I-III) are best described as showing a contagious dispersion, or clumping (Table 6). Quadrats I-III have variances which are larger than the mean, while quadrat IV has a variance similar to, but slightly less than the mean. Quadrats I-III showed a significant goodness of fit to the negative binomial model of dispersion at $p=0.05$. Quadrat IV fits the random dispersal (Poisson) model at a significance level of $p=0.05$.

Observed frequencies of beetle catches per trap were plotted for each of the four quadrats (Figure 5). Frequencies predicted by the Poisson and negative binomial models are superimposed on the histograms (shown as dots). For example, in quadrat I, there were no traps in which no beetles were caught, six traps which contained 1 beetle, 6 traps that contained 2 beetles, etc. At least one trap was

expected to contain no beetles, 3 traps were expected to contain 1 beetle, 4 traps were expected to contain 2 beetles, and so on.

III. Site Ecology

Methods

Stomion was collected from 46 different sites on 20 islands in the archipelago (Table 1). Many of the larger islands contained more than one site, while the smaller islands and rocks generally consisted of a single sampling site. At each collection site, some or all of the following variables were recorded: substrate type, vegetation zone, primary types of vegetation, elevation, and the presence of other species or genera. The number of individuals from the site were counted in the laboratory. The number of sites in which Stomion appeared with other genera was tabulated, as well as number of occurrences in each vegetation zone and elevation (Table 7). Occurrences of plants designated as primary vegetation and secondary vegetation, and substrate type were also tabulated (Table 8).

Results

Stomion was found to occur predominantly in the arid zone (Table 7). Among the 46 populations in which Stomion

were collected, ten populations (~22%) were collected in the littoral zone, at elevations usually less than 3 m. Three populations were collected at sites covering both littoral and arid zones. Thirty-one populations (~67%) were collected in the arid and transition zones, at elevations up to 300 metres, and two populations (~4%) were collected in the high elevation zones, one from the arid inversion zone at 1500 m (Cerro Azul), and the other in the humid fern/sedge zone at 1100 m (Volcan Alcedo).

In the littoral zone, Stomion was most often associated with salt tolerant bushes such as Cryptocarpus pyriformis (salt bush), Scaevola plumieri, and Ipomoea pes-capre. In the arid zone, the beetles were found under succulent plants such as Sesuvium portulacastrum, or herb mats such as Tiquilia darwinii. In the fern/sedge zone, Stomion were found among grasses at the Alcedo volcano rim. There is little evidence of substrate or plant preferences for individual species; rather, Stomion appears to be a generalist, and is found in association with many different plants and on various substrate types (Table 8). The most common plant recorded from the sampling sites was Cryptocarpus pyriformis and seven of the ten taxa were found in association with it at one or more sites. In addition, individual species are often found in association with a number of different plants at different sites. For example, Stomion laevigatum is found with Cordia sp., Cryptocarpus

pyriformis, Heliotropium sp., Waltheria sp., and herbs, shrubs, and mixed grasses. Six of the ten taxa are found in both littoral and arid zone habitats. Populations of S. longulum, S. galapagoensis leleupi, and S. sp. n. were not found in the littoral zone, but only in the arid zone. Sand and cinder are the most common substrate types on which Stomion is found, followed by rocks, ash and soil. All but two taxa are found on two or more different substrate types. The new species, which was collected at only two sites, was found only on rocks, and S. helopoides was found only on sand.

Stomion is often found in conjunction with other tenebrionid genera (Table 7). Of the 46 populations, Stomion was found with Ammophorus fourteen times, with Blapstinus seven times, and with Phaleria (a widely distributed, winged tenebrionid in which a Galápagos radiation has apparently not occurred) once. Stomion was found with combinations of two or three of these other genera at nineteen different sites. In total, Stomion was found co-existing with other genera at 41 of the 46 sites. The remaining five collections consisted solely of Stomion. One instance of strict sympatry (or at least parapatry) occurred among Stomion populations at the Tortuga Bay/Half-Way House sites on Santa Cruz. Stomion laevigatum was found in the littoral zone on sandy substrate, and S. longulum was found further up the trail in the arid zone on volcanic ash substrate.

Discussion

The transect study showed a general increase in the total number of individuals sighted over the course of the study. Beetle abundance reached a plateau of over 200 individuals sighted per evening, interrupted by two weeks of smaller catches in the middle of the study and remained steady at approximately 200 individuals for the remainder of the study. These abundances coincide in general with a number of climatic trends such as a decrease in minimum and maximum daily temperatures, as well as a decrease in rainfall and number of hours of sunlight per day as the cool/dry or "garua" season began toward the end of the study. On any given night, however, local environmental conditions affect beetle activity. The highest number of evening sightings occurred following days with the lowest number of hours of sunlight (less than five hours), perhaps as a result of lowered sand surface temperatures. In addition, the greatest species richness was experienced on evenings with the greatest degree of daytime relative humidity, suggesting that cooler temperatures and some moisture favours beetle activity. Indeed, oviposition is known to occur in some species only during rainy or wet periods (Watt, 1974). However, beetle activity was greatly reduced during heavy rains, such as on the first evening of collection.

There was some evidence of substrate division among the

species. In the transect study, Stomion laevigatum was rarely found past the sandy littoral zone, while Ammophorus bifoveatus and Blapstinus spatulus and B. lugubris were found both in the sand and volcanic rock substrate types. Among the four quadrats, all three genera were found in the highly vegetated quadrats, but Stomion predominated in the poorly vegetated sites. This suggests that cover and shade is a less important habitat requirement for Stomion than it is for Ammophorus and Blapstinus.

The number of recaptures in the mark and recapture study was too few to allow any estimation of population size or density for any of the species. The reasons for this may be due to a number of factors. One possibility is that at this site, population sizes and ranges are large, larger than the area covered by the four quadrats. Beetles, once marked, may have wandered out of the area, never to return. However, of the four beetles which were recaptured, each was found in the same quadrat in which it was marked. If these animals had large ranges, or good dispersal ability, some beetles would be expected to be recaptured in a different quadrat than that in which they were marked. Alternately, mortality rates may have been higher in marked beetles, e.g., the correction fluid may have been toxic (although no dead, marked beetles were found in the study area), or they may have been more visible to predators. As well, the mark may have rubbed off during the course of the study as the

beetle brushed against vegetation or sand while scavenging.

The ranges of the beetles may be inferred by their distribution within a quadrat. If beetles were caught more frequently in those traps at the periphery of the quadrat, this would suggest that their range is large, and that they wander in and out of the quadrat. On the other hand, if beetles are found in the central traps of the quadrat, the range of the beetles may not be much larger than the area covered by the quadrat. Visual inspection of the distribution does not show beetle concentrations in the peripheral traps (Figure 6). However, the beetles were found to be non-randomly distributed in three of the four quadrats. If all traps resulted in equal numbers of beetle catches throughout the duration of the study, this might suggest that ranges are small; individuals are repeatedly caught in the same area, suggesting little movement. This is supported by the fact that all four beetle recaptures occurred in the quadrat of origin. Tests of distribution models showed that beetles tended to be caught disproportionately in some traps week after week, and less frequently in other traps. One explanation is that the beetles may not travel far from their starting places, so that traps placed nearer to vegetation tended to catch more beetles. The beetles may also be emitting pheromones which attract other beetles to the same trap. In the least vegetated grid, beetle catch patterns were random. This may

be due to the need to wander further in search of suitable food sources or cover.

Both the transect and mark and recapture studies should be repeated over a longer time period, and during different seasons to verify these initial findings. In addition, the study should be carried out during a non "el Niño" year, to examine the effect this weather pattern may have had on beetle abundances. A study of the 1993 adult population may determine if the 1992 "el Niño" had any effect on reproduction among the 1992 population or recruitment rates for the 1993 cohort.

The ecological site data suggests that interspecific competition probably does not play a major role in the composition of local beetle communities. In 89 percent of the sites sampled containing Stomion, it was found with one or more other tenebrionid genera. If competition was a contributing factor, competitive exclusion -the presence of one species only, a predominance of one species- might be expected at some sites where resources are limited. Stomion are often found utilizing many plant and substrate resources, and therefore food is not likely to be a limiting factor in community structure.

However, there is some evidence that microhabitat subdivision may be a factor in multi-generic assemblages. For example, at the Granillo site on Isla Santa Cruz, Stomion was found scavenging along the dirt road while

Ammophorus was found nearby under the shrubs on the cinder field. In another case, at the North Shore site on Santa Cruz, Ammophorus was found under Cryptocarpus leaf litter, while Stomion was found under the leaf litter of the succulent tree Maytenus octogona. At the Aeropuerto site on San Cristóbal, Stomion was found under mats of the succulent plant Sesuvium, while Ammophorus was found primarily under prostrate mats of the herb Tiquilia.

Ninety-three percent of all Stomion populations were found in the dry, low altitude littoral and arid zones. This does not support the hypothesis that macrohabitat altitudinal "life zone" division is responsible for radiation of Stomion within the archipelago. Furthermore, all species seem to be utilizing many of the same plants and substrate types which also does not suggest microhabitat division. The only exception to this is the single case of parapatry/sympatry, where S. laevigatum and S. longulum are segregated between the littoral and arid zone at two overlapping or contiguous sites on Santa Cruz. A more in-depth study of interspecific feeding and resting behaviour in association with plants may help to answer this question.

In summary, then, these studies suggest that population sizes may be large, but restricted in geographic range by low individual vagility. Beetle densities are highest where vegetation is abundant. Beetle activity is dependent on

several environmental factors such as daily temperature and hours of sunlight. Overall abundances show seasonal trends. Stomion is probably a generalist scavenger, and thus far there is little evidence for niche partitioning playing a role in species distributions.

Chapter Two: Morphological Variation in Stomion.

Introduction

The genus Stomion is endemic to the Galápagos Islands (Van Dyke, 1953). The genus was described by G.R. Waterhouse (1845) who examined the collections made by Charles Darwin during his famous trip to the Galápagos. At that time, Waterhouse described three species: Stomion galapagoensis Waterhouse, S. laevigatum Waterhouse and S. helopoides Waterhouse. He placed them in the family Tentyriidae and the tribe Eurymetopini (Eschscholtz). No distributions were given for these species, because Darwin's specimens were not labelled with the individual island collection site.

M.L. Linell (1899) subsequently named three more species using specimens in the United States National Museum from the Clark University expedition in 1891, the 1887-88 U.S. Fish Commission expedition, and the Swedish expedition of 1852. He described S. carinipenne Linell from Floreana, S. piceum Linell from San Cristóbal, and S. bauri Linell from Isabela. K.G. Blair (1933) later recognized the first two of Linell's species to be only variations of S. galapagoensis Waterhouse. Stomion bauri Linell was identified by Blair as S. laevigatum Waterhouse. Blair himself named one additional species, S. linelli Blair, which he listed from the islands of Eden, Genovesa, and

Santa Cruz (1933). After corresponding with the British Museum, Blair decided that the specimens from Genovesa which he originally placed with S. linelli, actually belonged to S. laevigatum (1933).

Thus, four species were recognized until 1953 when E.C. Van Dyke re-examined the genus using specimens from the California Academy of Science's Templeton Crocker expedition of 1932, and the Academy's own 1905-06 expedition led by F.X. Williams. Van Dyke also studied Darwin's specimens described by Waterhouse in the Natural History Museum in London, as well as additional specimens from the American Natural History Museum. Van Dyke described five new species and one subspecies: S. obesum Van Dyke from Pinzón, Santa Fé, and Tortuga Islands; S. cribricollis Van Dyke from Darwin and Wolf Islands; S. longulum Van Dyke from Isabela and Santa Cruz Islands; S. longicornis Van Dyke from northeast Española Island; S. rugosum Van Dyke from Pinta Island; and S. galapagoensis punctipennis Van Dyke also from Española Island. Stomion galapagoensis leleupi Kaszab was described by Z. Kaszab (1970) from a high elevation site on Santa Cruz Island. The last additions to the genus were those of H. Franz (1985) who described Stomion laevigatum santacruensis Franz from Tortuga Bay, Santa Cruz Island, and S. galapagoensis pinzoni Franz from the island of Pinzón.

There is disagreement over the correct tribal placement of Stomion. Stomion is placed in the tribe Trimytini in some

catalogues (Blackwelder, 1944; Arnett, 1968). R.L. Aalbu places it in the tribe Triorophini in his classification of genera (Aalbu, unpublished 1992). J.T. Doyen first placed Stomion in the Trimytini (1991, pers. comm.) and later in the Epitragini (Gebien) in his tribal classification based on the structure of the spermatheca (Doyen, unpublished 1991). I place it here as a member of the tribe Trimytini until there is new evidence. This tribe contains 13 genera, all with New World distributions.

In his description of Stomion, Waterhouse noted the following character states which distinguished Stomion from other Tentyriinae: a truncated clypeus, an enlarged mentum which nearly covers the mandibles, and little or no indentation of the mentum for the maxillae. Some features which distinguish Stomion from other Galápagos Tenebrionidae are simple tarsal claws, eyes emarginate and always present, metafemur without apical ventral tooth, and abdomen without exposed intersegmental membranes between visible sternites (Peck, unpublished 1992).

In this study, a morphological examination of the genus Stomion was carried out in two parts. First, a standard taxonomic analysis of morphological characters was carried out on all of the presumptive species of Stomion. Museum specimens, original descriptions and a key by E.C. Van Dyke (1953) were used to test species concepts. These concepts were then applied to identify individuals in our field

collections.

Second, a two-part morphometric analysis of Stomion was done to test the species assignments made in the taxonomic analysis. Qualitative morphological data was used to construct a phenogram of morphological similarity among species of Stomion. Other genera from the tribe Trimytini were included as outgroups to test the generic status of Stomion. Morphometric methods were used to identify those dimensions of size or shape which are useful in species discrimination, and to attempt discrimination of species using quantitative data.

I. Standard Taxonomic Character Analysis

Material and Methods

Specimens examined were those from all collections made during 1992 field work in the Galápagos, and from specimens borrowed from the following museums: The California Academy of Sciences, The U.S. National Museum, the American Museum, the Los Angeles County Museum's Snodgrass and Heller expedition collection, and the Field Museum of Natural History, Chicago. Some specimens were also available from earlier expeditions carried out by S.B. Peck and colleagues in 1991 and 1989. Species concepts were tested on all collections using original descriptions (Waterhouse, 1845; Linell, 1899; Blair, 1933; Van Dyke, 1953; Kaszab, 1970;

Franz, 1985), the key of Van Dyke (1953) and by comparison with museum specimens which included type material of the following species: S. longicornis, S. galapagoensis, S. punctipennis, S. longulum, S. obesum, S. rugosum, and S. cribricollis. Individuals from our field collections were assigned species names.

Results

After examination of all available collections, eleven taxa could be identified using the existing key and descriptions (Table 9). Individuals from two populations on the island of Genovesa (BDAR, PHIL) could not be placed with any of the recognized species. Species distributions as known from the examined collections are mapped in Figure 7.

Members of the genus Stomion fall into into three main morphological types based on body sculpturing, especially of the elytra, or wing covers. Two species, S. laevigatum, and S. linelli have a smooth body surface, with very fine or no punctures whatsoever on the elytra. Four species, S. longulum, S. rugosum, S. obesum, and S. cribricollis, are recognized by longitudinal raised ridges which run the length of the elytra. Five taxa, S. galapagoensis, S. galapagoensis punctipennis, S. helopoides, S. longicornis, and the new species from Genovesa are recognized by coarse punctures on the elytra, usually forming indented striae. Striation is nearly obsolete in the

undescribed species and S. helopoides, but they are included in this group because they are coarsely punctured. The distributions of the three morphological types are shown in Figure 8.

II. Morphometric Analysis

Material and Methods

A. Qualitative Character Analysis

Individuals were chosen from material collected at the type localities. The specimens used and their localities are listed in Table 10. Other genera from the tribe Trimytini were used as outgroups to verify the generic status of Stomion. Among 13 genera listed in the Tribe Trimytini, only four could be acquired for comparison. The following were used as outgroups: Trientoma sp., Trimytis pruinus, Chilometopon castaneum, C. brachystomum, and Stibia sp.

Qualitative characters which are variable among species were selected from the descriptions, the key, and personal observations. These included characters involving size and shape of various body parts as well as external sculpture and punctation (Table 11). Character states were determined for 5-10 individuals of each species for 33 qualitative characters. Similarity measures were calculated between each presumptive species using the SIMQUAL module of NTSYS (Rohlf, 1992). The simple matching coefficient of Sokal and

Michener (1958) was employed to produce a similarity matrix:

$$S_{SN} = \frac{m}{n} = \frac{m}{(m+u)}$$

where m= number of matches, u= number of unmatches, and n= total number of characters. These similarities were then clustered using the SAHN module of NTSYS to group those species which are morphologically most similar. The average linkage cluster method was the algorithm used. Taxa are joined to a cluster when an average relationship with all other members in the cluster is met (Sokal and Sneath, 1963).

B. Quantitative Character Analysis

Where possible, ten individuals from each of 23 populations were used for morphometric analysis. The populations were chosen to include individuals of each presumptive species collected from the type localities, a second population from the same island, and where possible, a third population from a different island. In this way, geographic variation in morphology could be documented. Four species (S. rugosum, S. longulum, S. helopoides and S. laevigatum) were measured from three different sites, and five species (S. obesum, S. linelli, S. galapagoensis galapagoensis, S. galapagoensis punctipennis, S. cribricollis, and the undescribed species) were measured

from two sites. Stomion helopoides was measured from a single site. A single individual of S. longicornis was available for examination, so this species was omitted from this study. The species used, their localities and sample sizes are listed in Table 12.

Nineteen quantitative characters were measured for each of 226 specimens. These variables included continuous measure character states, some of which correspond to the qualitative traits. These measurements are illustrated in Figure 9. Measurements dealt with length and width of various structures of the body and antennae, as well as punctation on the pronotum and head. Measurements were made using a Wild Leitz® dissecting microscope, fitted with a Leitz video camera which captured the image on a monitor. Measurements were calibrated and stored using the JAVA® software system. Body measurements were made at 6x, and antennal measurements were made at 20x. Punctures were counted using an ocular microgrid at 20x, and included counts of all complete punctures in a 9x9 unit area of the grid placed at a landmark position on each specimen.

All statistics were calculated using SYSTAT (Wilkinson, 1988). Summary statistics were calculated for each population using the STATS module. Each variable was then tested for normality in all populations using the Kolmogorov-Smirnov test for normality. In all, 437 tests for normality were performed. An analysis of variance was

performed to first examine variation among species, then among sites assigned to the same species. Tukey's test was performed to identify those populations which differed significantly from one another for each variable. In all, 319 pairwise comparisons were examined between populations considered to belong to the same species.

The variables were then tested for correlation using the CORR module. Variables which were found to be very highly correlated ($r > 0.95$) were excluded from further analysis to avoid weighting the characters.

To examine morphological relationships among species and to attempt to discriminate species, both principle component analysis and canonical coefficients analysis were employed.

Principle component analysis is used to characterize the structure of a set of observations so that most of the variance between individuals is contained in the first few principle components (Chatfield and Collins, 1980). No a priori assumptions about species status are made. Principle component analysis was conducted on the raw measurements using the FACTOR module. Canonical coefficients analysis was done in the MGLH module. Canonical coefficients analysis is used when specimens can be allocated to species or groups. The procedure seeks to maximize the between-group variation while minimizing within-group differences (Reyment, et al, 1971).

Results

A. Qualitative Character Analysis

Scores for 33 qualitative characters show that species of Stomion share some characters not shared with other members of the tribe Trimytini (Table 13). Stomion differs from other members of the Trimytini primarily in the shape of the clypeus. The clypeus is truncated and always without lateral notches in Stomion, while members of the outgroup usually have a fully developed clypeus (Trimytis is the only exception), and always with deep lateral notches. Some members of the Trimytini have wings, while all species of Stomion are flightless and wingless. The lower tooth of the mandibles is bifurcated in other Trimytini while the tooth is truncated in species of Stomion. These differences support the hypothesis that Stomion is a valid genus.

A single phenogram of morphological similarity was produced using the average linkage cluster method. The resulting phenogram shows that Stomion forms a single phenetic group based on some shared character states which are not shared with other members of the Trimytini (Figure 10). Among the outgroup species, Trimytis pruinosus and Trientoma appear to share the most character states with Stomion, and are the first outgroup species to join the phenogram.

Some species pairs are suggested by the cluster analysis. Two subspecies, S. laevigatum laevigatum and S.

laevigatum santacruensis differ in only 2 of the 33 characters, and form a single cluster. Two other subspecies, S. galapagoensis galapagoensis and S. galapagoensis punctipennis group most closely to one another, but differ in six of the 33 characters. The subspecies S. galapagoensis leleupi clusters most closely with S. linelli, and is not clustered in the same phenad as S. galapagoensis galapagoensis. It differs from S. galapagoensis galapagoensis in 14 characters, and differs from S. linelli by only four characters. Stomion longulum and S. obesum also form a species pair.

The phenogram shows a division of Stomion into three clusters which correspond to the three morphological groups based on external sculpturing. However, distances between morphological group clusters is not great. The "ridged" and "smooth" groups have an average similarity of 64%, and the "smooth" and "punctured" group have an average similarity of 60%. To test the hypothesis that other characters support these morphological groups, three characters which describe elytral sculpturing (characters 7, 8, and 9 in Table 11) were removed from the data set. The similarity matrix and cluster algorithm were rerun. Four tied trees were produced using the average linkage method (Appendix 1). A consensus tree was produced in the CONSENSUS module of NTSYS using both the strict (Appendix 2) and majority rule (Appendix 3) methods. The three morphological groups are maintained in

two of the four trees. The "smooth" and "ridged" groups form a single cluster in the other two trees, while the "punctured" group remains intact in all four trees. All three species pairs are maintained in the four trees. Morphological groups break down in the consensus trees, which further shows that the distances between morphological group clusters is not significant.

B. Quantitative Character Analysis

Summary statistics were calculated for each of the ten presumptive taxa (Table 14). Of the 437 tests for normality, 28 (6%) showed non-normal distributions. At a five percent confidence interval, 22 tests might be expected to deviate from normality by random chance alone. Thus, these were treated as examples of random sampling error, and left in the data set.

An analysis of variance showed that there is significant variation in all 19 variables among species at $p < 0.01$ (Table 15). In addition, there is often variation among populations attributed to the same species. For species in which there were only two populations measured, 12 of the 19 variables showed significant differences between populations. For species in which there were three populations measured, 16 of the 19 variables showed significant differences. Tukey's test was performed for each variable on all pairwise comparisons of populations assigned

to each species to identify those populations whose means are significantly different. Of 319 pairwise comparisons, 43 comparisons were significantly different at $p < 0.05$. Some species in particular showed significant differences among populations at several variables. For example, measurements from Daphne and Rabida (assigned to S. linelli), differed significantly for PROWB, WIDT, ELYTWA, ANTL, SEG4L, SEG5L, SEG6L, and PPRO. Similarly, differences at eleven variables were also found between populations of S. galapagoensis punctipennis at Bahia Gardner, Manzanillo, and Punta Suarez, all on Española. Stomion laevigatum also showed significant differences in six variables between the three populations from two islands assigned to this species.

A Pearson correlation analysis of all variables showed that there is significant size related correlation of the variables. Only puncture counts on the head and pronotum were independent of size. Three variables were found to be very highly correlated with other variables ($r > 0.95$). The width of the pronotum at the midpoint was highly correlated to both the width of the pronotum at the base, as well as the width of the elytra at the base. The width of the pronotum at its base was also found to be highly correlated to the width of the elytra at the base. Finally, the body width as measured across the elytra was also highly correlated to the width of the elytra at the base. The following variables, then, were removed from further

analyses to avoid weighting of characters: pronotum width at middle (PROWM), pronotum width at base (PROWB), and body width (WIDT).

Principle component scores were calculated on the raw data of the sixteen remaining morphological characters (Table 16). The first three principle components had eigenvalues of 8.798, 2.465, and 1.442. All other eigenvalues were less than one, so character evaluation was based on the first three principle components. The first three principle components explained 54.8%, 15.4%, and 9.0% of the variation, respectively.

The first principle component separated individuals on the basis of general length and size components, with the highest scores for antennal length, total body length, and length of the 5th antennal segment. Other antennal segment lengths, as well as the width of the pronotum and elytra, had high component scores.

The second principle component separated individuals primarily by external sculpturing, as measured by the number of punctures on the pronotum and head.

The third principle component separated individuals based on a mixture of external punctuation and shape of the pronotum, based on high component scores for pronotum length and width measurements.

A scatter plot of the first two principle components shows a great deal of overlap among observations (Figure

11). Individuals are separated largely by size along the first axis and by punctuation along the second. Species with low scores on the first principle component have small body sizes (S. laevigatum, and S. rugosum). Species with high scores are those with larger body sizes (S. galapagoensis galapagoensis, S. galapagoensis punctipennis, and S. linelli). Species with low scores along the second principle component are those with few surface punctures on the head and pronotum (S. rugosum, S. galapagoensis punctipennis). Species which have high scores along the second principle component are those with high number of surface punctures (S. cribricollis, S. longulum). The second and third principle component scores were plotted to reflect distribution based on body shape, with size no longer a factor (Figure 12). Stomion rugosum, S. galapagoensis galapagoensis, and S. laevigatum are slightly distinguishable along the periphery of the plot, while all other species are highly overlapping.

To test the hypothesis that the genus Stomion is composed of three morphological groups, populations were coded according to smooth (A), punctured (B), or ridged (C) surface sculpture, and replotted. The plots show three highly overlapping groups with little separation between them. Member. of the three morphological groups are not separated by general size components (Figure 13) nor by body shape (Figure 14).

Population means were plotted for some characters which were identified by principle component analysis as contributing the most to overall variation among populations. Three of these bivariate plots seem to show division of the species into the same two groups. A plot of the width of the pronotum versus the length of the pronotum divides the populations into those with a pronotum which is nearly as long as wide, or quadrate shaped (S. laevigatum, S. rugosum, S. obesum, S. cribricollis, and S. longulum) and those with a pronotum which is wider than long, or transverse shaped (S. helopoides, S. linelli, the Genovesa populations, S. galapagoensis galapagoensis, and S. galapagoensis punctipennis) (Figure 15a). A plot of the elytra width versus length again divides the populations into the same two discrete groups: those which are long and thin in the abdomen (S. longulum, S. laevigatum, S. cribricollis, S. obesum, and S. rugosum) and those which are broader in body shape (S. galapagoensis punctipennis, S. galapagoensis galapagoensis, S. helopoides, the Genovesa populations, and S. linelli) (Figure 15b). The same two groups again are discriminated when the pronotum width at the base (PROWB) is plotted against the pronotum width at the apex (PROWA) (Figure 16a). Stomion galapagoensis gala, agoensis is separated from the first group along these dimensions, but is closer to this group than the group containing species which are narrower at the base. A plot of

the number of punctures on the head versus the number of pronotal punctures is less clear, although a linear relationship is suggested (Figure 16b). Stomion g. galapagoensis, S. galapagoensis punctipennis and S. helopoides have a low number of punctures on both the head and pronotum, S. linelli and S. laevigatum have a low number of pronotal punctures but a moderate number of head punctures, S. rugosum and S. obesum have moderate numbers of both head and pronotal punctures, and S. longulum, the Genovesa populations, and S. cribricollis have high numbers of both head and pronotal punctures.

Because the bivariate plots suggest that the species can be divided into two groups based on certain body dimensions, populations were coded for these two groups and principle components were replotted to test the hypothesis that Stomion is composed of two morphological groups based on body size and shape. Group A is comprised of individuals which are broad at the thorax and abdomen (i.e. galapagoensis punctipennis, S. galapagoensis galapagoensis, S. helopoides, the Genovesa populations, and S. linelli). Group B consists of species which are narrow both at the thorax and abdomen (S. longulum, S. laevigatum, S. cribricollis, S. obesum, and S. rugosum). A plot of the first two principle components shows two broadly overlapping groups (Figure 17). A plot of the second and third principle components shows a majority of individuals clustered toward the centre, with a few

outliers at each edge (Figure 18). The two groups are not well separated. The better separation of the first and second principle components suggest a size component to the observed separation.

A canonical coefficients analysis was used to minimize within-group variance and maximize between-group variances, to maximize discrimination among pre-assigned groups. By matching individual coefficient scores with group averages, individuals can be classified to the group in which they are closest to the mean. Classification of species was then tested against pre-assigned groups. Of the 226 measured animals, 201 individuals (89%) were classified to belong to the species in which they were originally assigned (Appendix 4). Stomion rugosum and S. helopoides were classified correctly in 100% of the cases. Stomion obesum, and S. galapagoensis punctipennis were classified correctly in 95% or greater of the cases. Stomion linelli showed the most deviation from the mean, as only 65% of these individuals were classified as belonging to S. linelli.

The first canonical coefficients show that general size variables contribute to overall variation (Table 17). The greatest contribution to discrimination along this axis comes from the width of the elytra at the apex (ELYTWA), and total body length (LENG). The number of punctures on the head was also a major contributor along this axis (PHEAD). The second canonical coefficients are also influenced by

variability in length and width (ELYTWA, LENG, PROWA), but also in the proportions of antennal segments (SEG4L, SEG5W).

A plot of the first and second canonical axes shows that there is considerable overlap among eight of the ten presumptive taxa (Figure 19). One species, S. rugosum, is clearly separated. It has low canonical scores along the second axis and lies separated from all other members of the genus. The new species is found overlapping primarily with S. longulum. A plot of the second and third canonical axes again show a clear separation of S. rugosum. Stomion laevigatum is nearly separated from the rest of the group. All other species form a single overlapping group. (Figure 20).

To again test the hypotheses that Stomion is comprised of three morphological groups, populations were coded as belonging to either the smooth (A), punctured (B), or ridged (C) groups, and the canonical analysis was rerun. The width of the elytra at the apex and the width of antennal segment five have the highest canonical coefficients. These two characters presumably contribute the most to discrimination of individuals along the first axis. Discrimination between individuals along the second axis is due to variation in the length of the antenna, and the number of punctures on the head. Classification of animals into preassigned groups was tested. Of 226 animals, 176 (78%) were placed into the "correct" group (Appendix 5). Eight-nine percent of "ridged"

individuals were classified into the ridged group. "Smooth" and "punctured" individuals were less successfully classified into the pre-assigned groups at 68% and 70%, respectively. A plot of the first two canonical axis shows a fairly good separation of the three groups, with some overlap among all groups (Figure 21).

To test that Stomion is composed of only two morphological groups, populations were coded as belonging to the two groups suggested by the bivariate plots (A= broad body shape, B= narrow body shape). The width of the elytra at the apex has the highest canonical coefficient. Discrimination among individuals is based largely on this character. A test of classification of individuals into preassigned groups shows 89% success in placing an individual into the "correct" group (Appendix 6). Broad bodied individuals were correctly classified in 87% of the cases, and narrow individuals were classified correctly in 91% of the cases.

Because of its distinctiveness from the rest of the genus, Stomion rugosum was removed from the data base, and the canonical analyses were repeated to try to further discriminate among the remaining species.

Body size (ELYTWA, ELYTL) and punctation (PHEAD, PPRO) again scored highly on the first and second canonical coefficients (Table 18). Of 195 tests, 172 individuals (88%) were classified to the species in which they were assigned

(Appendix 7). A plot of the first two canonical axes again shows overlap among all species (Figure 22). Stomion linelli, S. galapagoensis galapagoensis, and S. helopoides, in particular are highly overlapping. Stomion laevigatum is nearly separated from the group. A plot of the second and third canonical axes show S. laevigatum and S. galapagoensis galapagoensis to be partially separated from the group. All other species are highly overlapping (Figure 23).

A final attempt was made to discriminate among the species. Populations of Stomion laevigatum were also removed from the data set, so that only eight of the ten original taxa remained, and the canonical analysis was repeated. A plot of the first two canonical axes shows complete overlap of all species (Figure 24). In particular, the populations from Genovesa, S. cribricollis, and S. longulum are highly overlapping. Stomion galapagoensis punctipennis is nearly separated from the rest of the group. A plot of the second and third canonical axes shows a near separation of S. galapagoensis galapagoensis (Figure 25). All other species are highly overlapping. Classification of individual to the "correct" species was 87%.

Discussion

Generic Status

Species belonging to the genus Stomion form a cohesive morphological group. The distinctiveness of the genus is

supported by a cluster analysis of morphological similarity which clearly places other genera of the tribe Trimytini outside the cluster containing Stomion. Stomion, as a group, shows only 39% similarity with the nearest members of the outgroup.

Of the outgroups, Trientoma sp. and Trimytis pruinus are the most morphologically similar to Stomion. They are the first outgroups to join the tree. Both of these species have smooth external surfaces, although punctation is present in the three other outgroup species. Trimytis pruinus is probably the most closely related of the outgroups. It is the only examined species to share with Stomion the trait of truncated clypeus. However, until all other genera of the tribe Trimytini are examined, a sister genus can not be proposed.

Members of the tribe Trimytini are distributed throughout the new world, and are found from the southwest United States south to Chile and Argentina and as far east as the Greater Antilles. The tribe contains species which are winged as well as wingless (MacLachlan and Olson, 1990).

Oceanic currents likely aided in the transport of a Stomion ancestor to the Galápagos. Dispersal is possible both from North and Central American Pacific coastal regions via the California current, the North Equatorial Current, and the El Niño flow (Thornton, 1971). Likewise, dispersal from the South American Pacific coastal regions may be aided

by the Humboldt and South Equatorial Currents.

Discrimination of Species

While a standard taxonomic examination of the genus suggests that there are twelve taxa, species are not well distinguished using morphometric methods. Despite the high morphological similarity among members of the genus, both qualitative and quantitative character analysis shows that species discrimination is possible. Subspecies differ in from three to six different qualitative characters, and species differ in up to 11 different characters. A two-way ANOVA shows that species means differ significantly at 19 quantitative characters. Classification using canonical analysis places 88.9% of individuals into the "correct" species. While canonical analysis may not be necessary to identify new individuals, it proved to be a useful technique for species discrimination and identification of those characters with the greatest discriminating power.

Taxonomic characters which contribute most to variation among populations were identified from the principle component and canonical analyses. General size, especially length of some body parts such as overall body length, antennal length and length of antennal segment five were scored highly in the first principle component. Punctures on the head and pronotum scored highly in the second principle component.

Canonical coefficients analysis also showed that

general body size components are responsible for much of the variation among species. Body length, and the width of the elytra at the apex showed the highest canonical coefficients along the first two discriminant axes. Again, punctures on the head were important in discrimination of species. Thus while much of the variation among species is clearly due to size variation, body sculpturing is also an important component in species recognition. Classification of species into their pre-assigned groups shows that some species can be successfully differentiated. Stomion rugosum, S. helopoides, S. galapagoensis punctipennis, S. obesum, and S. cribricollis are correctly classified in 90% to 100% of the cases.

However, plots of both principle component and canonical axes show enormous overlap of species. Stomion rugosum is the only species which is visually distinguishable from all others in a plot of the first two canonical axes. A few other species, such as S. galapagoensis galapagoensis, S. galapagoensis punctipennis, S. laevigatum, S. cribricollis, and the new species from Genovesa are found at the periphery of canonical plots, suggesting some morphological divergence from the other species. These morphologically divergent species are all found on islands which are spatially isolated from other islands in the archipelago. Species which are found on the central islands such as S. longulum, S. obesum, and S.

linelli tend to show the greatest overlap. Stomion rugosum and S. cribricollis are found in the northern-most islands of Pinta, Marchena, Darwin, and Wolf. Stomion galapagoensis galapagoensis and S. galapagoensis punctipennis are found on the southern-most islands of Española and Floreana. It is likely that their geographic isolation has resulted in reduced gene flow into the populations, and greater morphological divergence. Time of isolation probably also plays a role in the morphological divergence observed in S. galapagoensis punctipennis. It is found on Española, one of the oldest islands in the archipelago. Thus, S. galapagoensis punctipennis has presumably had the greatest time to diverge. Stomion helopoides is found on San Cristóbal, another island whose rocks have been dated among the oldest in the archipelago. In contrast, it does not show marked morphological divergence from other species of the genus. This suggests that differential selection may be occurring among populations on different islands.

A plot of the first two canonical axes places the new species from Genovesa near S. cribricollis, S. longulum, and S. obesum. In particular, there is substantial overlap with S. longulum. Morphometric data, then, suggests that in body structure, the new species may belong to the group which is narrow in the thorax and abdomen. A plot of the number of punctures on the head and pronotum place it near S. cribricollis and S. longulum. However, bivariate scatter

diagrams of selected characters place the new species with S. galapagoensis, S. g. punctipennis and S. helopoides when certain body dimensions are examined.

There is clearly geographical variation in morphology among populations of some of the species. Tukey's test, performed on pairwise comparisons of sample means for each variable showed variation occurs particularly among populations of S. laevigatum, S. longulum, S. linelli, and S. galapagoensis punctipennis. All but the last of these four taxa are found on more than one island. Morphological divergence may be occurring among populations of those species where gene flow is reduced.

Biogeographical evidence supports the hypothesis of reproductive isolation among species. There are three cases of sympatry of two or more species on a single island. Sympatric distributions of Stomion occur on Española (2 species), Santa Cruz (3 species), and Isabela (2 species). There was no evidence of hybridization occurring on those islands which are home to more than one species. Morphological integrity is maintained, which shows an absence of interbreeding.

Most species are found on only a few, geographically close islands. This distribution of the species can be used as biogeographical evidence that speciation occurred on single islands, and colonizers then spread to other near-by islands. The flightless condition of Stomion certainly

limits its vagility and the possibility for dispersal and gene flow among demes. This is particularly true for chances of dispersal between islands, but geographical barriers may prevent dispersal on individual islands, as well.

Evolution of Species Groups

Distribution of the three morphological groups suggests that each group evolved in discrete areas of the archipelago. It may further be suggested on the basis of biogeographical evidence that group traits such as "ridges" or "punctures" would appear to have evolved once, and were dispersed to near-by islands. Species of the "punctured" group are found in the south and eastern part of the archipelago; they are found on Española, San Cristóbal, Floreana, and Genovesa. Species of the "smooth" group are found in the central and western islands; they are found on Santiago, Santa Cruz, several satellite islands between Santa Cruz and Santiago, and Fernandina and Isabela. The "ridged" group is found in the central and northern-most islands; they are distributed from Santa Cruz and Isabela to Pinta, Marchena, Darwin, and Wolf in the far north.

However, the morphological evidence supporting these three morphological groups is not strong. The cluster analysis of a similarity matrix based on 33 qualitative characters shows separation of the genus into these three groups, although distances between groups are slight. When traits involving elytra sculpturing are removed from the

data set, the three morphological groups are maintained in only two of the four resulting tied trees.

The principle component analysis does not show separation of the three groups when populations are coded according to surface sculpturing. In fact, bivariate plots of selected traits with the greatest contribution to overall variation suggest that there are two morphological groups based on body size and shape. A bivariate plot of surface punctures on the head and pronotum does not separate the species into morphological groups, but instead suggests that there is a linear relationship to punctation on the head and pronotum. Canonical analysis shows some discrimination of groups along the first two canonical axes, although full separation is not achieved. Classification into three pre-assigned morphological groups occurs correctly only in 78% of cases, while classification into two morphological groups occurs in 89% of cases.

Thus, the evidence is weak that Stomion is comprised of three morphological groups based on external sculpturing. Traits such as smooth or punctured surfaces may have arisen independently several times. Such surface sculpturing may have an adaptive advantage in some environments, and may arise as a result of response to local selection. Instead, there is some evidence which suggests that Stomion is comprised of two morphological groups based on body size and shape.

Nomenclature Changes

Some changes to the current nomenclature are required. All previously described species and one subspecies are recognized as being valid. One recombination results from assigning a subspecies to another species. One subspecies was found to be without evidence to support it, and another two remain in question. A new species is proposed from the island of Genovesa.

Stomion laevigatum santacruensis is not considered a valid subspecies because it differs little from the range of variation seen in other populations of S. laevigatum. It differs only in having very weak, feebly punctured ridges on the elytra. The overall body surface is smooth as in S. laevigatum Waterhouse, which also shows feeble punctuation on the elytra at other localities.

Animals from high elevation sites on Santa Cruz were examined and these fit Kazsab's description of Stomion galapagoensis leleupi. No type specimens of S. galapagoensis leleupi were available for examination, however. From this study, Stomion galapagoensis leleupi is considered to be a subspecies of S. linelli, not of S. galapagoensis, to which it was originally assigned. It clusters most closely with S. linelli in the cluster diagram of similarity based on qualitative characters. The shape of the pronotum and nearly smooth, convex abdomen place it clearly with S. linelli.

Stomion galapagoensis pinzoni was not encountered during this study, so its status remains unknown. Type material of Stomion galapagoensis pinzoni was not available. However, examination of collections from the island of Pinzón showed only examples of S. obesum. The status of S. galapagoensis pinzoni is therefore questionable.

E.C. Van Dyke's Stomion galapagoensis punctipennis stands as a good subspecies. It is found exclusively on Española, while S. galapagoensis galapagoensis is found on Floreana, Champion, and Gardner.

A small collection of animals from Genovesa in the Van Dyke collection, labelled S. helopoides, was misidentified. Stomion helopoides is known thus far only from San Cristóbal. The collections from Genovesa belong to the new morphotype. This new morphotype was collected at two additional sites in the 1992 field collections: Bahia Darwin and Prince Phillip's Steps, both on Genovesa. A new species is thus proposed from the island of Genovesa. Stomion denticula sp. n. is distinguished by numerous coarse punctures on the elytra which are evenly distributed over the surface and are not organized into striae and intervals. It also has a distinct dorsal tooth on the right mandible.

Key to Species

The following key and descriptions serve to distinguish each species:

- 1A. Pronotum and elytra smooth or with fine punctures.....2
- 1B. Pronotum and elytra distinctly marked with punctures and elytra with punctures or ridges.....4
- 2A. Pronotum widest at base, base 1.4x wider than apex; body large and robust (length= 7-9 mm width= 4-5 mm); sides of abdomen rounded.....3
- 2B. Pronotum apex and base nearly equal in width, base no more than 1.2x wider than apex; body size small and narrow (length= 6-8 mm, width= 3-4 mm); sides of abdomen parallel..... S. laevigatum
- 3A. Body surface shiny or feebly shiny; punctures on pronotum and elytra fine or absent.....S. linelli
- 3B. Body surface dull; punctures on pronotum fine and with short setae; punctures on elytra fine but forming weak striae..... S. linelli leleupi new comb.
- 4A. Pronotum 1.5-1.6x wider than long; punctures on pronotum coarse and widely spaced; elytra coarsely punctured with punctures usually in rows, forming distinct striae.....5
- 4B. Pronotum 1.2-1.3x wider than long; punctures on pronotum moderate to coarse, and close together; elytra marked with longitudinal ridges; or pronotum ≤ 1.5 x wider

- than long, but elytra with distinct ridges.....9
- 5A. Punctures on head, pronotum, elytra with setae.....S. longicornis
- 5B. Punctures on head, pronotum, elytra without setae.....6
- 6A. Elytral striae distinctly impressed, intervals raised.....7
- 6B. Elytral striae nearly obsolete, at same or nearly same height as intervals.....8
- 7A. Punctures in striae much coarser than those of intervals.....S. galapagoensis galapagoensis
- 7B. Punctures of striae and intervals of nearly the same size.....S. galapagoensis punctipennis
- 8A. Pronotum, elytra coarsely punctured, punctures on elytra evenly spaced in rows; punctures on pronotal disc sparse and irregular; ventral tooth on right mandible absent.....S. helopoides
- 8B. Pronotum, elytra finely to moderately punctured, punctures on elytra close together, rows indistinct; disc evenly punctured; ventral tooth on right mandible distinctly formed..... S. denticula (n.sp.)

- 9A. Head, pronotum, elytra rugosely punctured, punctures coarse, often running together.....S. rugosum
- 9B. Head, pronotum, elytra finely to coarsely punctured, punctures clearly separated.....10
- 10A. Elytra with coarse punctures between ridges, irregularly arranged on ridges.....S. cribricollis
- 10B. Elytra with fine punctures irregularly arranged in between and on top of ridges, striae obsolete.....11
- 11A. Elytra elongate, 1.4x longer than wide; body shiny, black; sides of elytra parallel.....S. longulum
- 11B. Elytra not elongate, 1.2x longer than wide; body dull, reddish; pronotum and abdomen convex.....S. obesum

Stomion cribricollis E.C. Van Dyke (Figure 26-3, 27a, 27b)
Stomion cribricollis Van Dyke, 1953:75. Holotype: Type 7386 in the California Academy of Sciences (CAS). (examined). Type locality: Wenman Island (=Wolf). Label data: 24.IX.1906 F.X. Williams.

Diagnosis: Length 7-9 mm, width 3-4 mm; body elongate, 2.2x longer than wide; pronotum nearly quadrate, 1.2-1.3x wider than long; pronotum widest at middle, slightly constricted at base; pronotum with coarse, shallow punctures, elytra with parallel ridges, coarsely punctured both between and on top of the ridges; dorsal tooth of right mandible present but weak, as in Figure 31a.

Stomion galapagoensis galapagoensis G.R. Waterhouse (Figure 26-1, 27c, 27d)

Stomion galapagoensis Waterhouse, 1845:29. Type locality: [Galápagos] probably Floreana. Lectotype to be designated by T.L. Finston in the British Museum of Natural History, London (BMNH).
Stomion carinipenne Linell, 1898:262. United States National Museum, New York (USNM) Type 1320 (examined). Type locality: Charles Island (=Floreana). Label data: Charles I. Galapagos Is. G. Baur collr. Red label: type 1320 USNM *Stomion carinipenne* type Linell.
Stomion carinatipenne Blair, 1933:477. (misspelled).
Stomion piceum Linell 1898:262. USNM type 1321 (examined). Type locality: Charles Island (=Floreana). Label data: Charles I. Acc 21,699 USFC. Red label: type no 1321 USNM *Stomion piceum* type Linell.

Diagnosis: Length 8-10 mm, width 4-5 mm; body large, broad, and often flattened, 2x longer than wide; pronotum transverse, 1.4-1.5x wider than long, coarsely, but shallowly punctured, apical margin nearly straight, widest at middle, nearly as wide at base, but sometimes constricted; elytra with striae formed by deep punctures, single irregular row of fine punctures in the intervals between the striae; dorsal tooth of right mandible present but weak, as in Figure 31a.

S. galapagoensis punctipennis E.C. Van Dyke (Figure 27e, 27f)
S. galapagoensis punctipennis Van Dyke, 1953:72. Holotype: type 7384 in CAS (examined). Type locality: Mood (=Española). Label data: Mood Is. II. 1906 F.X. Williams

Diagnosis: Length 8-10 mm, width 4-5 mm; body large, broad, and flattened, 2x longer than wide; pronotum transverse, 1.6x wider than long, coarsely punctured, apical margin very convex, widest at middle, nearly as wide at base; elytra with striae formed by deep punctures, double row of offset punctures in the intervals between the striae which are nearly as coarse as those in the striae; dorsal tooth of right mandible weak, as in Figure 31a.

Stomion helopoides G.R. Waterhouse (Figure 26-2, 28a, 28b)
Stomion helopoides Waterhouse, 1845:30. Type locality: [Galápagos] probably San Cristobal. Lectotype to be designated by T.L. Finston in the BMNH, London.
Stomion helopioides Linell, 1898: 263 (misspelled).

Diagnosis: Length 9-10 mm, width 4-5 mm; body large, broad, 2.0x longer than wide, densely punctured but with overall surface smooth; pronotum transverse, 1.5-1.6x wider than long, apex deeply concave, broadest at middle, distinctly narrowed at base, punctures coarse, sparse on disc; elytra evenly punctured throughout, striae barely impressed; dorsal tooth on right mandible absent, as in Figure 31b.

Stomion laevigatum G.R. Waterhouse (Figure 26-5, 28c, 28d)
Stomion laevigatus Waterhouse, 1845:30. Type locality: [Galápagos] probably either Isabela or Santiago. Lectotype to be assigned by T.L. Finston in the BMNH, London.

Diagnosis: Length 6-8 mm, width 3-4 mm; overall body surface smooth and somewhat shiny, 2.1x longer than wide; fine sparse punctures on pronotum and elytra; pronotum strongly convex at the apex; pronotum widest at middle, roughly the same width at the base as at the apex, constricted slightly at the base, 1.5-1.6x wider than long; elytra smooth with fine but distinct irregularly arranged punctures; sides of abdomen are parallel; dorsal tooth on right mandible present, moderately well developed, as in Figure 31c.

Stomion linelli K.G. Blair (Figure 26-6, 28e, 28f).
Stomion linelli Blair, 1933:478. Type locality: [Galapagos] probably either Eden or Indefatigable (=Santa Cruz). Lectotype to be designated by T.L. Finston in the BMNH, London

Diagnosis: Length 7-9 mm, width 4-5 mm; body broad, <2.0x longer than wide; overall body surface smooth; fine, sparse

punctures on pronotum and elytra; pronotum apical margin nearly straight; pronotum transverse, 1.7x wider than long, noticeably narrow at apex and broadens continually toward the base; elytra smooth with punctures very fine, sometimes obsolete, arranged in parallel rows; abdomen broad and convex, giving S. linelli a robust shape; dorsal tooth of right mandible present, well developed, as in Figure 31d.

Stomion linelli leleupi (Kaszab) new comb. (Figure 29a, 29b)
Stomion galapagoensis leleupi Kaszab 1976:187. Holotype male and paratypes in the Institut Royal Des Sciences naturelles De Belgique (not examined). Type locality: Santa Cruz. Label data: 12-17.II.1965, leg. J. & M. Leleup.

Diagnosis: Length 7-9 mm, width 4-5 mm; body broad, 2.0x longer than wide; overall body surface smooth, without striae or ridges, but with distinct punctures on pronotum and elytra; pronotum transverse, 1.7x wider than long, widest at base, base broader than apex; pronotal punctures distinct coarse, but not deep; elytra equally punctured; dorsal tooth of right mandible present, well developed, as in Figure 31d.

Stomion longicornis E.C. Van Dyke (Figure 26-7, 29c, 29d)
Stomion longicornis Van Dyke, 1953:79. Holotype: type 7388 in CAS (examined). Type locality Hood (=Española). Label data: February 1906 F.X. Williams.

Diagnosis: Length 8 mm, width 4 mm (Van Dyke, 1953); body broad, 2.0x longer than wide, body surface shiny, distinctly pilose on the head, apical margin of pronotum, and elytra; pronotum transverse, 1.4-1.5x wider than long, widest behind middle, punctures distinctly elongated; elytra are nearly evenly punctured in the striae and the intervals; dorsal

tooth on right mandible absent, as in Figure 31b.

Stomion longulum E.C. Van Dyke (Figure 26-4, 29e, 29f)
Stomion longulum Van Dyke, 1953:76. Holotype: type 7387 in CAS (examined). Type locality:
 Indefatigable (=Santa Cruz). Label data: 7.V.32 M. Willow Jr. Templeton Crocker Expd.

Diagnosis: Length 7-9 mm, width 3-4 mm; body elongate, 2.4x longer than wide, surface shiny; sides of abdomen are parallel; pronotum quadrate, 1.3-1.4x wider than long, with fine punctures, widest at middle, narrowed toward base; elytra marked by distinct parallel ridges; fine punctures arranged irregularly in intervals between ridges, single row of coarse punctures adjacent to ridges; dorsal tooth on right mandible present, moderately well developed, as in Figure 31c.

Stomion obesum E.C. Van Dyke (Figure 30a, 30b)
Stomion obesum Van Dyke, 1953:74. Holotype: type 7385 in CAS (examined). Type locality: Duncan (=Pinzón). Label data: 14-15.VII.1906. F.X. Williams.

Diagnosis: Length 7-9 mm, width 3-5 mm; body broad and convex, 2.0-2.1x longer than wide; pronotum slightly transverse, 1.5-1.6x wider than long, coarsely punctured, some punctures near margins are elongate, pronotum widest at middle, nearly as wide at base, sides rounded; elytra with parallel ridges, single row of weak punctures between ridges; thorax very convex, sides rounded; dorsal tooth on right mandible present, well developed, as in Figure 31d.

Stomion rugosum E.C. Van Dyke (Figure 26-8, 30c, 30d)
Stomion rugosum Van Dyke, 1953:80. Holotype: type 7389 in CAS (examined). Type locality: Abingdon (=Pinta). Label data: IX.1906 F.X. Williams.
Stomion rugosus Van Dyke, 1953:81.

Diagnosis: Length 6-8 mm, width 3-4 mm; body broad, 2.0x longer than wide; body coarsely and rugosely punctured; pronotum slightly transverse, 1.5x wider than long, widest behind middle, nearly as wide at base; elytra with rugose ridges, very coarsely punctured both between and on top of ridges, some punctures anastomosing; dorsal tooth on right mandible present, moderately well developed, as in Figure 31c.

Stomion denticula T.L. Finston new species (Figure 30e, 30f)
Stomion helopoides Waterhouse. Van Dyke, 1953:74.

Diagnosis: Length 8-10 mm, width 4-5 mm; body broad, convex, 2.0x longer than wide; striae and intervals of elytra nearly the same height, giving this species an overall smooth surface; pronotum transverse, 1.5x wider than long, coarsely, shallowly punctured, widest behind middle, slightly constricted at base; elytral punctures coarse along striae, smaller in intervals; right mandible with well developed dorsal tooth as in Figure 31d. The etymology of the name comes from the Latin meaning "small tooth".

In summary, Stomion appears to be a valid genus, separated from other Trimytini by several characters. Classic taxonomic examination of the genus shows that there are eight morphological species in the genus, and four

subspecies. These species form a morphologically cohesive group. However, both qualitative and quantitative character analyses uncovered a number of characters and combinations of characters which are useful for species discrimination. While there are clearly three main morphological groups based on external sculpturing, morphometric analysis do not support these groups. Instead, some evidence suggests the presence of only two morphological groups based on body size and shape. The external sculpture characters may have evolved independently several times, in response to local conditions.

Chapter Three: Population Genetics and Biochemical Systematics of Stomion.

Introduction

Morphological examination of Stomion has shown that it is a morphologically cohesive group, separated taxonomically into eight species and four subspecies. There are three main morphological groups based on external sculpturing. Morphometric data suggest that there may be two groups based on body size and shape. The genus is widespread in the archipelago, but each species is found on only one or a few islands which are geographically close. This distribution of Stomion suggests that speciation occurred on single islands, and was followed by dispersal to and colonization of other near-by islands.

The Galápagos Islands have been available for colonization for approximately three million years (Jackson, 1990). Stomion is considered to be a genus endemic to the Galápagos, having arisen from a single ancestor and evolving within the archipelago (Van Dyke, 1953). The time-frame for differentiation of these twelve taxa then, should be less than three million years.

The differentiation of a single lineage into many species can occur in a number of ways. Allopatric isolation is thought to be the primary mode of speciation among sexual, diploid organisms (Mayr, 1963). However, genetic

models of parapatric and sympatric speciation have been proposed for other speciation events (Endler, 1977). Selection, drift, and founder effects are some of the mechanisms which may help to produce new species under allopatric conditions. Darwin's finches are now a textbook case of insular speciation and adaptive radiation (Yang and Patton, 1981; Grant, 1981). Under differing environmental conditions provided by individual islands, isolated populations have adapted to the local conditions. The result is genetic and reproductive isolation, which is upheld even under conditions of secondary contact.

Radiation has occurred in other Galápagos organisms, as well. The giant tortoises, Geochelone elephantopus, and the lava lizards, Tropidurus spp. are two examples. Studying genetic patterns in Stomion may help to understand the processes of differentiation in an invertebrate species swarm. The beetles may have differentiated in response to differing environmental conditions of each new locality, or by allopatric isolation, where small population sizes, genetic drift, and founder effects act independently or together to produce the observed morphological divergence.

A two-part genetic study was carried out. Cellulose acetate electrophoresis was used to first examine the population structure of Stomion. Genetic structure at eight informative loci of 35 populations of Stomion were examined to try to understand the genetic patterns which underlie

speciation events in this genus. Second, a systematic study of some morphospecies was conducted at 21 loci to identify taxonomic markers between species. Morphospecies were tested for evidence that they were also genetic species. Genetic distances were used to calculate divergence times between species.

In these studies, genetic data are used as a second, independent character set to try to understand species relationships in Stomion and to test the validity of morphological species and species groups.

General Materials and Methods

Electrophoresis

Live beetles from each population were frozen on dry ice, and shipped to the laboratory in Ottawa where they were stored in a -80°C ultrafreezer until further analysis. As only a small piece of tissue is needed for cellulose acetate electrophoresis, each beetle was dissected, and a piece of tissue from the head was placed in a grinding well. This tissue was chosen over tissue from the thorax or abdomen, which may contain food particles, or eggs. These substances may interfere with banding patterns. The tissue was ground in 10 ~~micro~~microlitres of water, and the homogenate from 24

individuals was applied to each gel plate, in two rows of twelve animals. One standard (an individual of S. linelli linelli from Isla Daphne) was included in each row.

Electrophoresis was carried out using standard methods (Hebert and Beaton, 1988). Two buffer systems were employed: tris glycine (pH=8.5) was used for the following enzyme systems: hexokinase (Hk-2; the first locus could not be consistently resolved), mannose 6- phosphate isomerase (Mpi), phosphoglucomutase (Pgm-1; a second locus could not be consistently resolved), peptidase phenylalanine proline (Pep phe-pro) glutamate oxaloacetate transaminase, two loci: supernatant and mitochondrial forms (Got-s, Got-m), 6-phosphogluconate dehydrogenase (6Pgdh), phosphoglucoisomerase (Pgi), fumarase (Fum), aldehyde oxidase (Ao), arginine phosphokinase (Apk), peptidase leucyl glycine (Pep leu-gly), isocitric dehydrogenase, two loci: (Idh-1, Idh-2), and trehalase (Tre). Tris citrate (pH=7.3) was employed for the following enzyme systems: aconitase, two loci: (Acon-1, Acon-2), malic dehydrogenase, two loci: (Mdh-1, Mdh-2), and malic enzyme, two loci: (Me-1, Me-2).

Electrophoresis was carried out at approximately 2 milliamps (mA) per gel plate on tris glycine, and 8 mA per gel plate on tris citrate. Running times also varied with the buffer. Enzymes which were resolved in the tris glycine buffer ran for 16-20 minutes, and enzymes which were resolved in the tris citrate buffer ran for 25-30 minutes.

The protein products of these gene loci were visualized using staining protocols outlined in Hebert and Beaton (1988) and Murphy et al (1990).

The resulting bands were scored with respect to their relative mobilities: the slowest migrating electromorph was assigned a one; larger numbers indicate faster mobility. Electromorph mobilities were compared to the standard in each row. In addition, part way through the study, four individuals from a population were carried over to the next set of gels to provide a second source of comparison of electromorphs.

I. Population Structure of Stomion

Methods

Initially, 174 animals from six different populations were run for 20 commonly resolvable loci (Hebert and Beaton, 1988; Hsiao, 1989) in order to identify informative loci. The enzymes tested and number of loci is as follows:

phosphoglucosomerase, 1 locus: (Pgi), isocitrate dehydrogenase, 2 loci (Idh-1, Idh-2), phosphoglucomutase, 2 loci (Pgm-1, Pgm-2), malate dehydrogenase, 2 loci (Mdh-1, Mdh-2), aconitase, 2 loci (Acon-1, Acon-2), hexokinase, 2 loci (Hex-1, Hex-2), 6-phosphogluconate dehydrogenase, 1 locus (6Pgdh), malic enzyme, 2 loci (Me-1, Me-2), glutamate

oxaloacetate transaminase, 2 loci, supernatant and mitochondrial forms (Got-s, Got-m), fumarase, 1 locus (Fum), aldehyde oxidase, 1 locus (Ao), peptidase, phenylalanine proline, 1 locus (Pep phe-pro), alcohol dehydrogenase, 1 locus (Adh). Eight variable loci were found: Ik-2, Mpi, Pgm-1, Pep (phe-pro), Got-s, Got-m, 6Pgdh, and Pgi. Where possible, 44 individuals from each population were analyzed for these eight loci. The populations used for electrophoretic analysis and their sample sizes are shown in Table 19. Nine taxa were represented by the 35 populations: Stomion denticula, S. galapagoensis galapagoensis, S. galapagoensis punctipennis, S. helopoides, S. laevigatum, S. linelli linelli, S. longulum, S. obesum, and S. rugosum.

Analyses of electrophoretic data were carried out using BIOSYS (Swofford and Selander, 1991). Genetic variability measures were calculated for all populations. This included mean number of alleles per locus, percentage of polymorphic loci, and mean heterozygosity using both direct count (the proportion of individuals sampled that were actually heterozygous) and expected Hardy-Weinberg methods. A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95. Heterozygosity was tested for correlation to ecological variables, such as island area, height, and age. Genotype frequencies were tested against Hardy-Weinberg expectations using a chi-square goodness-of-fit test. Levene's correction for small sample

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sizes was employed. Allele frequencies were calculated for each locus. A chi-square contingency analysis was performed at two levels to test for frequency differences among groups. First, chi-square analyses were performed to test for frequency differences among the nine taxa. Next, individual taxa were examined for frequency differences among populations assigned to that species. Hierarchical F-statistics were calculated to examine gene frequency divergence among populations (Wright, 1940). The formula used is as follows:

$$F = \frac{\sigma_p^2}{\bar{p}(1-\bar{p})} ; 1 - F_{it} = (1 - F_{is})(1 - F_{st})$$

where F_{is} and F_{it} are the fixation indices of individuals relative to the subpopulation and total population respectively. The number of migrants was estimated from F-statistics using the following formula:

$$F_{st} = \frac{1}{(4N_{em} + 1)} ; N_{em} = \frac{(\frac{1}{F_{st} - 1})}{4}$$

where N_{em} = effective number of migrants per generation. Roger's genetic distance measures were calculated between all pairwise comparisons of populations. This distance measure was chosen over the distance measure of Nei because

multidimensional scaling requires metricity of the data (Wilkenson, 1988).

$$D_R = \left(\frac{1}{L} \right) \sum_L \frac{\sqrt{\sum (x_i - y_i)^2}}{2}$$

where L= total number of loci.

Scaling of genetic distances in two dimensions was performed using SYSTAT (Wilkenson, 1988) to examine spatial relationships among populations.

Results

Genetic variability over the eight informative loci is shown in Table 20 for each of the 35 populations. Sample sizes averaged over all loci ranged from 4.0 to 49.6, and the mean sample size was 32.4. The mean number of alleles per locus ranged from 1.6 to 3.1. The percentage of polymorphic loci ranged from 12.5% to 87.5%. The mean individual heterozygosity ranged from 0.039 to 0.272.

Genetic variability measures show that Stomion has a moderate to high level of genetic variation in comparison to other Galápagos organisms. Data are compiled for Stomion, Darwin's finches (Geospiza) (Yang and Patton, 1981), the Giant Tortoises (Geochelone) (Marlow and Patton, 1981), lava lizards, (Tropidurus) (Wright, 1983) and geckos

(Phyllodactylus) (Wright, 1983) (Table 21a). Stomion ranks highest in average heterozygosity of these five groups of Galápagos organisms and ties with Phyllodactylus for greatest number of alleles at a locus. However, it ranks lower in proportion of polymorphic loci and mean number of alleles per locus than some other taxa.

Because no genetic data are available for other Galápagos invertebrates, data from other island archipelagos will be used for comparison. Variability data are compiled for the land snails Cerion (Gould et al, 1975), Partula, (Johnson et al, 1986a), and Samoana (Johnson et al, 1986b), and the Hawaiian fruit flies Drosophila (Carson and Johnson, 1975). Variability in Stomion appears to be more typical of other island invertebrate populations (Table 21b). Stomion ranks in the middle of five taxa at average individual heterozygosities, and second in the average number of alleles per locus. It has the greatest total number of alleles per locus, and is second in proportion of polymorphic loci.

Average individual heterozygosities in Stomion were mapped for each population to look for geographical evidence of bottlenecking (Figure 32). There is no apparent geographical trend in heterozygosity levels which might suggest that bottle-necking occurred with subsequent colonizing events. If a bottle-neck had occurred with colonization events, heterozygosity might be expected to

decrease from east to west, with island age. Reduced heterozygosity levels might be observed if each new population was founded with a small subset of the genetic variation present in the parent population. Heterozygosity was found to have no correlation with island age ($r=0.355$; $p=0.075$), island area ($r=0.025$; $p=0.893$), or height ($r=0.074$; $p=0.692$).

Allele frequencies were calculated for all populations at eight loci (Table 22). Populations were then pooled for each species and allele frequencies recalculated (Table 23). A chi-square contingency analysis showed significant frequency differences at all loci among species (Table 24). However, there are also significant frequency differences at a majority of loci (70% at $p<0.05$) among populations assigned to the same species (Table 25). However, unique alleles were found in low frequency in some species. For example the 1 allele at Hk-2 was found only in 2 populations of S. linelli linelli, BALT and EDEN, at frequencies of 0.045 and 0.033, respectively. Likewise, the 7 allele at 6Pgdh was found in low frequency only in the LIDO and AERO populations of S. helopoides. Other than the occurrence of a few rare alleles, then, all alleles are shared by two or more species. No species markers were found at any of the eight loci.

Two loci in particular show geographic trends in the distribution of allele frequencies. At the

phosphoglucosomerase locus (Pgi), the 2 allele is common in the southeastern islands of Española and San Cristóbal, and decreases in frequency in the central islands, and is completely absent in the northern islands of Pinta and Marchena, where the common allele is the 3 allele (Figure 33). Supernatant glutamate oxaloacetate transaminase (Got-s) also shows a geographical pattern (Figure 34). The 4 allele is common in the southeastern islands, and is replaced by the 3 allele in the northern islands. A third common allele, the 5 allele, is found in high frequency in the central and western islands of Santa Cruz and Isabela.

Population genotype frequencies were compared to those expected by Hardy-Weinberg predictions for each polymorphic locus. Of 128 tests against Hardy-Weinberg predictions, 63 (49.2%) were found to violate predictions. In each case, the deviation was due to a heterozygote deficiency.

Genetic divergence among populations and among islands is high. F- statistics show that the proportion of total allelic variance due to variation among the subgroups is substantial, averaging 0.496 among populations and 0.302 among islands (Table 26). Gene flow is restricted between subgroups. Estimates of the effective number of migrants shows that the number of migrants between subgroups is less than one migrant per generation. This level of migration is not enough to overcome the effect of drift, therefore genetic heterogeneity of the subgroups results.

There is also substantial subdivision among populations within some species (Table 27). F-statistics for individual species range from a low of 0.073 in S. helopoides to a high of 0.455 in S. longulum. Gene flow among populations is substantial in three species, S. helopoides, S. galapagoensis galapagoensis and S. galapagoensis punctipennis as shown by the estimated number of migrants between populations.

Multidimensional scaling of genetic similarities of all 35 populations shows three species which are genetically distinct (Figure 35a). Stomion helopoides, S. galapagoensis punctipennis, and S. rugosum form discrete clusters, while all other species form one overlapping group.

When all populations from the same island are circled, a geographical pattern emerges (Figure 35b). There is a relationship between geographical distance and genetic distance of populations. In fact, when turned on its side, the plot represents a crude map of the Galápagos Islands. Populations from San Cristóbal and Española, the most southeasterly islands, are found at the bottom right of the "map". Populations from Isabela and Santa Cruz, two central islands, are found in the centre of the map, and the most northerly populations, from Pinta and Marchena, are found at the top of the map. Many of the small satellite islands are clustered between Santa Cruz and Isabela. Of the major islands, only Santa Fé and Floreana cluster more closely to

the central islands than their geography would predict.

Morphological groups were circled to test for genetic correlations to morphology. When populations are circled which have punctured, ridged, or smooth external sculpturing, three overlapping clusters are formed (Figure 36a). When populations are divided into two morphological groups based on body size and shape, there is still considerable overlap among clusters (Figure 36b).

II. Systematic Analysis of Stomion

Methods

Individuals of each of nine morphospecies were selected for this study. Where possible, each morphospecies was represented by two populations from different islands, such that all major islands, and some of the smaller islands were represented. The individuals were analyzed for an additional 13 loci in order to gather systematic data and to estimate divergence time among species. The sample sizes chosen for a systematic study should reflect the amount of polymorphism expected (Baverstock and Moritz, 1990). The pilot study showed that ten of the 13 additional loci used in this systematic study were monomorphic (Ao, Fum, Idh-1,2, Acon-1,2, Mdh-1,2, and Me-1,2), therefore sample sizes are small (n=2-13). Three new enzyme loci were tested which were not

used in the pilot study. These were arginine phosphokinase (Apk), peptidase leucyl-glycine (Pep, leu-gly), and trehalase (Tre). The populations from which the individuals were selected are listed in Table 28. In addition to the eight loci screened in the population genetics survey, then, the following loci were included in the systematic study: Ao, Apk, Fum, Pep (leu-gly), Idh-1, Idh-2, Acon-1, Acon-2, Mdh-1, Mdh-2, Me-1, Me-2, and Tre-1 for a total of 21 loci. Individuals of Stomion cribricollis, and S. longicornis were not available for systematic analysis.

All calculations were carried out using BIOSYS (Swofford and Selander, 1981). Allele frequencies were calculated for each taxon at the 13 additional loci and combined with frequency data from the previous eight locus survey. Roger's genetic distance (1972) was calculated for all pairwise comparisons of taxa. These distance measures were used in an average linkage cluster diagram to group allozymically similar taxa. In order to examine genetic relationships among taxa which are independent of the assumption that evolution occurs at a constant rate, a phylogeny was produced using the Distance-Wagner procedure. This procedure was used to estimate a phylogeny from Roger's genetic distances using the multiple addition criterion. Branch lengths are sought which equal the genetic distances between species. Two other speciose genera of Galápagos tenebrionids, Ammophorus and Blapstinus were used as

outgroups in the Distance-Wagner phylogeny to root the resulting tree.

Nei's genetic distances (1972) were used to calculate genetic identity (I), using the following formula:

$$D = -\ln I; I = \ln^{-1}(-D)$$

This was done to compare genetic identity within and between species of Stomion to those of other organisms from the literature.

Nei's genetic distances were also used to calculate divergence times between each species and a reference species (S. helopoides). Estimated genetic divergence times between the reference species and all other species were plotted against the inferred geological age difference between species (the difference in age of the island on which each species is found from the reference site, LIDO on San Cristóbal).

Using the generally accepted model of allozyme divergence under no selection, each unit of Nei's genetic distance is equivalent to approximately 19 million years of evolutionary divergence (Sarich, 1972; Carlson, 1978; Vawter et al, 1980). These studies showed that allozyme divergence occurs at a regular rate, and this calibration was substantiated by data from fish populations which were separated by the emergence of the isthmus of Panama.

Results

All but two of the 13 additional loci were monomorphic for the same allele in all individuals (Table 29). One species marker was found at the Fum locus. Individuals of S. rugosum were fixed for a faster allele than is found in all other species. An additional polymorphism was discovered at the peptidase (Pep-leu-gly) locus.

Nei's genetic identities between all pairwise comparisons of taxa were classified as those which measured within species identities and those which measured between species identities. A plot of these identities shows that there is substantial overlap of within and between species identities (Figure 37). Measures of within species identity ranged from 0.891 to 0.988. The average within species identity is 0.947. Measures of between species identities ranged from 0.696 to 0.996. The average between species identity is 0.884. A one-way analysis of variance showed that these means are significantly different ($F= 33.957$; $df=1,557$; $p<0.001$).

Genetic identities in Stomion are higher than expected for between species comparisons, and lower than expected for within species comparisons when compared to other organisms (Table 30). Thorpe (1982) compiled faunal genetic identity data for a large number of mainly North American, continental species. His study showed that 80% of genetic

identities between populations of a single species lie at or above $I=0.95$. In Stomion, only 43% of intraspecific identities are at or above $I=0.95$. Furthermore, Thorpe found that among congeneric species, only 5% of genetic identities are greater than $I=0.80$, while in Stomion, 90% fall above this level of identity.

When compared to other Galápagos organisms, patterns of genetic identities in Stomion are intermediate to those of other taxa (Table 31). The Giant Tortoise (Geochelone) and Darwin's Finches (Geospiza) show very high levels of between species (or races) comparisons ($I > 0.90$ in all cases). Stomion shows a low of 0.70 identity between different species, with an average between species identity of 0.88.

Among other island invertebrates, four species of the land snail genus Samoana had average identities of 0.95 among populations in the Society Islands in French Polynesia. Another land snail, Partula, had average identities of 0.89 over seven species on the island of Moorea.

A cluster analysis of genetic distances of all species shows concordance to the pattern seen in multidimensional scaling of populations. Stomion rugosum is the most genetically divergent, due largely to the fixed difference at Fum (Figure 38). Two other taxa, S. helopoides, and S. galapagoensis punctipennis form a single cluster. Stomion linelli and S. longulum also form a single cluster, as do S.

obesum, S. laevigatum, and S. denticula. Stomion galapagoensis galapagoensis forms a cluster quite distinct from that containing S. galapagoensis punctipennis. Morphological groups based on external sculpturing and body size and shape are randomly distributed throughout the dendogram.

In order to make estimates of divergence times among species, the population of S. helopoides from San Cristóbal, (LIDO) is taken as the reference species. This species was chosen because it is one of the most genetically divergent of the group, and because it comes from an island whose rocks have been aged as among the oldest in the archipelago (Cox, 1983). Nei's genetic distance was calculated between the LIDO population and all other populations (Appendix 7). Taking one unit of Nei's genetic distance (D) as equal to 19 million years of divergence, the divergence times were calculated between S. helopoides and all other species (Table 32). In cases where two divergence estimates were made for a species, the divergence times are averaged to give one estimate of divergence among species (Table 33). Divergence times range from a low of 1.18 million years, between S. helopoides and S. galapagoensis punctipennis to a high of 6.29 million years between S. helopoides and S. rugosum.

The age of the island as reported by Cox (1983) where a species was collected was subtracted from the age of San

Cristóbal (the oldest island) to give the geological difference in ages between species. This inferred geological age difference was plotted against estimated genetic divergence times to test the "clock-like" rate of allozyme divergence (Figure 39). A regression analysis was done to determine the slope and significance of the line. The regression analysis showed a significant positive correlation between genetic divergence and the geological age difference of species ($r=0.603$, $p<0.05$).

The Distance-Wagner phylogeny shows much the same groupings as the cluster diagram of genetic distances (Figure 40). Stomion helopoides appears to be the ancestral species of the genus, sharing a common ancestor with S. galapagoensis punctipennis and with the common ancestor of all other species. Stomion galapagoensis punctipennis is again well separated from the clade containing S. galapagoensis galapagoensis. Stomion linelli forms its own clade, but shares a common ancestor with a population of S. longulum. Stomion rugosum also forms a distinct clade and the Marchena population shows the greatest divergence and distance from the root. Five taxa show confusing phylogenetic patterns. The two populations each of Stomion obesum, S. laevigatum, and S. longulum are split among different clades. In addition, the two S. galapagoensis subspecies are found in separate clades.

Discussion

Reduced levels of genetic variability are characteristic of island and cave populations of vertebrates when compared to continental populations. (Nevo, 1978). However, this pattern is not observed in invertebrates (Nevo, 1978).

Variability in natural populations is best measured by average heterozygosity and mean number of alleles per locus (Nei, et al, 1975). The average heterozygosity in Stomion is higher than that in the Galápagos vertebrates for which data are available. However, invertebrates in general show higher levels of genetic variability than do vertebrates (Nevo, 1978). No data are available for Galápagos invertebrates, although comparisons can be made with other island invertebrate populations such as the Hawaiian Drosophila and the land snails Partula and Samoana from the Society Islands.

Invertebrate species from other island archipelagos show comparable levels of variability to Stomion. In fact, heterozygosity may be slightly lower in Stomion than the average estimates of 7.4% and 10.7% reported in other insects (Nevo, 1978; Graur, 1985). If heterozygosity of 17.8% over eight polymorphic loci in Stomion is extrapolated to include the monomorphic loci, Stomion would have an approximate average heterozygosity of only 7.1%. Genetic

variability is high in the Hawaiian Drosophila, but this may be due to the incidence of chromosomal inversions (White, 1978). Their rapid morphological and genetic evolution may have been driven by complex social and mating behaviour which resulted in reproductive isolation (Carson and Kaneshiro, 1976).

It is difficult to assess whether a population bottle-neck occurred during the colonization of new populations of Stomion. Rare alleles donate little to the heterozygosity level of the parent population, therefore heterozygosity in newly founded populations may be nearly as high as the parent population (Futuyma, 1986). Alternately, population sizes may have quickly rebounded after founding, which acts to regain levels of heterozygosity, although the total number of alleles prior to the bottle-neck may not be recovered at the same rate (Nei, et al, 1975).

Heterozygosity in Stomion is not correlated to either island size, height, or age. Nor is there a geographical pattern to heterozygosity which might suggest that the population went through a bottle-neck during founding events. This is in contrast to the pattern which was seen among populations of the Giant Tortoises. In Geochelone, heterozygosity is highest in the easternmost populations on Española, and decreases gradually westward. This is likely due to a reduction in variability associated with founder events in each successive colonization (Marlow and Patton,

1981). No such pattern exists in Stomion, which supports the hypothesis that a severe bottleneck did not occur during colonization of Stomion.

With the exception of a few, rare alleles, all species of Stomion share the same alleles at eight polymorphic loci, although in different frequencies. Chi-square contingency tests show frequencies differ significantly among species. Eleven additional loci were monomorphic for the same allele in all species. Only one complete allelic substitution was found among species. Stomion rugosum is fixed for a faster allele at Fum than is found in any other species. The general congruence of allelic composition supports the hypothesis that Stomion is a monophyletic genus, arising from a single ancestral colonization. Rare, unique alleles may represent mutations which have occurred in the evolution of this genus. Assuming that each unique allele represents one mutation event, the visible mutation rate in Stomion can be roughly estimated. There are four unique alleles in 20 loci over all 35 populations. Using a three million year time frame (the age of the archipelago as determined by geological data) as the amount of time available for the evolution of Stomion, the mutation rate is one mutation per locus every 15 million years. Furthermore, assuming there is one generation per year gives a rate of 6.7×10^{-8} mutations per locus per generation. Mutations in Drosophila were estimated at 4×10^{-6} per locus per generation (Mukai and

Cockerham, 1977), although estimates vary considerably among loci (Futuyma, 1986). Kimura and Ohta (1971) estimated the rate of mutation in protein loci to be 10^{-7} per year. Further comparisons with other invertebrate and island groups may aid in understanding if the mutation rate in Stomion is unusually slow, or falls within the range of other observed rates of mutation.

A substantial proportion of the variable loci deviate from Hardy-Weinberg expectations of genotype frequencies. In all cases, the deviation was due to a heterozygote deficit. Heterozygote deficiencies result when population sizes are small or when inbreeding occurs (Futuyma, 1986). The ecological study showed that while Stomion populations may be large, individuals have low vagility. Thus, the conditions may be right for inbreeding to occur in localized populations. Geographical barriers such as recent lava flows may present enough of a barrier to gene flow to isolate populations, resulting in genetic drift and loss of heterozygosity. This is shown very clearly in the Giant Tortoises, where five distinct races inhabit each of five volcanoes on Isabela. Here, the rough and barren lava fields between volcanoes present a geographic barrier to gene exchange (Marlow and Patton, 1981; Jackson, 1991).

Further evidence that populations behave as isolated, inbreeding subunits comes from the results of genetic diversity analyses. F-statistics show significant inbreeding

within populations, and restricted gene flow among populations. Gene flow results in the genetic homogenization of populations (Lewontin, 1973). It has been shown that if there is no selection acting on populations, very few migrants are necessary to keep populations genetically similar (Wright, 1940).

Examination of the genetic diversity of populations of individual species again shows substantial subdivision among some populations. F-statistics show that genetic divergence is particularly high among populations of S. longulum, and S. obesum. Populations of these species are found on more than one island, a situation where barriers to gene flow might be expected. Furthermore, in species for which populations are restricted to single islands, such as S. helopoides, and S. galapagoensis punctipennis, genetic variance among populations is lower, suggesting that gene flow among populations is more substantial.

Clearly, isolating barriers are present among populations, especially those on different islands. Nothing is known about the ability of tenebrionids to survive or remain afloat in salt water, but the evidence suggests that gene flow between populations on different islands may be a rare event.

A relationship between geographical distance and genetic distance is shown by multidimensional scaling of populations. Those populations which are geographically

closest are also genetically most similar. The first dimension represents a north-south axis, and the second dimension represents an east-west axis. The resulting "map" suggests that colonization and speciation occurred in a stepping-stone fashion. Dispersal has occurred primarily between islands which are in close proximity.

The distribution of Stomion populations in two-dimensional space can be used to make some conclusions about the relationships among species in the genus. Stomion helopoides and S. galapagoensis punctipennis show large genetic distance from other populations. In addition, their distributions on the oldest islands in the archipelago, San Cristóbal and Española, respectively, can be used to suggest that these two species are the oldest of the genus. They have presumably had the most time to diverge. Stomion rugosum is also a genetically distinct species. It is found only on the northern islands of Pinta and Marchena. This genetic distance is probably a result more of geographical isolation than temporal isolation, as Pinta and Marchena are among the youngest islands in the archipelago, but are separated from the rest of the archipelago by a large water gap. The remaining species on the central islands are genetically less differentiated. All of the south and central islands lie on the shallow Galápagos platform 400 m below sea level. Pinta and Marchena are separated from this group by a seafloor depth of 1200 to 2000 m. The central

islands are separated by depths sometimes less than 200 m and may have been attached by high ridges during the Pleistocene, when sea level dropped by as much as 45 m (Jackson, 1991). This may explain the lack of genetic differentiation among species in the central islands (*S. longulum*, *S. laevigatum*, and *S. linelli*), and the greater differentiation of species on the southeastern islands (*S. helopoides* and *S. g. punctipennis*).

McArthur and Wilson (1967) proposed that the degree of isolation of populations and the amount of immigration into them would have an important effect on population structure. *Stomion* shows higher levels of between species genetic identities, and lower levels of within species identities than other continental taxa. Since colonization of isolated island archipelagos is likely to be an extremely rare event, the radiation of a group of species from a single lineage will result in a greater degree of genetic similarity, especially in young islands such as the Galápagos. On the other hand, the isolation of individual islands, and the limited gene flow between islands, can result in greater differentiation between species. However, *Stomion* shows minimum and mean between species genetic identities which fall between those of other Galápagos organisms. Identities among Darwin's Finches may be high because morphological and genetic differentiation has apparently occurred in less time than has been available for *Stomion*. Estimated divergence

times among finch species are calculated to be about one million years (Grant, 1981). There may also be a greater possibility for gene flow among Darwin's Finches. Some finches are known to move between islands, and hybridization may be occurring between species such as those on Daphne Major (Grant, 1986). The lower identities seen among species of the lizards and geckoes may be due to decreased dispersal abilities resulting in lower incidences of gene flow. The lizards probably arose from a single ancestor, but two colonizations are possible (Wright, 1983). This may contribute to low interspecific genetic identities.

Using Thorpe's (1982) observations for species' genetic relationships ($I > 0.80$ in 90% of interspecific comparisons), S. obesum, S. galapagoensis galapagoensis, S. galapagoensis punctipennis, and S. helopoides show sufficient genetic divergence from other taxa to merit species status. If we raise the criterion to $I > 0.85$ (78% of interspecific comparisons), only Stomion rugosum shows genetic divergence great enough from other taxa to be considered a separate species. It is doubtful that the subspecies S. galapagoensis galapagoensis and S. galapagoensis punctipennis share a recent common ancestor. The genetic evidence suggests that they are only distantly related, and that any morphological similarity is likely the result of convergence.

Clearly, genetic divergence among Stomion species does not mirror that observed in more ancient, continental taxa.

While classic taxonomic examination of qualitative characters of Stomion suggests that there are twelve taxa in the genus, morphometric examination of the genus shows only a few to be quantitatively distinguishable. Stomion rugosum, S. laevigatum, S. cribricollis, S. galapagoensis, S. galapagoensis punctipennis, and S. denticula can be distinguished from other members of the genus using various quantitative methods, while S. longulum, S. linelli linelli, S. obesum, and S. helopoides form a morphometrically indistinguishable group. The genetic data is not in complete concordance with the morphological findings. However, a lack of correlation between phenograms based on morphological and allozyme data has been observed in a number of organisms (Patton, 1984; Aquadro and Kilpatrick, 1981). A well known Galápagos example of morphological and genetic disconcordance comes from the Giant Tortoises. There is no correlation between the two main carapace types (dome and saddle-back) and genetic data, suggesting that the saddle-back type arose independently several times (Marlow and Patton, 1981). In Stomion, the three major morphological types (punctured, ridged, and smooth surface) are distributed throughout the genetic phenogram, with no apparent similarity among members of these groups. The lack of homology of these external characters as uncovered by allozymes suggests that smooth, punctured, and ridged surfaces may have evolved

independently several times, perhaps in response to environmental variables.

The 21 locus systematic study was used to estimate divergence times among species. Nei's genetic distance among species was converted to divergence time in millions of years. Most estimated divergence times from the reference species fall within the time frame available for colonization as estimated by geological data. Divergence times of each species from S. helopoides range from 1.18 million years in S. galapagoensis punctipennis to 6.29 million years in S. rugosum. Stomion rugosum may show greater genetic differentiation because of its geographic isolation. It is separated by great distance over water. Alternately, the archipelago may be older than any of the present day islands (Christie, et al, 1992). Submerged seamounts east of the Galápagos with geological features suggestive of a history above water have been dated at ten million years. These now-submerged islands may have once been colonized by Galápagos predecessors, greatly extending the time available for colonization. This may explain the great genetic divergence seen between the Galápagos land and marine iguanas, whose divergence time from a common ancestor is estimated between 15 and 20 million years (Wyles and Sarich, 1983). Finally, strong selective pressures may be accelerating the rate of genetic divergence between some taxa.

A scatter plot and correlation analysis of genetic divergence times between species and geological age divergence shows a positive correlation ($r=0.603$, $p<0.05$). Allozyme divergence has occurred at a clock-like rate in Stomion. The evidence seems to suggest that selection has not played a role in driving genetic divergence between species of Stomion, instead, genetic differentiation has been neutral and regular. This is further support for the hypothesis that colonization and speciation occurred in a stepping-stone manner; the oldest and most divergent species live on the oldest islands, and the youngest islands are home to the newest species. New islands were colonized as they became available.

The Distance-Wagner tree can also be used to make some hypotheses about the progression of colonization and speciation within Stomion. It suggests that S. helopoides gave rise to S. galapagoensis punctipennis and the common ancestor of all other species. Stomion linelli was the next species to evolve, which might explain its close association with S. helopoides and S. galapagoensis punctipennis in body size and shape. These species all belong to a group of species which have broad bodies and a transverse pronotum. Stomion longulum on Santa Cruz (BARR) shares a common ancestor with S. linelli. This was the first appearance of the second body shape, that which is long and narrow, and with a more quadrate pronotum. This Santa Cruz population of

S. longulum may have been the source population for S. longulum on Isabela (NVIL). Alternately, they may simply share the same common ancestor which evolved into S. linelli in one case, and a common ancestor of the remaining species in another case, while retaining its S. longulum phenotype on two different islands. The problems inherent in using genetic distances to infer phylogenies arise at this point. Stomion obesum and S. laevigatum both appear to have evolved twice on different islands. Populations of each of these two species do not appear to share recent common ancestors. Stomion galapagoensis galapagoensis from Floreana (FLBB) and Gardner (GARD) is evolutionarily far removed from S. galapagoensis punctipennis on Española (BGAR, MANZ), largely due to a near substitution of alleles at the Pgi locus.

Nonetheless, some broad conclusions may be drawn. The species in the first two clades are probably the older, more primitive members of the genus, and species in the remaining clades are more recently derived. Geological data of the Galápagos Islands supports this decision. San Cristóbal, Española and Santa Cruz are the oldest of the islands at about three million years (Cox, 1983). This phylogeny suggests that these populations were the founders for all other species on the newer island formations.

The phylogeny suggests that the three morphological types arose independently several times. The punctured species appear to have three separate origins. Stomion

helopoides and S. galapagoensis punctipennis from San Cristóbal share a common ancestor, however, Stomion denticula and S. galapagoensis galapagoensis arose much later. They share a common ancestor with S. obesum and S. laevigatum. Punctation was either lost in these latter two species, or punctation appeared independently in S. denticula and S. galapagoensis galapagoensis. The ridged surface appears to have arisen at least twice, first in Stomion longulum, and later in S. obesum and S. rugosum. Smooth surfaces may have arisen once; Stomion laevigatum may have evolved from a S. linelli ancestor.

Additional phylogenies should be tested using methods such as transformation of genotypes into character data (Miyamoto, 1983), or by using allele frequencies as character data (Swofford and Berlocher, 1987).

In summary, genetic variability in Stomion is comparable to that of other invertebrates. There is no evidence of a population bottle-neck occurring during the evolution of Stomion. However, populations are isolated and show the effects of inbreeding. The geography presents barriers to gene flow among populations, both within and between islands. Species share the same major alleles, supporting the hypothesis of a monophyletic origin. Divergence times between species are largely within the time-frame given by the age of the archipelago, and divergence in Stomion has occurred at a clock-like rate.

General Conclusions

Morphological and genetic data give some conflicting results in the interpretation of the evolutionary history of Stomion. While a classical taxonomic examination of the genus suggests that there are twelve taxa, morphological and genetic similarities are high, often making discrimination of species ambiguous.

Both principle component and canonical coefficients analyses show enormous overlap of species. Plots of these analyses show only one species, Stomion rugosum, that is visually distinguishable from the others. Thus, while some external characters, such as punctation, have diverged among species, dimensions of body size and shape have changed little. Does this mean that Stomion is composed of only two species, Stomion rugosum and another species which shows a wide range of variation in external sculpturing? While species are not visually discriminated in two dimensional space, classification of specimens using their individual canonical scores places them in the "correct" species grouping with 89% success. Some species were classified correctly in 100% of the cases.

Allozyme data show that there are only three species that can be distinguished genetically. Stomion rugosum, S. galapagoensis punctipennis, and S. helopoides show allelic substitutions or frequency shifts at some loci which separate them from all other members of the genus. The only

other conclusion that can be drawn from the allozyme data is that Stomion galapagoensis galapagoensis and S. galapagoensis punctipennis should be considered separate species. They are not closely related allozymically, and in fact are not found in the same clade, and have not shared a recent common ancestor. However, the morphological evidence shows repeatedly that they are very similar both in body size and shape, and also in other qualitative characters. The two subspecies form a pair in the phenogram of 31 qualitative characters, and remain paired even after removal of data describing elytral punctation. Thus, while convergence may be responsible for similar punctation in the two taxa, body size and shape dimensions, and other qualitative characters place them as close relatives. In the principle component and canonical coefficients analyses, the two subspecies show consistently overlapping distributions about their means.

Stomion longulum, S. obesum, and S. laevigatum also show ambiguous allozymic phylogenetic patterns. Populations of each species are divided among different clades, often sharing only distant common ancestors. Thus, the genetic evidence suggests that there are perhaps only four species: S. rugosum, S. galapagoensis punctipennis, S. helopoides, and one which includes all other morphotypes.

The morphological analysis presents the strongest data set. Species can be reliably identified using taxonomic keys

and descriptions, and canonical classification of individuals to the "correct" species is highly successful. The genetic data, in contrast, give results which are internally conflicting, and are not easily wedded to the morphological findings.

What are the factors, then, which result in low interspecific genetic identities and high intraspecific genetic identities? Why do morphotypes not have corresponding genotypes?

High interspecific genetic similarities result from the fact that species of the genus Stomion were likely derived from a single colonization event. The rate of random mutations over time (generally believed to be 10^{-6} - 10^{-7} per locus per generation) is such that little genetic differentiation occurs in a three million year time-frame. Thus, Stomion species have not had time for detectable levels of genetic divergence to occur.

We must consider selection and random genetic drift as possible driving forces of genetic divergence between populations of the same species. The islands themselves are isolated entities, with little possibility for gene flow among them. Populations on a single island may also be isolated by topographical barriers such as barren lava fields. This isolation and resulting lack of migration permits random genetic drift between populations to occur. Under the neutral allele hypothesis, random chance

determines which alleles become fixed in any given, isolated population.

Differential selection may also be occurring among populations on different islands, but the overall environmental uniformity of islands makes this a less feasible explanation for genetic divergence. Selection may, however, be partly responsible for the accelerated rate of genetic divergence observed in one species, S. rugosum.

Thus, the morphological data is chosen as having the most weight for an interpretation of the evolutionary history of Stomion, and a morphospecies concept is adopted as one that most reflects the true biological species involved. The twelve morphological taxa presented in Table 9 will be considered valid based on qualitative and quantitative morphological evidence. The use of other molecular techniques, such as restriction fragment length polymorphisms in the mitochondrial DNA molecule may help resolve the genetic quandary. The mitochondrial DNA molecule evolves at a faster rate than nuclear DNA and is a useful tool in systematic studies where allozyme analyses fail. Inter-taxon hybridization studies can test if reproductive isolating mechanisms have arisen between the species. If there are genetic barriers to successful crossing and hybridization, this proves their specific status. But, the lack of isolating mechanisms in allopatric taxa does not prove they are the same species.

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Table 1: List of sampling sites and abbreviations used in text.

Island	Site	Abbreviation
Baltra	military beach	BALT
Bartolomé		BART
Champion		CHAM
Caamaño		CAAM
Daphne	sendero	DAPH
Eden		EDEN
Española	Bahia Gardner	BGAR
Española	Manzanillo	MANZ
Española	Punta Suarez	PTSU
Fernandina	Cerro Verde	FERN
Floreana	Black Beach	FLBB
Floreana	Las Cuevas	FLCU
Floreana	Punta Cormorant	FLPC
Gardner	at Floreana	GARD
Genovesa	Bahia Darwin	BDAR
Genovesa	Pr. Phillips Steps	PHIL
Isabela	Alcedo Rim	ARIM
Isabela	Cerro Azul	AZUL
Isabela	N. Villamil	NVIL
Isabela	Tagus Cove	TAGU
Isabela	Volcan Darwin	VDAR
Isabela	W. Villamil	WVIL
Marchena	SW Playa	MARC
Pinta	forest	FORE
Pinta	Playa Ibettson	IBET
Plaza Sur		PLAZ
Rabida	Red Beach	RABI
San Cristóbal	aeropuerto	AERO
San Cristóbal	Punta Lido	LIDO
San Critsóbal	Baquerizo	BAQU

Table 1, continued.

Island	Site	Abbreviation
Santa Cruz	barranco	BARR
Santa Cruz	Conway Bay	CONW
Santa Cruz	Santa Rosa	ROSA
Santa Cruz	iguana pens	PENS
Santa Cruz	Granillo	GRAN
Santa Cruz	Half-Way House	HALF
Santa Cruz	North Shore	SHOR
Santa Cruz	tortoise corral	CORR
Santa Cruz	Bahia de Tortuga	BTOR
Santa Fé	beach	SFEB
Santa Fé	trail	SFTR
Santa Fé	plateau	SFEP
Santiago	Bahia Sullivan	SULL
Santiago	Playa Espumilla	SGPE
Seymour		SEYM
Tortuga		TORT

Table 2. The number of individuals of each of four species of tenebrionids counted at the Tortuga Bay transect site on Isla Santa Cruz, Galápagos. Sl= S. laevigatum, Bl= B. lugubris, Bs= B. spatulus, Ab= A. bifoveatus, TI= total number of individuals, TS= total number of species.

WEEK	Sl	Bl	Bs	Ab	TI	TS
1	2	0	0	0	2	1
2	9	4	37	37	87	4
3	4	44	58	96	202	4
4	1	0	53	74	128	3
5	5	19	65	73	162	4
6	1	14	80	112	207	4
7	1	8	89	110	208	4
8	2	19	69	113	203	4

Table 3. Pearson correlation matrix of species abundance and diversity with seven environmental conditions. T= temperature at 18:00 hours, PP= daily precipitation, H= relative humidity at 18:00 hours, SOL= number of sunlight hours, TMAX= maximum daily temperature, TMIN= minimum daily temperature, TPP= total precipitation in the week preceding the collection. Species abbreviations are as in Table 2.

Factor	T	PP	H	SOL
S1	0.385	-0.162	0.394	0.384
B1	-0.227	-0.376	0.071	-0.349
Bs	-0.23*	-0.82*	0.521	-0.73*
Ab	-0.87*	-0.77*	0.369	-0.76*
TI	-0.85*	-0.80*	0.425	-0.74*
TS	-0.697	-0.94*	0.710*	-0.511

Factor	TMAX	TMIN	TPP
S1	0.480	0.247	-0.068
B1	-0.354	0.108	-0.362
Bs	-0.959*	-0.679	-0.859*
Ab	-0.960*	-0.523	-0.807*
TI	-0.935*	-0.510	-0.836*
TS	-0.699	-0.464	-0.929*

*p<0.05

Table 4. The total number of individuals marked and recaptured for each species for all four quadrats. Amm= Ammophorus Bla= Blapstinus Sto= Stomion.

Quad I.						
week	marked			recaptured		
	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>
1	3	10	9	0	0	0
2	6	9	12	0	0	0
3	0	9	8	0	1	0
4	0	7	8	0	1	0
5	1	1	6	0	0	0

Quad II.						
week	marked			recaptured		
	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>
1	3	12	13	0	0	0
2	13	21	19	0	1	0
3	5	16	26	0	0	0
4	2	11	13	0	0	0
5	2	8	13	1	0	0

Quad III.						
week	marked			recaptured		
	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>
1	0	0	6	0	0	0
2	0	0	5	0	0	0
3	0	2	4	0	0	0
4	0	1	1	0	0	0
5	0	1	1	0	0	0

Quad IV.						
week	marked			recaptured		
	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>	<u>Amm</u>	<u>Bla</u>	<u>Sto</u>
1	1	0	8	0	0	0
2	1	0	6	0	0	0
3	0	1	6	0	0	0
4	0	0	3	0	0	0
5	0	0	4	0	0	0

Table 5. The frequency with which beetles were caught in traps during the mark and recapture study. The number of beetles represents the number of beetles found in a single trap; the frequency represents the number of traps which contained the corresponding number of beetles.

NO. BEETLES	FREQUENCY			
	QI	QII	QIII	QIV
0	0	0	15	10
1	6	0	5	7
2	6	2	2	7
3	1	0	1	1
4	5	5	1	
5	1	2	1	
6	2	1		
7	2	7		
8	1	2		
9	1	2		
10		1		
11		0		
12		0		
13		0		
14		1		
15		1		
16		1		

Table 6. Mean number of catches per trap, standard deviation, dispersion index and chi-square values for random (Poisson) distribution model tests for each of four quadrats in the mark and recapture study. DF=24. Quadrat IV fits the random distribution model. Quadrats I-III fit a negative binomial distribution model.

quad	$\bar{x}$	s^2	DI	χ^2
I	3.76	6.25	1.67	40.08
II	7.12	13.20	1.85	44.40
III	0.84	1.90	2.25	54.00
IV	0.96	0.88	0.91	21.84*

*p=0.05

Table 7. Vegetation zone, elevation, and other genera at sites in the Galápagos Islands where Stomion was found. Amm=Ammophorus, Bla=Blapstinus, Pha=Phaleria. 0= none.

site	species	zone	elev.(m)	genera
BALT	linelli	arid	20	Amm
BART	linelli	littoral	10	0
CAAM	laevigatum	littoral	2	Pha
CHAM	g. galap.	arid	5	Amm, Bla
DAPH	linelli	arid	120	Amm
EDEN	linelli	arid	10	Amm
BGAR	g. punct.	littoral	2	Bla
MANZ	g. punct.	littoral	2	0
PTSU	g. punct.	arid	10	Amm, Bla
FERN	laevigatum	arid	140	Amm
FLBB	g. galap.	littoral	10	Amm, Bla
FLCU	g. galap.	arid	5	Amm
FLPC	g. galap.	littoral	3	Amm, Bla
GARD	g. galap.	arid	50	Bla
BDAR	sp. n.	arid	3, 10	Bla
PHIL	sp. n.	arid	20	Bla
ARIM	laevigatum	pampa	1100	Bla
AZUL	longulum	arid inv.	1500	Bla
NVIL	longulum	arid	2	Amm, Bla
TAGU	laevigatum	arid	20	Amm, Bla
VDAR	laevigatum	arid	300	Amm
WVIL	longulum	arid	1	Amm, Bla
MARC	rugosum	arid	10	Amm
FORE	rugosum	transition	200	Amm
IBET	rugosum	arid	1	0
PLAZ	laevigatum	arid	10	Amm, Bla
RABI	linelli	litt/arid	20	Amm, Bla, Pha
AERO	helopoides	littoral	2	Amm, Bla
LIDO	helopoides	littoral	2	Amm, Bla
BAQU	helopoides	arid	10	Amm
BARR	longulum	arid	40	Amm
PENS	longulum	arid	15	Amm, Bla
GRAN	g. leleupi	arid	300	Amm
HALF	longulum	arid	10	Amm, Bla
SHOR	laevigatum	littoral	10	Amm, Bla
CORR	longulum	arid	15	Amm
BTOR	laevigatum	litt/arid	10	Amm, Bla
CONW	laevigatum	litt/arid	2	Bla
ROSA	g. leleupi	arid	140, 300	Amm, Bla
SFEB	obesum	littoral	3	Amm, Bla, Pha
SFTR	obesum	arid	10-50	Amm, Bla
SFEP	obesum	arid	120	Amm
SULL	laevigatum	arid	3	0
SGPE	laevigatum	arid	5	Amm, Bla
SEYM	linelli	arid	10	0
TORT	obesum	arid	40	Amm

Table 8. Primary (veg 1) and secondary (veg 2) vegetation and substrate type at sites in the Galápagos Islands where Stomion was collected. 0= none.

site	species	veg 1	veg 2	substrate
BALT	linelli	Parkinsonia	Tiquilia	sand
BART	linelli	Rhizophora	0	sand
CAAM	laevigatum	Cryptocarpus	0	sand
CHAM	g. galap.	Sesuvium	0	rocks
DAPH	linelli	Tiquilia	Sesuvium	cinder
EDEN	linelli	Opuntia	grass	ash
BGAR	g. punct.	Cryptocarpus	0	sand
MANZ	g. punct.	Iboemoea	Cryptocarpus	sand
PTSU	g. punct.	Cryptocarpus	Cordia	cinder
FERN	laevigatum	Waltheria	scrub	ash
FLBB	g. galap.	Ipoemoea	Cryptocarpus	sand
FLCU	g. galap.	Waltheria	Bursera	ash
FLPC	g. galap.	Scaevola	Cryptocarpus	sand
GARD	g. galap.	succulents	Portulaca	rocks
BDAR	sp. n.	Cryptocarpus	Bursera	rocks
PHIL	sp. n.	grass	Bursera	rocks
ARIM	laevigatum	grass	0	soil
AZUL	longulum	mats	shrubs	ash
NVIL	longulum	Tiquilia	0	marl
TAGU	laevigatum	Waltheria	grass	soil
VDAR	laevigatum	grass	Cordia	soil, rocks
WVIL	longulum	Tiquilia	grass	sand
MARC	rugosum	Waltheria	grass	ash
FORE	rugosum	Palo Santo	grass	ash
IBET	rugosum	Cryptocarpus	0	sand
PLAZ	laevigatum	Sesuvium	grass	rocks
RABI	linelli	Cryptocarpus	0	sand
AERO	helopoides	Cryptocarpus	Tiquilia	sand
LIDO	helopoides	Cryptocarpus	Scaevola	sand
BAQU	helopoides	Cryptocarpus	Tiquilia	sand
BARR	longulum	Opuntia	grass	cinder
PENS	longulum	grass	0	cinder
GRAN	g. leleupi	herbs	grass	cinder
HALF	longulum	Opuntia	grass	cinder
SHOR	laevigatum	Maytenus	Cryptocarpus	sand
CORR	longulum	grass	0	cinder
BTOR	laevigatum	Scaevola	Heliotropium	sand
CONW	laevigatum	Cryptocarpus	0	sand
ROSA	g. leleupi	Bursera	herbs	rocks
SFEB	obesum	Cryptocarpus	grass	sand
SFTR	obesum	grass	Opuntia	cinder
SFEP	obesum	Opuntia	Scalesia	cinder
SULL	laevigatum	Conocarpus	0	sand
SGPE	laevigatum	Cordia	Waltheria	sand
SEYM	linelli	Bursera	herbs	cinder
TORT	obesum	Sesuvium	Portulaca	cinder

Table 9. Species which were identified using classical taxonomic methods. Distributions of all examined material are listed.

Species	Distribution
<u>Stomion cribricollis</u>	Darwin, Wolf
<u>S. galapagoensis galapagoensis</u>	Floreana, Gardner at Floreana, Champion
<u>S. galapagoensis punctipennis</u>	Española
<u>S. longicornis</u>	Española
<u>S. helopoides</u>	San Cristóbal
<u>S. obesum</u>	Pinzón, Santa Fé, Tortuga
<u>S. laevigatum</u>	Santa Cruz, Isabela, Fernandina, Caamaño, Plaza Sur
<u>S. linelli linelli</u>	Eden, Santa Cruz, Daphne Major, Seymour Norte, Baltra, Rabida, Bartolomé
<u>S. galapagoensis leleupi</u>	Santa Cruz
<u>S. longulum</u>	Santa Cruz, Isabela
<u>S. rugosum</u>	Pinta, Marchena
<u>S. sp. n.</u>	Genovesa

Table 10. Species used in qualitative morphological character analysis of Stomion and other members of the tribe Trimytini.

Species	Locality
<u>Stomion cribricollis</u>	Darwin
<u>S. galapagoensis galapagoensis</u>	Floreana, Las Cuevas
<u>S. galapagoensis punctipennis</u>	Española, Manzanilla
<u>S. galapagoensis leleupi</u>	Santa Cruz, Santa Rosa
<u>S. helopoides</u>	San Cristóbal, Baquerizo
<u>S. laevigatum laevigatum</u>	Santiago, Pl. Espumilla
<u>S. laevigatum santacruensis</u>	Santa Cruz, Tortuga Bay
<u>S. linelli</u>	Rabida, Red Beach
<u>S. longicornis</u>	Española
<u>S. longulum</u>	Santa Cruz, barranco
<u>S. obesum</u>	Tortuga
<u>S. rugosum</u>	Pinta, forest
<u>S. sp. n.</u>	Genovesa, Bahia Darwin
<u>Chilometopon brachystomum</u>	Mexico, Baja California
<u>C. castaneum</u>	California
<u>Stibia sp.</u>	California
<u>Trientoma sp.</u>	Puerto Rico
<u>Trimytis pruinosus</u>	Colorado

Table 11. Characters, character states and their assignments to eleven morphotypes of Stomion, and five outgroup genera.

character	character state
1. pronotum length:width	1. length<width 2. length≈width
2. pronotum apex:base	1. apex<base 2. apex=base 3. apex>base
3. clypeus shape	1. truncated 2. rounded 3. pointed
4. antennal mounds	1. flat or nearly flat 2. distinctly raised
5. antennal length	1. length<pronotum 2. length≈pronotum 3. length>pronotum
6. pronotal punctures	1. absent 2. fine 3. moderate 4. coarse
7. elytra carinae	1. none 2. present, no striae 3. present, striae
8. strial punctures	1. present 2. absent
9. interval punctures	1. present 2. absent
10. elytra surface	1. smooth 2. marked
11. pronotum apex margin	1. concave 2. straight
12. pronotum base margin	1. sinuate 2. convex 3. straight
13. elytra width:length	1. 0.60-0.65 2. 0.66-0.70 3. 0.71-0.75 4. 0.76-0.80

Table 11, continued

character

14. body surface	1. dull 2. shiny
15. marginal bead	1. absent 2. present on 3 sides 3. present on 4 sides
16. anterior pronotal angles	1. right or nearly right 2. acute
17. posterior pronotal angles	1. right or nearly right 2. acute
18. 3 rd antennal segment length: width	1. <3.0 2. 3.0-3.5 3. 3.6-4.0
19. elytra disc punctures	1. absent 2. fine 3. coarse
20. abdominal sternite punctures	1. absent 2. fine 3. coarse
21. submentum punctures	1. absent 2. fine 3. coarse
22. clypeus length	1. 0.5-0.8 2. 0.81-1.1 3. >1.1
23. right dorsal tooth	1. distinct 2. weak 3. absent
24. left dorsal tooth	1. present 2. absent
25. ventral tooth	1. truncated 2. bi-cusped
26. canthus	1. <1/4 2. 1/4 3. >1/4

Table 11, continued

character	character state
27. ultimate antennal segment	1. round 2. elongate
28. head:thorax	1. <0.5 2. 0.5-0.6 3. >0.6
29. scutellum size	1. small 2. large
30. scutellum shape	1. transverse 2. triangular 3. round 4. half circle
31. flightless	1. yes 2. no
32. clypeus notch	1. present 2. absent
33. lateral ridge above eye	1. ends at eye 2. extends to clypeus

Table 12. Species and localities used for the morphometric analysis of 19 measured character states.

Species	Island	Site

<u>S. cribricollis</u>	Darwin Wolf	
<u>S. g. galapagoensis</u>	Floreana	Las Cuevas Punta Cormoran
<u>S. g. punctipennis</u>	Española	Manzanillo Bahia Gardner
<u>S. helopoides</u>	San Cristóbal	Baquerizo
<u>S. laevigatum</u>	Santiago	Pl. Espumilla
	Isabela	Bahia Sullivan Alcedo Rim
<u>S. linelli</u>	Daphne Rabida	Red Beach
<u>S. longulum</u>	Santa Cruz	barranco
	Isabela	iguana pens Cerro Azul
<u>S. obesum</u>	Santa Fé Tortuga	beach
<u>S. rugosum</u>	Pinta Marchena	Pl. Ibettson
<u>S. sp. n.</u>	Genovesa	Pr. Phillip's Bahia Darwin

Table 13. Matrix of scores for twelve taxa of Stomion for 33 qualitative morphological characters. Rows= characters listed in table 11. Columns= taxa: S. longulum S. galapagoensis galapagoensis S. galapagoensis punctipennis S. obesum, S. linelli S. rugosum S. laevigatum laevigatum S. cribricollis S. longicornis Trientoma spp. Trimytis pruinus Chilometopon castanum C. brachystomum Stibia spp. S. sp.n. S. helopoides S. galapagoensis leleupi S. laevigatum santacruensis

1.	2	1	1	2	1	2	1	2	1	1	1	2	2	2	1	1	1	1
2.	2	1	1	2	1	2	2	2	1	2	1	3	3	3	1	1	1	2
3.	2	2	2	2	2	2	2	2	2	3	1	1	1	3	2	2	1	1
4.	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1	1
5.	1	2	2	1	1	1	2	2	3	2	1	3	3	2	1	1	1	2
6.	2	3	3	2	1	4	1	2	3	2	2	3	3	2	3	3	1	1
7.	2	3	3	2	1	2	1	3	3	1	1	3	3	3	1	1	1	2
8.	2	1	1	2	2	2	2	1	1	2	2	1	1	1	2	2	2	2
9.	1	1	1	1	2	1	2	1	1	2	1	1	1	1	1	1	1	1
10.	2	2	2	2	1	2	1	2	2	1	1	2	2	2	2	2	1	1
11.	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1
12.	1	1	1	1	1	1	1	1	3	1	2	1	1	3	1	1	1	1
13.	2	3	4	3	2	3	2	3	2	4	3	1	1	2	4	2	2	2
14.	2	1	2	1	2	1	2	1	2	1	2	2	2	2	1	1	2	2
15.	3	3	3	3	3	3	3	3	2	1	3	2	3	3	2	2	3	3
16.	2	1	2	2	2	2	1	1	2	2	2	2	2	2	1	2	2	1
17.	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1
18.	2	2	2	3	2	2	2	3	2	1	2	2	3	2	1	2	2	2
19.	2	3	3	2	1	3	1	3	3	1	1	3	3	2	3	3	2	2
20.	1	1	2	1	1	3	2	2	3	2	2	2	3	2	2	3	1	2
21.	3	3	3	2	3	3	2	2	3	2	3	3	3	3	2	3	3	2
22.	1	2	2	1	1	1	1	1	1	1	2	1	2	3	1	2	1	1
23.	1	2	3	1	1	2	2	2	3	1	3	3	3	1	1	3	1	2
24.	2	2	2	2	2	2	2	2	2	1	1	1	1	1	2	2	2	2
25.	1	1	1	1	1	1	1	1	1	2	2	2	2	2	1	1	1	1
26.	1	1	1	1	1	1	1	1	1	3	3	1	1	1	1	1	1	1
27.	1	1	1	1	1	1	1	1	2	1	1	2	2	1	1	1	1	1
28.	1	1	1	1	1	2	2	2	1	1	2	2	2	3	1	1	2	2
29.	2	2	2	2	2	2	2	2	2	1	1	2	2	1	2	2	2	2
30.	1	2	1	4	1	1	4	4	2	3	1	4	4	1	1	4	1	4
31.	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1
32.	2	2	2	2	2	2	2	2	2	1	1	1	1	1	2	2	2	2
33.	1	1	1	1	1	1	1	1	1	2	2	2	2	2	1	1	1	1

Table 14. Mean, standard deviation, and range of 19 morphometric measurements for ten presumptive species of Stomion. Number in parentheses is sample size.

	dent (21)	rugos (31)	long (29)	g.gal (20)
PROL	2.22 0.193 1.95- 2.67	1.92 0.186 1.60- 2.29	2.02 0.151 1.69- 2.27	2.16 0.179 1.84- 2.54
PROLM	3.36 0.271 2.90- 3.36	2.90 0.251 2.38- 3.52	2.83 0.194 2.47- 3.25	3.22 0.192 2.87- 3.66
PROMB	3.11 0.238 2.71- 3.64	2.90 0.24 2.38- 3.60	2.69 0.192 2.31- 3.00	3.19 0.179 2.90- 3.63
PROWA	2.26 0.138 1.99- 2.47	2.03 0.160 1.44- 2.33	2.08 0.148 1.82- 2.36	2.18 0.138 1.94- 2.47
LENG	8.57 0.564 7.65- 9.58	7.23 0.484 6.44- 8.38	7.96 0.528 6.88- 8.97	8.81 0.462 7.87- 9.79
WIDT	4.25 0.312 3.62 4.86	3.64 0.259 3.12- 4.26	3.40 0.251 2.88- 4.08	4.28 0.228 3.80- 4.28
ELYTL	5.23 0.462 4.41- 6.40	4.60 0.355 3.81- 5.45	4.89 0.446 4.13- 5.64	5.71 0.400 4.93- 6.64
HEADW	1.65 0.140 1.37- 2.04	1.55 0.144 1.28- 1.87	1.55 0.129 1.31- 1.78	1.68 0.121 1.50- 1.91
ELYTWA	3.31 0.250 2.82- 3.78	2.99 0.234 2.43- 3.53	2.78 0.208 2.41- 3.24	3.39 0.190 3.11- 3.82

Table 14, cont'd.

	<u>sq. ft.</u>	<u>cubic ft.</u>	<u>tons</u>	<u>sq. gal.</u>
SEG3L	0.36 0.029 0.31- 0.41	0.26 0.023 0.21- 0.31	0.31 0.036 0.22- 0.37	0.35 0.050 0.20- 0.43
ANTL	2.30 0.136 2.10- 2.59	1.80 0.119 1.63- 2.05	2.06 0.121 1.76- 2.29	2.45 0.214 1.99- 2.84
SEG4L	0.25 0.015 0.21- 0.27	0.18 0.015 0.16- 0.22	0.22 0.019 0.17- 0.25	0.27 0.030 0.19- 0.32
SEG5L	0.23 0.017 0.20- 0.28	0.17 0.014 0.14- 0.20	0.20 0.018 0.16- 0.23	0.24 0.027 0.18- 0.28
SEG6L	0.21 0.018 0.16- 0.26	0.16 0.017 0.13- 0.21	0.18 0.017 0.14- 0.23	0.23 0.031 0.16- 0.27
SEG4W	0.13 0.008 0.12- 0.15	0.10 0.008 0.08- 0.11	0.12 0.010 0.10- 0.14	0.12 0.010 0.10- 0.14
SEG5W	0.13 0.009 0.12- 0.15	0.10 0.009 0.08- 0.12	0.12 0.010 0.10- 0.14	0.12 0.01 0.11 0.14
SEG6W	0.13 0.009 0.11- 0.15	0.10 0.008 0.08- 0.11	0.13 0.011 0.10- 0.15	0.12 0.010 0.11- 0.14
PHEAD	41.19 3.683 36.0- 48.0	34.45 4.032 26.0- 42.0	38.62 3.416 33.0- 45.0	26.05 2.438 22.0- 31.0
PPRO	25.67 2.309 21.0- 30.0	21.81 2.54 16.0- 27.0	24.69 3.486 14.0- 30.0	17.00 1.026 15.0- 19.0

Table 14, continued.

	<u>obes</u> (20)	<u>line</u> (20)	<u>laev</u> (30)	<u>crib</u> (18)
PROL	0.19 0.200 1.49- 2.39	2.06 0.208 1.58- 2.48	1.80 0.186 1.56- 2.32	2.05 0.104 1.88- 2.24
PROWM	2.98 0.174 2.60- 3.36	3.46 0.277 3.06- 3.96	2.76 0.324 2.32- 3.53	2.89 0.145 2.63- 3.13
PROWB	2.87 0.205 2.45- 3.30	3.44 0.37 2.91- 4.11	2.65 0.365 2.14- 3.55	2.81 0.151 2.53- 3.05
PROWA	2.10 0.109 1.89- 2.26	2.33 0.168 2.12- 2.61	1.99 0.170 1.73- 2.39	2.14 0.102 1.94- 2.34
LENG	7.90 0.548 6.98- 9.08	8.66 0.641 7.25- 9.55	7.24 0.706 6.16- 8.73	8.26 0.572 7.21- 9.07
WIDT	3.80 0.361 3.20- 4.84	4.36 0.406 3.80- 5.10	3.38 0.384 2.83- 4.32	3.76 0.185 3.48- 4.02
ELYTL	4.91 0.024 3.74- 5.81	5.58 0.556 4.50- 6.67	4.49 0.470 3.66- 5.37	5.12 0.511 4.14- 6.02
HEADW	1.51 0.080 1.32- 1.69	1.70 0.125 1.50- 1.92	1.49 0.129 1.22- 1.82	1.52 0.116 1.37- 1.77
ELYTWA	2.98 0.198 2.55- 3.32	3.58 0.360 2.97- 4.30	2.72 0.372 2.13- 3.60	2.95 0.168 2.66- 3.26

Table 14, cont'd.

	<u>obes</u>	<u>line</u>	<u>laev</u>	<u>crib</u>
SEG3L	0.34 0.042 0.24- 0.41	0.38 0.039 0.32- 0.46	0.31 0.046 0.11- 0.14	0.34 0.046 0.26- 0.44
ANTL	2.17 0.156 1.92- 2.52	2.36 0.247 1.93- 2.85	2.00 0.170 1.63- 2.41	2.31 0.174 2.04 2.72
SEG4L	0.24 0.024 0.18- 0.28	0.27 0.030 0.22- 0.35	0.22 0.029 0.16- 0.28	0.21 0.019 0.17- 0.24
SEG5L	0.22 0.019 0.18- 0.25	0.24 0.026 0.20- 0.29	0.20 0.027 0.15- 0.28	0.23 0.029 0.18- 0.27
SEG6L	0.20 0.018 0.17- 0.23	0.22 0.027 0.16- 0.27	0.18 0.021 0.15- 0.23	0.21 0.019 0.17- 0.24
SEG4W	0.12 0.007 0.10- 0.13	0.12 0.007 0.11- 0.13	0.12 0.011 0.11- 0.14	0.14 0.012 0.12- 0.16
SEG5W	0.12 0.007 0.10- 0.13	0.12 0.007 0.11- 0.15	0.12 0.010 0.10- 0.14	0.14 0.012 0.12- 0.16
SEG6W	0.12 0.007 0.11- 0.13	0.13 0.010 0.11- 0.15	0.12 0.013 0.10- 0.15	0.14 0.015 0.12- 0.18
PHEAD	34.60 3.016 30.0- 42.0	31.05 3.332 26.0- 37.0	31.03 4.081 24.0- 39.0	40.22 2.922 35.0- 45.0
PPRO	20.45 3.170 16.0- 28.0	15.65 7.177 7.0- 25.0	15.20 5.261 3.0- 23.0	27.50 2.383 24.0- 34.0

Table 14, continued.

	<u>g.pun</u> (29)	<u>helop</u> (08)		<u>g.pun</u> (29)	<u>helop</u> (08)
PROL	2.10 0.338 1.62- 2.85	2.31 0.261 1.96- 2.69	SEG3L	0.34 0.035 0.28- 0.40	0.306 0.023 0.27- 0.33
PROUM	3.43 0.262 2.95- 4.00	3.58 0.25 3.23 3.93	ANTL	2.38 0.225 1.89- 2.69	2.23 0.157 2.03- 2.48
PROMB	3.40 0.321 2.87- 4.06	3.60 0.253 3.26- 3.88	SEG4L	0.25 0.023 0.19- 0.30	0.23 0.012 0.21- 0.24
PROWA	2.39 0.183 2.04- 2.77	2.46 0.169 2.28- 2.75	SEG5L	0.23 0.022 0.19- 0.28	0.22 0.020 0.19- 0.25
LENG	8.99 0.632 7.92- 10.1	9.09 0.537 8.41- 9.95	SEG6L	0.22 0.024 0.16- 0.26	0.21 0.021 0.18- 0.24
WILT	4.41 0.38 3.73- 5.21	4.49 0.309 4.16- 4.98	SEG4W	0.13 0.017 0.09- 0.16	0.13 0.012 0.11- 0.14
ELYTL	5.72 0.448 4.86- 6.95	5.98 0.374 5.65 6.83	SEG5W	0.13 0.015 0.10- 0.16	0.13 0.01 0.12- 0.15
HEADW	1.69 0.130 1.45- 1.90	1.70 0.161 1.52- 1.98	SEG6W	0.13 0.016 0.10- 0.16	0.13 0.012 0.12- 0.16
ELYWA	3.65 0.326 3.05- 4.31	3.77 0.294 3.36- 4.12	PHEAD	24.24 1.431 22.0- 27.0	28.38 1.061 27.0- 30.0
PPRO	11.52 1.184 9.0- 14.0	17.62 1.996 14.0- 20.0			

Table 15. An analysis of variance for 19 variables among species.

Variable	DF	F
PROL	9, 216	10.638*
PROWM	9, 216	33.017*
PROWA	9, 216	20.796*
PROWB	9, 216	31.720*
LENG	9, 216	36.803*
WIDT	9, 216	46.422*
ELYTL	9, 216	30.614*
HEADW	9, 216	11.016*
ELYTWA	9, 216	42.625*
SEG3L	9, 216	21.327*
ANTL	9, 216	37.581*
SEG4L	9, 216	33.470*
SEG5L	9, 216	30.201*
SEG6L	9, 216	28.098*
SEG4W	9, 216	30.218*
SEG5W	9, 216	32.735*
SEG6W	9, 216	23.923*
PHEAD	9, 216	81.172*
PPRO	9, 216	55.881*

*P<0.0001

Table 16. The first three principle components calculated on 16 morphological variables. The first three principle components account for 79.2% of total variance.

eigenvalues	8.768	2.465	1.442

VARIABLE	PCI	PCII	PCIII
PROL	0.693	0.017	0.495
PROWA	0.833	-0.256	0.337
LENG	0.899	-0.152	0.246
ELYTL	0.782	-0.298	0.187
HEADW	0.685	-0.400	0.363
ELYTWA	0.818	-0.437	0.213
SEG3L	0.767	0.228	-0.236
ANTL	0.907	0.090	-0.215
SEG4L	0.826	0.125	-0.377
SEG5L	0.869	0.094	-0.252
SEG6L	0.858	-0.014	-0.255
SEG4W	0.665	0.582	-0.041
SEG5W	0.675	0.587	0.004
SEG6W	0.636	0.542	-0.030
PHEAD	-0.266	0.710	0.344
PPRO	-0.273	0.608	0.563

Table 17. Standardized canonical coefficients for the first two discriminant functions calculated from 16 morphological variables.

variable	DFI	DFII

PROL	0.116	-0.305
PROWA	0.043	0.364
LENG	0.577	0.670
ELYTL	-0.326	0.015
HEADW	0.338	-0.248
ELYTWA	-0.829	-0.845
SEG3L	0.224	-0.159
ANTL	-0.197	0.144
SEG4L	-0.114	0.345
SEG5L	0.150	0.264
SEG6L	-0.050	0.019
SEG4W	-0.113	0.180
SEG5W	0.095	0.411
SEG6W	-0.087	0.102
PHEAD	0.774	-0.070
PPRO	0.410	0.042

Table 18. Standardized canonical coefficients for the first two discriminant functions calculated from 16 morphological variables. Populations of S. rugosum have been removed.

variable	DFI	DFII
PROL	-0.071	0.153
PROWA	0.041	-0.299
LENG	-0.436	-0.409
ELYTL	0.183	0.568
HEADW	-0.255	-0.270
ELYTWA	0.711	1.028
SEG3L	-0.245	-0.381
ANTL	0.214	0.551
SEG4L	0.077	0.208
SEG5L	-0.188	0.188
SEG6L	0.049	0.006
SEG4W	0.033	-0.005
SEG5W	-0.112	-0.018
SEG6W	0.063	-0.483
PHEAD	-0.795	0.124
PPRO	-0.432	0.651

Table 19. Populations and sample sizes used in the electrophoretic examination of Stomion.

Island	Site	Sample Size	Species
Baltra	BALT	44	<u>S. linelli</u>
Bartolomé	BART	44	<u>S. linelli</u>
Caamaño	CAAM	42	<u>S. laevigatum</u>
Daphne	DAPH	49	<u>S. linelli</u>
Eden	EDEN	15	<u>S. linelli</u>
Española	BGAR	37	<u>S. g. punctipennis</u>
	MANZ	50	<u>S. g. punctipennis</u>
	PTSU	44	<u>S. g. punctipennis</u>
Floreana	FLBB	9	<u>S. g. galapagoensis</u>
	FLCU	38	<u>S. g. galapagoensis</u>
Gardner	GARD	36	<u>S. g. galapagoensis</u>
Genovesa	DARW	25	<u>S. denticula</u>
Isabela	ARIM	44	<u>S. laevigatum</u>
	AZUL	44	<u>S. longulum</u>
	NVIL	44	<u>S. longulum</u>
	TAGU	43	<u>S. laevigatum</u>
	WVIL	16	<u>S. longulum</u>
Marchena	MARC	38	<u>S. rugosum</u>
Pinta	FORE	18	<u>S. rugosum</u>
	IBET	36	<u>S. rugosum</u>
Rabida	RABI	12	<u>S. linelli</u>
San Cristóbal	AERO	30	<u>S. helopoides</u>
	LIDO	33	<u>S. helopoides</u>
Santa Cruz	BARR	44	<u>S. longulum</u>
	BTOR	44	<u>S. laevigatum</u>
	GRAN	44	<u>S. linelli</u>
	HALF	4	<u>S. longulum</u>
	PENS	44	<u>S. longulum</u>
Santa Fé	SHOR	15	<u>S. linelli</u>
	SFEB	44	<u>S. obesum</u>
	SFEP	9	<u>S. obesum</u>
Santiago	SFTR	16	<u>S. obesum</u>
	SGPE	44	<u>S. laevigatum</u>
Seymour	SEYM	13	<u>S. linelli</u>
Tortuga	TORT	30	<u>S. obesum</u>

Table 20. Genetic variability at 8 loci in all populations. Standard errors are in parenthesis. A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.

	Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic	heterozygosity	
					Direct- count	HdyWbg expected
1	LIDO	30.0 (2.9)	2.5 (.6)	37.5	.203 (.115)	.226 (.109)
2	MANZ	49.6 (.4)	2.0 (.4)	25.0	.076 (.052)	.136 (.082)
3	SFEB	44.0 (.0)	3.4 (.5)	75.0	.230 (.063)	.285 (.082)
4	BART	44.0 (.0)	2.1 (.4)	37.5	.131 (.073)	.128 (.071)
5	MAFC	36.9 (.7)	2.0 (.4)	37.5	.039 (.018)	.096 (.047)
6	FLCU	40.3 (.4)	2.8 (.5)	37.5	.164 (.074)	.225 (.084)
7	BALT	40.9 (2.7)	2.4 (.2)	75.0	.185 (.038)	.248 (.057)
8	BARR	43.9 (.1)	2.6 (.5)	25.0	.134 (.062)	.152 (.072)
9	BGAR	31.5 (3.3)	2.3 (.3)	75.0	.158 (.049)	.234 (.066)
10	SGPE	43.9 (.1)	2.9 (.4)	50.0	.217 (.077)	.269 (.093)
11	DARW	25.0 (.0)	2.1 (.2)	37.5	.085 (.042)	.159 (.067)
12	TORT	30.0 (.0)	2.5 (.3)	75.0	.158 (.051)	.213 (.061)
13	EDEN	14.5 (.5)	2.4 (.4)	50.0	.178 (.072)	.245 (.090)
14	SFEP	8.9 (.1)	1.8 (.3)	62.5	.141 (.058)	.183 (.071)
15	PTSU	43.9 (.1)	2.9 (.4)	50.0	.163 (.073)	.185 (.069)
16	GRAN	43.5 (.5)	3.1 (.2)	62.5	.230 (.073)	.279 (.078)
17	AZUL	44.0 (.0)	1.8 (.3)	37.5	.139 (.073)	.153 (.078)
18	NVIL	43.5 (.4)	2.4 (.4)	75.0	.264 (.071)	.304 (.076)
19	IBET	35.8 (.2)	2.1 (.2)	50.0	.119 (.054)	.142 (.063)
20	GARD	36.0 (.0)	2.1 (.2)	50.0	.101 (.071)	.179 (.081)

Table 20, continued.

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic	heterozygosity	
				Direct- count	HdyWbg expected
21. TAGU	42.9 (.1)	2.3 (.3)	75.0	.128 (.040)	.159 (.043)
22. SHOR	14.5 (.3)	2.4 (.3)	62.5	.217 (.059)	.272 (.074)
23. AERO	25.8 (3.6)	2.3 (.5)	50.0	.128 (.052)	.174 (.089)
24. SFTR	15.4 (.4)	2.4 (.4)	75.0	.188 (.070)	.284 (.081)
25. FORE	17.4 (.3)	1.6 (.3)	37.5	.094 (.057)	.089 (.053)
26. BTOR	41.8 (1.7)	2.9 (.3)	87.5	.221 (.053)	.309 (.067)
27. CAAM	41.8 (.2)	2.0 (.3)	62.5	.163 (.051)	.244 (.079)
28. RABI	11.4 (.6)	1.5 (.2)	62.5	.272 (.083)	.274 (.082)
29. ARIM	44.0 (.0)	2.0 (.2)	50.0	.068 (.021)	.096 (.027)
30. DAPH	48.9 (.1)	1.6 (.3)	12.5	.078 (.069)	.076 (.062)
31. PENS	43.3 (.5)	2.3 (.4)	50.0	.125 (.054)	.168 (.072)
32. HALF	4.0 (.0)	1.5 (.2)	50.0	.156 (.066)	.147 (.059)
33. WVIL	14.5 (1.4)	2.3 (.2)	87.5	.222 (.051)	.254 (.061)
34. FLBB	9.0 (.0)	1.6 (.3)	37.5	.167 (.084)	.173 (.086)
35. SEYM	12.8 (.3)	2.0 (.3)	37.5	.156 (.074)	.210 (.094)

Table 21a. Variability measures in some Galápagos organisms. Numbers in parentheses represent the proportion of loci which are polymorphic.

taxon	no. species or races	no. loci	no. poly- morphic loci	no. alleles ----- range	mean	H
<u>Stomion</u>	8	20	8(0.40)	1-7	2.84	0.178
<u>Geospiza</u>	5	27	18(0.67)	1-6	2.30	0.102
<u>Geochelone</u>	7	20	4(0.20)	1-6	1.45	0.130
<u>Tropidurus</u>	6	20	18(0.90)	1-6	3.60	0.050
<u>Phyllo- dactylus</u>	7	20	20(1.00)	2-7	3.45	0.029

Table 21b. Variability measures in some island invertebrate taxa.

taxon	no. species or races	no. loci	no. poly- morphic loci	no. alleles ----- range	mean	H
Insecta						
<u>Stomion</u>	8	20	4(0.40)	1-7	2.84	0.178
<u>Drosophila</u>	2	11	4(0.36)	1-4	--	0.218
Gastropoda						
<u>Samoana</u>	4	20	4(0.25)	1-4	1.35	0.020
<u>Partula</u>	7	23	18(0.78)	1-6	3.39	0.166
<u>Cerion</u>	1	18	4(0.22)	1-2	1.22	0.271

Table 22. Allele frequencies at eight loci for 35 populations of Stomion. Abbreviations are as in Table 19.

Locus	Population								
	LIDO	MANZ	SFEB	BART	MARC	FLCU	BALT	BARR	BOAR
HK-2									
(N)	33	50	44	44	38	38	44	44	37
1	.000	.000	.000	.000	.000	.000	.045	.000	.000
2	.000	.000	.000	.000	.026	.026	.091	.000	.000
3	1.000	1.000	.989	.989	.974	.974	.864	.966	.743
4	.000	.000	.011	.011	.000	.000	.000	.034	.257
5	.000	.000	.000	.000	.000	.000	.000	.000	.000
MPI									
(N)	32	50	44	44	38	40	44	44	27
1	.000	.000	.011	.000	.000	.000	.000	.000	.000
2	.016	.000	.057	.000	.053	.000	.000	.011	.000
3	.031	.000	.136	.068	.934	.162	.182	.170	.352
4	.578	.980	.523	.909	.013	.650	.739	.648	.648
5	.375	.020	.239	.023	.000	.150	.090	.148	.000
6	.000	.000	.034	.000	.000	.038	.000	.023	.000
PGM-1									
(N)	33	50	44	44	38	41	41	44	38
1	.000	.000	.011	.000	.000	.000	.000	.000	.000
2	.000	.000	.023	.000	.013	.012	.049	.023	.079
3	.045	1.000	.864	1.000	.987	.988	.951	.977	.789
4	.955	.000	.080	.000	.000	.000	.000	.000	.118
5	.000	.000	.023	.000	.000	.000	.000	.000	.013
PEP									
(N)	33	50	44	44	38	41	44	44	38
1	.000	.000	.045	.000	.000	.000	.000	.011	.000
2	.000	.090	.295	.000	1.000	.037	.011	.250	.013
3	.803	.830	.602	1.000	.000	.951	.989	.727	.947
4	.045	.080	.057	.000	.000	.012	.000	.011	.039
5	.152	.000	.000	.000	.000	.000	.000	.000	.000
GOT-M									
(N)	33	50	44	44	32	39	44	44	14
1	.000	.000	.000	.000	.000	.013	.000	.000	.000
2	.000	.000	.898	.000	.750	.769	.000	.000	.000
3	1.000	.960	.102	1.000	.250	.218	.864	1.000	.929
4	.000	.040	.000	.000	.000	.000	.136	.000	.071

Table 22, continued.

Locus	Population								
	LIDO	MANZ	SFEB	BART	MARC	FLCU	BALT	BARR	BGAR
GOT-S									
(N)	10	50	44	44	37	41	22	44	22
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.023	.000	.000	.000	.023	.000
3	.000	.000	.011	.955	1.000	.000	.773	.977	.000
4	1.000	1.000	.943	.023	.000	1.000	.227	.000	1.000
5	.000	.000	.045	.000	.000	.000	.000	.000	.000
6	.000	.000	.000	.000	.000	.000	.000	.000	.000
6PGDH									
(N)	33	47	44	44	35	41	44	44	38
1	.258	.394	.000	.000	.000	.024	.000	.000	.000
2	.197	.426	.000	.000	.028	.427	.000	.023	.263
3	.136	.128	.955	.148	.903	.329	.000	.955	.737
4	.197	.053	.045	.307	.028	.183	.375	.023	.000
5	.167	.000	.000	.545	.042	.037	.625	.000	.000
6	.045	.000	.000	.000	.000	.000	.000	.000	.300
7	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGI									
(N)	33	50	44	44	38	41	44	43	38
1	.000	.000	.000	.034	.000	.000	.000	.000	.000
2	.985	.990	.261	.045	.000	.000	.045	.000	.987
3	.015	.010	.716	.920	1.000	.976	.932	.988	.013
4	.000	.000	.023	.000	.000	.024	.023	.012	.000
5	.000	.000	.000	.000	.000	.000	.000	.000	.000

Locus	Population								
	SGPE	DARW	TORT	EDEN	SFEP	PTSU	GRAN	AZUL	NVIL
HK-2									
(N)	44	25	30	15	9	44	44	44	44
1	.000	.000	.000	.033	.000	.000	.000	.000	.000
2	.000	.000	.000	.400	.000	.034	.023	.000	.023
3	.989	.940	.933	.567	1.000	.966	.966	1.000	.977
4	.011	.060	.050	.000	.000	.000	.011	.000	.000
5	.000	.000	.017	.000	.000	.000	.000	.000	.000

Table 22, continued.

Locus	Population								
	SGPE	DARW	TORT	EDEN	SFEP	PTSU	GRAN	AZUL	NVIL
6PGDH									
(N)	44	25	30	15	9	43	44	44	43
1	.000	.000	.000	.033	.000	.012	.000	.011	.000
2	.000	.280	.000	.133	1.000	.709	.023	.000	.058
3	1.000	.660	.000	.567	.000	.163	.159	.000	.256
4	.000	.060	.950	.100	.000	.081	.500	.989	.651
5	.000	.000	.050	.167	.000	.035	.318	.000	.035
6	.000	.000	.000	.000	.000	.000	.000	.000	.000
7	.000	.000	.000	.000	.000	.000	.000	.000	.000
PGI									
(N)	44	25	30	15	9	44	44	44	44
1	.000	.000	.000	.067	.000	.034	.000	.000	.000
2	.125	.300	.000	.000	.167	.943	.068	.386	.000
3	.545	.700	.750	.933	.833	.023	.886	.614	.614
4	.295	.000	.000	.000	.000	.000	.045	.000	.386
5	.034	.000	.250	.000	.000	.000	.000	.000	.000
HK-2									
(N)	35	36	43	15	30	16	18	44	42
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.057	.000	.000	.000	.000	.031	.028	.000	.000
3	.943	1.000	1.000	1.000	1.000	.969	.972	.977	1.000
4	.000	.000	.000	.000	.000	.000	.000	.000	.000
5	.000	.000	.000	.000	.000	.000	.000	.023	.000
MPI									
(N)	36	36	42	14	30	16	17	43	42
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.333	.000	.012	.036	.000	.063	.265	.000	.000
3	.597	.028	.000	.143	.017	.156	.706	.000	.012
4	.069	.361	.929	.786	.850	.531	.029	.372	.667
5	.000	.611	.060	.036	.133	.188	.000	.581	.012
6	.000	.000	.000	.000	.000	.063	.000	.047	.310

Table 22, continued.

Locus	Population								
	IBET	GARD	TAGU	SHOR	AERO	SFTR	FORE	BICR	CAAM
PGM-1									
(N)	36	36	43	15	30	16	18	44	42
1	.000	.000	.000	.000	.000	.000	.000	.011	.000
2	.042	.014	.058	.000	.000	.094	.000	.034	.000
3	.903	.986	.907	.967	.067	.906	.944	.920	.857
4	.056	.000	.035	.033	.850	.000	.056	.034	.143
5	.000	.000	.000	.000	.683	.000	.000	.000	.000
PEP									
(N)	36	36	43	15	30	16	18	44	42
1	.000	.000	.000	.000	.000	.281	.000	.000	.000
2	.014	.069	.081	.033	.000	.000	.000	.284	.119
3	.986	.931	.919	.967	.983	.656	1.000	.693	.881
4	.000	.000	.000	.000	.017	.063	.000	.000	.000
5	.000	.000	.000	.000	.000	.000	.000	.023	.000
GOT-M									
(N)	35	36	43	15	30	13	16	42	41
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.871	.944	.907	.400	.000	.846	1.000	.000	.488
3	.129	.056	.093	.600	1.000	.154	.000	.405	.512
4	.000	.600	.000	.000	.000	.000	.000	.595	.000
GOT-S									
(N)	36	36	43	14	1	14	16	30	41
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.000	.028	.000	.250	.000	.000	1.000	.667	.000
4	.000	.972	.000	.750	1.000	1.000	.000	.333	.561
5	.000	.000	1.000	.000	.000	.000	.000	.000	.439
6	.000	.000	.000	.000	.000	.000	.000	.000	.000
6PGDH									
(N)	36	36	43	13	25	16	18	43	42
1	.000	.000	.000	.000	.020	.000	.000	.000	.000
2	.014	.389	.012	.000	.000	.000	.000	.035	.012
3	.986	.514	.163	.577	.000	.906	1.000	.930	.988
4	.000	.097	.826	.385	.120	.094	.000	.035	.000
5	.000	.000	.000	.038	.380	.000	.000	.000	.000
6	.000	.000	.000	.000	.160	.000	.000	.000	.000
7	.000	.000	.000	.000	.320	.000	.000	.000	.000

Table 23. Allele frequencies pooled by species. ggal= S. galapagoensis galapagoensis, helo= S. helopoides, gpun= S. galapagoensis punctipennis, long= S. longulum, obes= S. obesum, rugo= S. rugosum, line= S. linelli, dent= S. denticula.

	Species								
Locus	ggal	helo	gpun	long	obes	laev	rugo	line	dent

HK-2									
(N)	83	63	131	196	99	217	91	236	25
1	.000	.000	.000	.000	.000	.000	.000	.011	.000
2	.012	.000	.011	.008	.005	.000	.038	.047	.000
3	.988	1.000	.916	.982	.970	.993	.962	.939	.940
4	.000	.000	.073	.010	.020	.002	.000	.004	.063
5	.000	.000	.000	.000	.005	.005	.000	.000	.000
MPI									
(N)	85	62	121	196	99	215	91	234	25
1	.000	.000	.000	.000	.005	.000	.000	.017	.000
2	.000	.008	.000	.003	.035	.009	.203	.004	.000
3	.100	.024	.198	.099	.121	.095	.758	.179	.020
4	.524	.710	.769	.832	.667	.693	.038	.771	.960
5	.359	.258	.029	.059	.146	.133	.000	.028	.020
6	.018	.000	.004	.008	.025	.070	.000	.000	.000
PGM-1									
(N)	86	63	132	196	99	217	92	233	25
1	.000	.000	.000	.005	.005	.005	.000	.000	.000
2	.012	.000	.023	.143	.035	.021	.022	.017	.020
3	.988	.056	.917	.786	.869	.929	.946	.974	.980
4	.000	.905	.057	.051	.071	.046	.033	.009	.000
5	.000	.040	.004	.015	.020	.000	.000	.000	.000
PEP									
(N)	86	63	132	193	99	217	92	236	25
1	.029	.000	.000	.005	.096	.000	.000	.000	.000
2	.047	.000	.042	.075	.141	.113	.418	.033	.020
3	.919	.889	.913	.891	.727	.880	.582	.966	.980
4	.006	.032	.045	.028	.035	.002	.000	.011	.000
5	.000	.079	.000	.000	.000	.005	.000	.000	.000
GOT-M									
(N)	84	63	108	195	95	214	83	236	25
1	.006	.000	.000	.000	.011	.000	.000	.000	.000
2	.869	.000	.000	.300	.916	.591	.849	.044	.960
3	.125	1.000	.958	.700	.074	.292	.151	.926	.000
4	.000	.000	.042	.000	.000	.117	.000	.030	.040

Table 23, continued.

Locus	Species								
	ssal	helo	spun	long	obes	laev	rufo	line	dent
GOT-S									
(N)	86	11	116	182	97	201	89	200	25
1	.000	.000	.000	.000	.000	.002	.000	.000	.000
2	.000	.000	.000	.005	.005	.007	.000	.023	.000
3	.012	.000	.000	.239	.175	.254	1 .000	.705	.000
4	.988	1 .000	.987	.143	.799	.425	.000	.262	1 .000
5	.000	.000	.013	.602	.021	.311	.000	.010	.000
6	.000	.000	.000	.011	.000	.000	.000	.000	.000
6PGDH									
(N)	86	58	128	192	99	216	90	232	25
1	.012	.155	.148	.003	.000	.000	.000	.002	.000
2	.366	.112	.473	.023	.091	.012	.017	.013	.280
3	.453	.078	.320	.456	.571	.627	.956	.170	.660
4	.140	.164	.047	.500	.323	.354	.011	.293	.060
5	.029	.259	.012	.016	.015	.007	.017	.519	.000
6	.000	.095	.000	.000	.000	.000	.000	.002	.000
7	.000	.138	.000	.000	.000	.000	.000	.000	.000
PGI									
(N)	86	63	122	195	99	217	92	236	25
1	.000	.024	.011	.000	.000	.005	.011	.013	.000
2	.006	.968	.973	.103	.177	.081	.000	.049	.300
3	.983	.008	.015	.774	.737	.839	.984	.915	.700
4	.012	.000	.000	.123	.010	.065	.005	.023	.000
5	.000	.000	.000	.000	.076	.012	.000	.000	.000

Table 24. Chi square contingency analysis of allele frequency differences at eight polymorphic loci among species of Stomion.

Locus	No. of alleles	Chi-square	D.F.	P
HK-2	5	157.606	32	.00000
MPI	6	1175.035	40	.00000
PGM-1	5	1356.863	32	.00000
PEP	5	616.019	32	.00000
GOT-M	4	1305.985	24	.00000
GOT-S	6	1749.912	40	.00000
6PGDH	7	2471.375	48	.00000
PGI	5	1732.740	32	.00000
(Totals)		10565.540	280	.00000

Table 25. Chi-square contingency analysis of populations assigned to species of Stomion. Data were available for only one population of S. denticula, therefore no analysis was performed.

SPECIES : OBESUM				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	4	11.606	9	.23642
MPI	6	36.604	15	.00145
PGM-1	5	12.951	12	.37265
PEP	4	68.411	9	.00000
GOT-M	3	12.372	6	.05417
6PGDH	4	365.405	9	.00000
PGI	4	53.463	9	.00000

SPECIES : LINELLI				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	4	106.933	18	.00000
MPI	5	81.768	24	.00000
PGM-1	3	41.260	12	.00004
PEP	3	20.833	12	.05288
GOT-M	3	166.138	12	.00000
6PGDH	6	292.462	30	.00000
PGI	4	47.149	18	.00020

SPECIES : RUGOSUM				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	2	1.075	2	.58426
MPI	3	23.929	4	.00008
PGM-1	3	6.854	4	.14382
PEP	2	179.948	2	.00000
GOT-M	2	10.882	2	.00433
6PGDH	4	9.021	6	.17238
PGI	3	9.855	4	.04294

Table 25, continued.

SPECIES : GALAPAGOENSIS				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	2	2.397	2	.30160
MPI	4	39.437	6	.00000
PGM-1	2	.246	2	.88423
PEP	4	46.562	6	.00000
GOT-M	3	13.293	4	.00993
6PGDH	5	25.808	8	.00113
PGI	3	3.595	4	.46365

SPECIES : LONGULUM				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	3	16.258	10	.09247
MPI	5	103.044	20	.00000
PGM-1	5	234.665	20	.00000
PEP	4	99.768	15	.00000
GOT-M	2	301.926	5	.00000
6PGDH	5	248.260	20	.00000
PGI	3	202.352	10	.00000

SPECIES : LAEVIGATUM				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	4	23.750	15	.06946
MPI	5	435.955	20	.00000
PGM-1	4	46.175	15	.00005
PEP	4	65.971	15	.00000
GOT-M	3	498.468	10	.00000
6PGDH	4	499.276	15	.00000
PGI	5	158.683	20	.00000

Table 25, continued.

SPECIES : HELOPOIDES				
Locus	No. of alleles	Chi-square	D.F.	P
MPI	4	11.443	3	.00955
PGM-1	3	6.134	2	.04656
PEP	3	11.061	2	.00396
6PGDH	7	58.106	6	.00000
PGI	3	4.249	2	.11952

SPECIES : PUNCTIPENNIS				
Locus	No. of alleles	Chi-square	D.F.	P
HK-2	3	57.623	4	.00000
MPI	4	49.842	6	.00000
PGM-1	4	30.395	6	.00003
PEP	3	15.215	4	.00428
GOT-M	2	.755	2	.68573
6PGDH	5	148.359	8	.00000
PGI	3	6.653	4	.15538

Table 26. Hierarchical F-statistics of all populations combined across loci. F_{st} = genic diversity among subgroups, $1-F$ = genic diversity within subgroups, and N_m = estimated number of migrants per generation.

comparison				
subgroup (s)	total group (t)	F_{st}	$1-F$	N_m

population	island	0.277	0.723	0.652
population	total	0.496	0.504	0.254
island	total	0.302	0.698	0.578

Table 27. Genic diversity among subpopualtions (F_{st}) combined across loci for individual species, and the estimated number of migrants per generation among subpopulations (N_m).

species	no. islands	no. populations	F_{st}	N_m
<hr/>				
<u>S. galapagoensis</u> <u>galapagoensis</u>	2	3	0.107	2.09
<u>S. galapagoensis</u> <u>punctipennis</u>	1	3	0.146	1.46
<u>S. helopoides</u>	1	2	0.073	3.17
<u>S. laevigatum</u>	4	6	0.384	0.401
<u>S. linelli</u>	7	7	0.252	0.742
<u>S. longulum</u>	2	6	0.455	0.299
<u>S. cbesum</u>	2	4	0.298	0.589
<u>S. rugosum</u>	2	3	0.368	0.429

Table 28. Populations from which individuals were selected for electrophoretic examination at 21 loci.

Species	Island	Site
<hr/>		
<u>S. galapagoensis</u> <u>galapagoensis</u>	Floreana Gardner	FLBB GARD
<u>S. galapagoensis</u> <u>punctipennis</u>	Española	BGAR MANZ
<u>S. helopoides</u>	San Cristóbal	LIDO
<u>S. laevigatum</u>	Isabela Santiago	TAGU SGPE
<u>S. linelli</u>	Baltra Daphne	BALT DAPH
<u>S. longulum</u>	Isabela Santa Cruz	NVIL BARR
<u>S. obesum</u>	Santa Fé Tortuga	SFEB TORT
<u>S. rugosum</u>	Marchena Pinta	MARC FORE
<u>S. denticula</u>	Genovesa	DARW

Table 29. Allele frequencies for 16 populations of Stomion at 21 enzyme loci. Abbreviations as in Table 28.

Locus	Population								
	TORT	SFED	MARC	BALT	BARR	BGAR	MANZ	LIDO	SGPE
HK-2									
(N)	30	44	38	44	44	37	50	33	44
1	.000	.000	.000	.045	.000	.000	.000	.000	.000
2	.000	.000	.026	.091	.000	.000	.000	.000	.000
3	.933	.989	.974	.864	.034	.743	1.000	1.000	.989
4	.050	.011	.000	.000	.000	.257	.000	.000	.011
5	.017	.000	.000	.000	.000	.000	.000	.000	.000
MPI									
(N)	30	44	38	44	44	27	50	32	44
1	.000	.011	.000	.000	.000	.000	.000	.000	.000
2	.000	.057	.053	.000	.011	.000	.000	.016	.034
3	.067	.136	.934	.132	.170	.352	.000	.031	.375
4	.933	.523	.013	.739	.548	.648	.980	.578	.580
5	.000	.239	.000	.795	.146	.000	.020	.375	.011
6	.000	.034	.000	.000	.023	.000	.000	.000	.000
PGM-1									
(N)	30	44	38	41	44	38	50	33	44
1	.000	.011	.000	.000	.000	.000	.000	.000	.011
2	.033	.023	.013	.049	.023	.079	.000	.000	.011
3	.817	.864	.987	.951	.977	.789	1.000	.045	.966
4	.117	.080	.000	.000	.000	.118	.000	.955	.011
5	.033	.023	.000	.000	.000	.013	.000	.000	.000
6	.000	.000	.000	.000	.000	.000	.000	.000	.000
PEPPF									
(N)	30	44	38	44	44	38	50	33	44
1	.000	.045	.000	.000	.011	.000	.000	.000	.000
2	.033	.295	1.000	.011	.250	.013	.090	.000	.000
3	.967	.602	.000	.989	.727	.947	.830	.803	.989
4	.000	.057	.000	.000	.011	.039	.080	.045	.011
5	.000	.000	.000	.000	.000	.000	.000	.152	.000
GOT-M									
(N)	30	44	32	44	44	14	50	33	44
1	.033	.000	.000	.000	.000	.000	.000	.000	.000
2	.967	.898	.750	.000	.000	.000	.000	.000	.625
3	.000	.102	.250	.864	1.000	.929	.960	1.000	.375
4	.000	.000	.000	.136	.000	.071	.040	.000	.000

Table 29, continued.

Locus	Population								
	TORT	SFEB	MARC	BALT	BARR	BGAR	MANZ	LIDO	SGPE
6PGDH									
(N)	30	44	36	44	44	38	47	33	44
1	.000	.000	.000	.000	.000	.000	.394	.258	.000
2	.000	.000	.028	.000	.023	.263	.426	.197	.000
3	.000	.955	.903	.000	.955	.737	.128	.136	1.000
4	.950	.045	.028	.375	.023	.000	.053	.197	.000
5	.050	.000	.042	.625	.000	.000	.000	.167	.000
6	.000	.000	.000	.000	.000	.000	.000	.045	.000
PGI									
(N)	30	44	38	44	43	38	50	33	44
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.261	.000	.045	.000	.987	.990	.985	.125
3	.750	.716	1.000	.932	.988	.013	.010	.015	.545
4	.000	.023	.000	.023	.012	.000	.000	.000	.295
5	.250	.000	.000	.000	.000	.000	.000	.000	.034
6	.000	.000	.000	.000	.000	.000	.000	.000	.000
FUM									
(N)	2	2	2	2	8	13	10	2	7
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	1.000	.000	.000	.000	.000	.000	.000
3	1.000	1.000	.000	1.000	1.000	1.000	1.000	1.000	1.000
APK									
(N)	2	2	2	2	2	2	2	2	2
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AC									
(N)	2	2	2	2	8	13	10	2	7
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PEPLG									
(N)	2	2	2	2	2	2	2	2	2
1	.250	.000	1.000	.000	.000	.000	.000	.250	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	.750	1.000	.000	1.000	1.000	.750	1.000	.500	1.000
4	.000	.000	.000	.000	.000	.250	.000	.250	.000

Table 29, continued.

Locus	Population								
	TORT	SFEB	MARC	BALT	BARR	BGAR	MANZ	LILG	SGPE
ME-2									
(N)	2	2	2	2	8	13	10	2	7
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TRE									
(N)	2	2	2	2	2	2	2	2	2
1	.000	.000	.000	.000	.000	.000	.000	.000	.000
2	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Locus	Population						
	DARW	NVIL	GARD	TAGU	FORE	DAPH	FLBB
HK-2							
(N)	25	44	36	44	18	49	9
1	.000	.000	.000	.000	.000	.000	.000
2	.000	.023	.000	.000	.028	.000	.000
3	.940	.977	1.000	1.000	.972	1.000	1.000
4	.060	.000	.000	.000	.000	.000	.000
5	.000	.000	.000	.000	.000	.000	.000
MPI							
(N)	25	44	36	43	17	48	9
1	.000	.000	.000	.000	.000	.083	.000
2	.000	.000	.000	.012	.265	.000	.000
3	.020	1.000	.028	.000	.706	.271	.111
4	.960	.000	.361	.930	.029	.646	.611
5	.020	.000	.611	.058	.000	.000	.278
6	.000	.000	.000	.000	.000	.000	.000
PQM-1							
(N)	25	44	36	44	18	49	9
1	.000	.000	.000	.000	.000	.000	.000
2	.020	.011	.014	.057	.000	.010	.000
3	.980	.693	.986	.886	.944	.990	1.000
4	.000	.227	.000	.034	.016	.000	.000
5	.000	.068	.000	.000	.000	.000	.000
6	.000	.000	.000	.023	.000	.000	.000

Table 30. Percentage of Stomion and other taxa (Thorpe, 1982) belonging to genetic identity classes.

identity		percent	
		<u>Stomion</u>	others

within species	I>0.95	43	80
	I>0.90	86	93
	I>0.85	100	98
between species	I>0.85	78	3
	I>0.80	90	5

Table 31. Minimum and mean genetic identities between species of some Galápagos organisms.

genus	no. species/races	min. I	mean I
<hr/>			
<u>Stomion</u>	8	0.70	0.88
<u>Geospiza</u>	5	0.90	0.96
<u>Geochelone</u>	7	0.93	0.96
<u>Tropidurus</u>	6	0.29	0.76
<u>Phyllodactylus</u>	7	0.38	0.72

3 of/de 3

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010A
(ANSI and ISO TEST CHART No. 2)

Table 32. Nei's genetic distances (D) and estimated divergence times in millions of years (MY) of each species from the reference site LIDO (S. helopoides). Island ages (Cox 1983) are subtracted from the age of the reference site to give an inferred geological age difference of species from the reference species.

population	species	D	t (my)	inferred age (my)
<hr/>				
GARD	<u>S. galapagoensis</u> <u>galapagoensis</u>	0.199	3.78	2.0
BGAR	<u>S. galapagoensis</u> <u>punctipennis</u>	0.057	1.08	0
MANZ	<u>S. galapagoensis</u> <u>punctipennis</u>	0.067	1.27	0
SGPE	<u>S. laevigatum</u>	0.150	2.85	2.0
TAGU	<u>S. laevigatum</u>	0.160	3.04	2.3
BALT	<u>S. linelli</u>	0.125	2.38	0
DAPH	<u>S. linelli</u>	0.143	2.72	0
BARR	<u>S. longulum</u>	0.128	2.43	0
NVIL	<u>S. longulum</u>	0.134	2.55	2.3
TORT	<u>S. obesum</u>	0.170	3.23	2.3
SFEB	<u>S. obesum</u>	0.160	3.04	0.3
MARC	<u>S. rugosum</u>	0.363	6.90	2.3
FORE	<u>S. rugosum</u>	0.299	5.68	2.3
DARW	<u>S. denticula</u>	0.159	2.85	2.0

Table 33. Average estimated divergence times for each species from the reference species S. helopoides.

species	no. estimates	t(my)
<hr/>		
<u>S. galapagoensis</u> <u>galapagoensis</u>	1	3.78
<u>S. galapagoensis</u> <u>punctipennis</u>	2	1.18
<u>S. laevigatum</u>	2	2.94
<u>S. linelli</u>	2	2.55
<u>S. longulum</u>	2	2.49
<u>S. obesum</u>	2	3.14
<u>S. rugosum</u>	2	6.29
<u>S. denticula</u>	1	3.02

Figure 1. The islands of the Galápagos.

Figure 2. Major vegetation zones found on some Galápagos Islands (from Peck and Kukalova-Peck, 1991)

Figure 3. Abundances of four species of beetles over an eight week period at the transect site. Ab= Ammophorus bifoveatus, Bl= Blapstinus lugolus, Bs= B. spatulus, Sl= Stomion laevigatum.

Figure 4. Arrangement of four quadrats for mark and recapture study. Each quadrat contained 25 unbaited pit-fall traps, and covered an area of 64m².

1

2

3

4

Figure 5. Observed (bars) and expected (dots) distribution of beetles in traps among four quadrats. Expected frequencies were calculated based on negative binomial (Quadrats I-III) and Poisson (Quadrat IV) models.

Figure 6. Distribution of beetle catches among four quadrats (I-IV) each containing 25 pit-fall traps.

Figure 7. Distribution of species in the genus Stomion.

✱ S. cribricollis

● S. linelli

● S. denticula

□ S. longicornis

* S. galapagoensis galapagoensis

▲ S. longulum

◎ S. galapagoensis punctipennis

▼ S. obesum

✱ S. helopoides

☆ S. rugosum

⊛ S. laevigatum

Figure 8. Distribution of the three morphological groups of Stomion.

✱ punctured

● smooth

▲ ridged

Figure 9. Nineteen morphological measurements taken on 226 individuals of the genus Stomion.

1. length of pronotum (PROL)
2. width of pronotum at middle (PROWM)
3. width of pronotum at base (PROWB)
4. width of pronotum at apex (PROWA)
5. total body length (LENG)
6. body width (WIDT)
7. length of elytra (ELYTL)
8. width of head between eyes
9. width of elytra at apex (ELYTWA)
10. length of antennal segment 3 (SEG3L)
11. total length of antenna (ANTL)
12. length of antennal segment 4 (SEG4L)
13. length of antennal segment 5 (SEG5L)
14. length of antennal segment 6 (SEG6L)
15. width of antennal segment 4 (SEG4W)
16. width of antennal segment 5 (SEG5W)
17. width of antennal segment 6 (SEG6W)
18. number of punctures on head (PHEAD)
19. number of punctures on pronotum (PPRO)

Figure 10. UPGMA clustering of a similarity matrix based on 33 qualitative characters. Species are labeled with morphological type (P= punctured, R= ridged, S= smooth) and body shape (1= broad, 2= narrow) O= outgroup.

Figure 11. First and second principle components of 23 populations of *Stomion*.

S. cribricollis P=WOLF, Q=DARW

S. galapagoensis galapagoensis D=FLCU, S=FLPC

S. galapagoensis punctipennis E=MANZ, F=BGAR, W=PTSU

S. helopoides T=BAQU

S. laevigatum I=SGPE, L=ARIM, R=SULL

S. linelli H=DAPH, J=RABI

S. longulum C=BARR, U=AZUL, V=PENS

S. obesum G=TORT, O=SFEB

S. rugosum B=IBET, K=FORE, M=MARC

S. sp. n. A=PHIL, N=BDAR

Figure 12. Scatter plot of the 2nd and 3rd principle components for 23 populations of Stomion.

S. cribricollis P=WOLF, Q=DARW

S. galapagoensis galapagoensis D=FLCU, S=FLPC

S. galapagoensis punctipennis E=MANZ, F=BGAR, W=PTSU

S. helopoides T=BAQU

S. laevigatum I=SGPE, L=ARIM, R=SULL

S. linelli H=DAPH, J=RABI

S. longulum C=BARR, U=AZUL, V=PENS

S. obesum G=TORT, O=SFEB

S. rugosum B=IBET, K=FORE, M=MARC

S. sp. n. A=PHIL, N=BDAR

Figure 13. The first two principle components calculated on 23 populations of Stomion. Populations are coded for three morphological groups based on external sculpturing. A=punctured, B=ridged, C=smooth.

Figure 14. The second and third principle components calculated on 23 populations of *Stomion*. Populations are coded for morphological groups based on external sculpturing. A=punctured, B=ridged, C=smooth.

Figure 15a.
ELYTL

Figure 15b.

Figure 15. Bivariate plots of population means for ten taxa of *Stomion*. *S. cribricollis* P,Q; *S. galapagoensis* *galapagoensis* D,S; *S. galapagoensis punctipennis* E,F,W; *S. helopoides* T; *S. laevigatum* I,L,R; *S. linelli* H,J; *S. longulum* C,U,V; *S. obesum* G,O; *S. rugosum* B,K,M; *S. sp. n.* A,N.

a. Length of pronotum (PROL) versus width of pronotum (PROWM).

b. Length of elytra (ELYTL) versus width of elytra (WIDT).

Figure 16a.

Figure 16b.

Figure 16. Bivariate plots of population means for ten taxa of *Stomion*. *S. cribricollis* P,Q; *S. galapagoensis* galapagoensis D,S; *S. galapagoensis punctipennis* E,F,W; *S. helopoides* T; *S. laevigatum* I,L,R; *S. linelli* H,J; *S. longulum* C,U,V; *S. obesum* G,O; *S. rugosum* B,K,M; *S. sp. n.* A,N.

a. Width of pronotum at apex (PROWA) versus width of pronotum at base (PROWB).

b. Number of punctures on pronotum (PPRO) versus number of punctures on head (PHEAD).

Figure 17. The first two principle components calculated on 23 populations of Stomion. Populations are coded for two morphological groups based on body size and shape. A=broad, B=narrow.

Figure 18. The second and third principle components calculated on 23 populations of *Stomion*. Populations are coded for two morphological groups based on body size and shape. A=broad, B=narrow.

Figure 19. The first and second canonical axes of ten taxa of Stomion based on variation at 16 quantitative characters. A=denticula, B= rugosum, C=longulum, D=galapagoensis galapagoensis, E=galapagoensis punctipennis, F=obesum, G=linelli, H=laevigatum, I=cribricollis, J=helopoides.

Figure 20. The second and third canonical axes of ten taxa of Stomion based on variation at 16 quantitative characters. A=denticula, B=rugosum, C=longulum, D=galapagoensis, E=galapagoensis punctipennis, F=obesum, G=linelli, H=laevigatum, I=cribricollis, J=helopoides.

Figure 21. The first and second canonical axes of ten taxa of *Stomion*, coded for morphological group based on external sculpturing. A= smooth, B= punctured, C= smooth.

Figure 22. The first and second canonical axes of nine taxa of Stomion. Populations of S. rugosum have been removed from the data set. A=denticula, B=longulum, C=galapagoensis galapagoensis, D=galapagoensis punctipennis, E=obesum, F=linelli, G=laevigatum, H=cribricollis, I=helopoides.

Figure 23. The second and third canonical axes of nine taxa of Stomion. Populations of S. rugosum have been removed from the data set. A=denticula, B=longulum, C=galapagoensis galapagoensis, D=galapagoensis punctipennis, E=obesum, F=linelli, G=laevigatum, H=cribricollis, I=helopoides.

Figure 24. First and second canonical axes of eight taxa of Stomion. Populations of S. rugosum and S. laevigatum have been removed from the data set. A=denticula, C=longulum, D=galapagoensis galapagoensis, E=galapagoensis punctipennis, F=obesum, G=linelli, I=cribricollis, J=helopoides.

Figure 25. Second and third canonical axes of eight taxa of *Stomion*. Populations of *S. rugosum* and *S. laevigatum* have been removed from the data set. A=*denticula*, C=*longulum*, D=*galapagoensis galapagoensis*, E=*galapagoensis punctipennis*, F=*obesum*, G=*linelli*, I=*cribricollis*, J=*helopoides*.

Figure 26. Species belonging to the genus Stomion. From Van Dyke, 1953. a. S. galapagoensis galapaagoensis; b. S. helopoides; c. S. cribricollis; d. S. longulum; e. S. laevigatum; f. S. linelli; g. S. longicornis; h. S. rugosum. Scale=4x.

Figure 27. Scanning electron micrographs of the head and pronotum (18x), and the elytra disc (300x). Inset: pronotal disk, 100x. A,B: S. cribricollis; C,D: S. galapagoensis galapagoensis; E,F: S. galapagoensis punctipennis.

Figure 28. Scanning electron micrographs of the head and pronotum (18x) and the elytra disc (300x). Inset: pronotal disk, 100x. A,B: S. helopoides; C,D: S. laevigatum; E,F: S. linelli linelli.

Figure 29. Scanning electron micrographs of the head and pronotum (18x) and the elytra disc (300x). Inset: pronotal disk, 100x. A,B: S. linelli leleupi; C,D: S. longicornis; E,F: S. longulum.

Figure 30. Scanning electron micrographs of the head and pronotum (18x) and the elytra disc (300x). Inset: pronotal disk, 100x. A,B: S. obesum; C,D: S. rugosum; E,F: S. denticula.

Figure 31. Scanning electron micrographs of the range in tooth development on the right mandible (80x). A. S. galapagoensis galapagoensis, B. S. helopoides, C. S. longulum, D. S. denticula.

Figure 32. Average individual heterozygosities for 35 populations of Stomion based on eight polymorphic loci.

Figure 33. Geographical variation among 35 populations of Stomion at the Pgi locus. Sections of the pie represent the proportion of that allele in the population.

Figure 34. Geographical variation among 35 populations of Stomion at the Got-s locus. Sections of the pie represent the proportion of that allele in the population.

Figure 35. Scaling in two dimensions of Roger's similarity of 35 populations of Stomion.

a. Populations are clustered by species:

S. denticula J
S. galapagoensis galapagoensis D, S, h
S. galapagoensis punctipennis G, H, N
S. helopoides V, W
S. laevigatum I, T, Z, a, c
S. linelli B, E, L, O, U, b, i
S. longulum F, P, Q, e, f, g
S. obesum A, K, M, X
S. rugosum C, R, Y

b. Populations are clustered by island:

major islands	satellites
-----	-----
Española G, H, N	
Floreana D, h	Gardner S
Genovesa J	
Isabela P, Q, T, c, g	Tortuga K
Pinta R, Y	
Rabida b	
Marchena C	
San Cristóbal V, W	
Santa Cruz F, O, U, X, Z, e, f	Baltra E
	Caamaño a
	Eden L
	Seymour i
Santa Fé A, M, X	
Santiago I	Bartolomé B

Figure 35a.

Figure 35b.

Figure 36. Scaling in two dimensions of Roger's similarity of 35 populations of Stomion.

a. Populations are clustered by morphological types:

punctured D, G, H, J, N, S, V, W, h
ridged A, C, F, K, M, P, Q, R, X, Y, e, f, g
smooth B, E, I, L, O, T, U, Z, a, b, c, d, i

b. Populations are clustered by body size and shape:

group 1 (broad) B, D, E, G, H, J, L, N, O, S, U, V, W, h
group 2 (long, narrow) A, C, F, I, K, M, P, Q, R, T, X, Y,
Z, a, c, e, f, g

Figure 36a.

Figure 36b.

Figure 37. Genetic identities within and between species of Stomion.

Figure 39. Nei's genetic distances between species of Stomion and a reference species (LIDO) plotted against the inferred geological age of the species in million of years (MY).

Figure 40. Distance-Wagner tree of 16 populations of Stomion based on a Roger's genetic distance matrix. Species are labelled with morphological type (P=punctured, R=ridged, S=smooth) and body shape (group 1= broad, group 2= long, narrow).

Solution tree number 1

Appendix 1. Four tied UPGMA trees produced from a similarity matrix of a reduced set of qualitative characters of Stomion and other Trimytini.

Solution tree number 2

Appendix 1, continued.

Solution tree number 3

Appendix 1, continued.

Solution tree number 4

Appendix 1, continued.

	1.000	2.000	3.000	4.000	5.000	6.000
1.000	18	0	1	0	0	2
2.000	0	31	0	0	0	0
3.000	1	0	24	0	0	0
4.000	0	0	0	17	0	0
5.000	0	0	0	1	28	0
6.000	1	0	0	0	0	19
7.000	0	0	0	1	2	3
8.000	0	1	0	0	1	1
9.000	0	0	2	0	0	0
10.000	0	0	0	0	0	0
TOTAL	20	32	27	19	31	25

	7.000	8.000	9.000	10.000	TOTAL
1.000	0	0	0	0	21
2.000	0	0	0	0	31
3.000	0	0	4	0	29
4.000	1	0	0	2	20
5.000	0	0	0	0	29
6.000	0	0	0	0	20
7.000	13	0	0	1	20
8.000	2	25	0	0	30
9.000	0	0	16	0	18
10.000	0	0	0	8	8
TOTAL	16	25	20	11	226

Appendix 4. Table of group (ROWS) by predict (COLUMNS).

1= *S. denticula*, 2= *S. rugosum*, 3= *S. longulum*, 4= *S. galapagoensis galapagoensis*, 5= *S. galapagoensis punctipennis*, 6= *S. obesum*, 7= *S. linellii*, 8= *S. laevigatum*, 9= *S. cribricollis*, 10= *S. helopoides*.

	1.000	2.000	3.000	TOTAL
1.000	34	10	6	50
2.000	5	55	18	78
3.000	7	4	87	98
TOTAL	46	69	111	226

Appendix 5. Table of group (ROWS) by predict (COLUMNS). 1= smooth, 2= punctured, 3= ridged

	1.000	2.000	TOTAL
1.000	85	13	98
2.000	11	117	128
TOTAL	96	130	226

Appendix 6. Table of group (ROWS) by predict (COLUMNS). 1= BROAD, 2= NARROW.

Pop	1	2	3	4	5	6	7	8	
1 SFEB	*****								
2 MARC	.176	*****							
3 BALT	.100	.300	*****						
4 BARR	.092	.259	.089	*****					
5 BGAR	.089	.290	.104	.095	*****				
6 MANZ	.114	.350	.092	.073	.026	*****			
7 PESP	.017	.204	.086	.075	.060	.092	*****		
8 GENO	.018	.224	.097	.109	.084	.092	.023	*****	
9 TORT	.065	.253	.088	.158	.149	.134	.073	.037	
10 NVIL	.079	.209	.089	.090	.073	.120	.040	.107	
11 GARD	.080	.217	.132	.114	.159	.195	.096	.067	
12 TAGU	.044	.261	.075	.075	.121	.105	.054	.025	
13 LIDO	.160	.363	.125	.128	.057	.067	.150	.159	
14 PINT	.084	.116	.195	.181	.194	.247	.082	.104	
15 DAPH	.113	.289	.026	.042	.103	.095	.084	.104	
16 FLBB	.037	.184	.117	.074	.135	.173	.053	.032	

Pop	9	10	11	12	13	14	15	16	
9 TORT	*****								
10 NVIL	.139	*****							
11 GARD	.099	.155	*****						
12 TAGU	.004	.122	.098	*****					
13 LIDO	.170	.134	.199	.160	*****				
14 PINT	.151	.115	.153	.135	.299	*****			
15 DAPH	.112	.075	.163	.099	.143	.188	*****		
16 FLBB	.067	.124	.012	.062	.197	.112	.130	*****	

Appendix 7. Nei's genetic distance matrix of 16 populations of Stomion.

END

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FIN