Incipient non-adaptive radiation by founder effect?
Oliarus polyphemus Fennah, 1973 – a subterranean model case.
(Hemiptera: Fulgoromorpha: Cixiidae)

Dissertation

zur Erlangung des akademischen Grades

doctor rerum naturalium

(Dr. rer. nat.)

im Fach Biologie

eingereicht an der

Mathematisch-Naturwissenschaftlichen Fakultät I

der Humboldt-Universität zu Berlin

von

Diplom-Biologe Andreas Wessel
geb. 30.11.1973 in Berlin

Präsident der Humboldt-Universität zu Berlin
Prof. Dr. Christoph Markschies

Dekan der Mathematisch-Naturwissenschaftlichen Fakultät I
Prof. Dr. Lutz-Helmut Schön

Gutachter/innen:
1. Prof. Dr. Hannelore Hoch
2. Prof. Dr. Dr. h.c. mult. Günter Tembrock
3. Prof. Dr. Kenneth Y. Kaneshiro

Tag der mündlichen Prüfung: 20. Februar 2009

Incipient non-adaptive radiation by founder effect?
Oliarus polyphemus Fennah, 1973 – a subterranean model case.
(Hemiptera: Fulgoromorpha: Cixiidae)

Doctoral Thesis

by

Andreas Wessel

Humboldt University Berlin
2008

Dedicated to Francis G. Howarth,
godfather of Hawai'ian cave ecosystems,

and

to the late Hampton L. Carson,
who inspired modern population thinking.

Ua mau ke ea o ka aina i ka pono.

Zusammenfassung

Die vorliegende Arbeit hat sich zum Ziel gesetzt, den Populationskomplex der hawai'ischen Höhlenzikade *Oliarus polyphemus* als Modellsystem für das Studium schneller Artenbildungsprozesse zu erschließen. Dazu wurde ein theoretischer Rahmen aus Konzepten und daraus abgeleiteten Hypothesen zur Interpretation bekannter Fakten und Erhebung neuer Daten entwickelt. Im Laufe der Studie wurde zur Erfassung geografischer Muster ein GIS (Geographical Information System) erstellt, das durch Einbeziehung der historischen Geologie eine präzise zeitliche Einordnung von Prozessen der Habitatsukzession erlaubt. Die Muster der biologischen Differenzierung der Populationen wurden durch morphometrische, ethometrische (bioakustische) und molekulargenetische Methoden erfasst.

Die Untersuchungen ergaben das folgende Muster, welches im Hinblick auf die zu Grunde liegenden Prozesse zu interpretieren war: Auf Hawai'i Island kommen Populationen der weit verbreiteten und stark troglomorphen *Oliarus polyphemus* in jungen Höhlen mit einem abgestuften Alter von 38 bis etwa 1.000 Jahren vor (mit der Ausnahme von Pink Pistillaria Cave mit einem Alter von etwa 8.000 Jahren). Der Populationskomplex stellt sich in genetischen Analysen als Monophylum dar; die Verbreitung über das untersuchte Gebiet hat in den letzten 10.000 Jahren subterran im Anschluss an eine einmalige evolutionäre Transformation zur troglobionten Lebensweise stattgefunden. Die untersuchten Populationen sind bezüglich der Morphologie und noch mehr des Verhaltens so stark voneinander differenziert, dass sie in 13 Fällen als eigene Unterarten und in vier Fällen sogar als eigene Arten hypothetisiert werden. Die Mittelwerte der phänotypischen Differenzierungen zeigen weder eine Korrelation mit der geografischen Distanz der Höhlen zueinander noch eine klinale Verteilung. Keine der untersuchten morphologischen oder ethologischen Unterschiede lassen sich als irgendwie geartete Anpassungen an Unterschiede in den Habitaten interpretieren. Die Variabilität der Ausprägung der Merkmale ist jedoch negativ mit dem Alter der Höhlen korreliert. Die Verbreitung von *O. polyphemus s.l.* erfolgt wahrscheinlich über ungerichtetes individuelles Migrationsverhalten, einzelne oder sehr wenige Individuen fungieren als Gründer neuer Populationen, die voneinander separiert sind. Somit ist das Alter der Höhlen auch als maximales Alter für den Genpool der dort lebenden Populationen anzunehmen.

Die nicht-adaptive Differenzierung der Populationen kann durch eine Folge von Gründereffekten nach dem „Founder flush"-Modell von H. L. Carson erklärt werden. Zur Veranschaulichung und zum Verständnis des Mechanismus wurde dieses verbale Modell unter Verwendung der bildlichen Metapher der adaptiven Landschaft als „Peak move" (Gipfelverschiebung) im Gegensatz zum klassischen

Mechanismus des „Peak shift“ (Gipfelwechsel) interpretiert. Dieser „Peak move“ kommt durch die Ausbildung eines adaptiven Plateaus während der ersten Phase des „Founder flush“ durch stark verminderte sexuelle Selektion, die anschließende freie „Besiedlung“ dieses Plateaus und letztendlich den Zusammenbruch der (effektiven) Population und damit des Plateaus zustande. Die erneute Ausbildung eines Gipfels erfolgt mit einer bestimmten Wahrscheinlichkeit an anderer Stelle in der adaptiven Landschaft als bei der Elternpopulation – eine Gipfelverschiebung ist das Ergebnis.

Die genetische Differenzierung der Populationen passt zur Interpretation der Ausbreitung des *O. polyphemus s.l.*-Komplexes mit der Entstehung der neuen Höhlenhabitate während der letzten 10.000 Jahre. Allerdings sind die Substitutionsraten um bis zu 100-fach höher, als für die entsprechenden „molekularen Uhren“ durchschnittlich angenommen. In Übereinstimmung mit neueren Studien ist dies durch die Aufeinanderfolge von tausenden Gründerereignissen mit anschließenden Gründereffekten zu erklären.

Selbst bei konservativen Annahmen zur Entstehung von *O. polyphemus s.l.* (d.h. bei Annahme des Alters von Hawai’i Island als Alter des Gesamtkomplexes) gehören die sich ergebenden Differenzierungs- bzw. Speziationsraten zu den schnellsten bekannten; beim Ansetzen von realistischen Szenarien finden wir hier den mit Abstand schnellsten Radiationsprozess, der für Arthropoden dokumentiert ist.

Contents

Vorwort

Die Evolutionsbiologie, d.i. die Gesamtheit der evolutionsbiologisch arbeitenden Wissenschaftler, sieht sich stetig vor der Aufgabe ihren Gegenstand und ihre Methoden zu bestimmen. Dieser Prozess ist nicht kontinuierlich und geradlinig, er verläuft vielmehr in Phasen und mit Sprüngen, der Weg ist gepflastert mit hitzigen Debatten, manche im Nachhinein kaum noch verständlich. Wer aufmerksam zurückschaut sieht Sackgassen und Umwege und kann aus dieser Rückschau vieles für die Bewertung der heutigen Erfolge und Triumphe lernen. So manche Erkenntnis muss mehrfach gefunden werden, um Wirkung auf diesen Prozess auszuüben. Die heutige, an Triumphen so reiche Wissenschaft, muss sich um so dringender von Zeit zu Zeit ihrer geistigen Grundlagen versichern. Nur durch den Blick zurück ist ein souveränes Vorwärtsschreiten möglich.

Die Evolutionsbiologie droht sich derzeit zu verlieren zwischen kritik- und distanzloser Methodeneuphorie und Verengung des theoretischen Blickes auf ihre Grundlagen. Molekulare Analytik hat von evolutionsökologischen bis hin zu systematisch-taxonomischen Studien Einzug gehalten und verspricht, viele ihrer Probleme zu lösen. Es ist jedoch eine Illusion, dass eine neue Methodik das Verständnis des Lebendigen vereinfachen würde, da doch die Komplexität Kennzeichen des Lebens selbst ist. Wir schauen nur etwas tiefer hinein – und sehen mehr Fragen als je zuvor. Auf der anderen Seite hat sich eine mathematische Biologie das Prädikat einer Theoretischen Biologie exklusiv zugeeignet, ohne dass ein fundierter Paradigmenwechsel stattgefunden hätte. Entfernt davon, die Verdienste eines mathematisch-kybernetischen Ansatzes geringzuschätzen, muss die Arbeit an einer umfassenden Theorie der Biologie, die im Kern eine Entwicklungstheorie ist, jedoch auf einer breiten philosophischen Grundlage erfolgen.

Erfolgreiche evolutionsbiologische Arbeit kann, wie alle Wissenschaft, nur durch theoriebasierte Beobachtung und Experiment erfolgen, welche durch strenge Prüfung klar formulierter Hypothesen auf die Theorie zurückwirken. Es gibt keine objektive Datenanalyse oder Datenakkumulation ohne Vorannahmen, die automatisch zur Erkenntnis führt. Ebensowenig können theoretische Ansätze fruchtbar werden, die nicht von Anfang an von intimen Wissen um reale biologische Systeme getragen werden. Ein theoretisch arbeitender Biologe muss halt auch einmal eine "Tiefenbohrung" absolviert haben und "seine Viecher" kennen.

Unabhängig vom Fortschreiten der theoretischen Evolutionsbiologie an ihren Rändern ist es ebenso eine Herausforderung und Notwendigkeit für den Zusammenhalt der Biologie als eigenständiger Disziplin, allen Biologen bestimmte Grundeinsichten mit Nachdruck zu vermitteln. Leben existiert nur in Form von einzelnen Lebewesen, die allesamt, so sie heute noch existieren, Ergebnis eines vier Milliarden Jahre langen, ununterbrochene, unumkehrbaren, einmaligen und unwiederholbaren Prozesses sind. Evolutiver Wandel findet auf der Ebene von Populationen statt, die Annahme einer "zweite Evolution" oder Makroevolution ist zur Erklärung des evolutiven Wandels nicht nötig und damit metaphysisch. Die komplexen Prozesse, die zur Vielfalt und Angepasstheit des Lebendigen geführt haben sind so vielfältig wie das Lebendige selbst, wer hofft einfache Regeln oder gar Gesetze zu finden, wird scheitern. Bezüglich der Frage nach der Entstehung der Arten, werden wir akzeptieren müssen, dass jeder Speziationsvorgang einmalig ist, nicht nur historisch gesehen, sondern auch in Bezug auf die spezifischen Mechanismen; wie können also nur Konzepte suchen, die uns im Verständnis dieser Prozesse – an deren einem Ende auch wir selbst stehen – helfen.

Die vorliegende Arbeit soll in ihrem Herangehen an diese Fragen beispielhaft sein. Im Ergebnis wird ein neues Modellsystem erschlossen und Konzepte formuliert, getestet und modifiziert. Ziel ist es nicht Fragen zu beantworten, sondern sie in der Folge präziser stellen zu können. Falls es in dieser Studie trotzdem gelingen sollte einige Fragen zu klären, so werden sich jeweils Dutzende neuer ergeben.

A.W. Ternate, 19. September 2005

Foreword

Scientists working in the field of evolutionary biology are constantly facing the task of defining the scope of their subject as well as its methods. This process is neither continuous nor linear, but rather erratic, and frequently accompanied by animated debates, the point of which may seem – with the benefit of hindsight – enigmatic. An attentive observer looking back in time will discover dead ends and detours, and may learn a good deal from such retrospective to aid him in judging the successes and triumphs of today. In order to influence this process, some insights have to be gained several times independently. Present-day science is rich in triumphs, thus even increasing the need to occasionally remind itself about its conceptual background. A confident progress can only be achieved by looking back.

Current evolutionary biology is in danger of being eroded between an uncritical euphoria about new methods and a narrow theoretical perspective on its fundamental concepts. Molecular analyses have become a standard tool for studies ranging from evolutionary ecology to systematics and taxonomy, and hold the promise of solving many current problems. However, the hope that new methods will simplify the comprehension of life is but an illusion, as complexity is inherent to life itself. They just help us to take a better look – which inevitably results in an even higher number of questions. On the other hand the entire field of theoretical biology is now exclusively associated with ‘mathematical biology’, without a fundamental change of the prevailing paradigms, though. While the merits of this mathematical-cybernetic approach should not be easily disregarded, a wider philosophical fundament must be aimed at for making progress towards a more universal theory of biology, which is basically a theory of development in the widest sense of the word.

Successful studies in evolutionary biology do progress, as does all of science, by observations and experiments conducted within a theoretical framework. They may, through a strict assessment of clearly stated hypotheses, re-assert influence on the underlying theory. There is no objective assumption-free analysis or accumulation of data, which automatically leads to new perceptions. Just as little may be expected from theoretical approaches which lack a solid fundament of knowledge about real biological systems. There is no way even for a theoretical biologist to avoid getting at least once a thorough dose of practical experience and knowing ‘his critters’.

Independent of the progress of theoretical evolutionary biology at its margins, the challenge and necessity to impress certain fundamental issues upon all biologists, if biology is to remain a distinct and unified scientific discipline, remains: life only exists in individual organisms, all of which – provided they made it – are the result of a four billion year long, unbroken, irreversible, unique and unrepeatable process. Evolutionary change takes place on the population level; consequently it is unnecessary and metaphysic to invoke a 'second evolution' or macroevolution in order to explain it. As the complex processes, which have produced the diversity and adaptation evident in the living world, are no less diverse than life itself, attempts to discover simple rules or even laws will remain futile. With respect to the origin of species we will have to accept that each speciation process is unique, not just historically but also concerning the specific mechanisms involved; we can only seek concepts, thus, which will improve our understanding of these processes – we ourselves are but one of their results.

This study is intended to exemplarily address these questions. In its course a new model system has been established, and concepts are formulated, tested and modified. The aim here is not to provide definite answers, but rather to allow the more precise posing of questions. Even if this study should succeed to gain some answers, each of these is certain to give rise to a dozen new questions.

A.W. Ternate, September 19, 2005

1 Introduction – the question and the model system

> Nachdem die grosse Idee der Entwicklung in Bezug auf die organische Welt einmal durchgedrungen, die fruchtbare Hypothese der Descendenzlehre in die Wissenschaft als berechtigt aufgenommen worden ist, steht jetzt neben zahlreichen andern und grossen Aufgaben vor Allem auch diejenige vor unsern Blicken, die Ursachen zu erforschen, welche die Umwandlung einer organischen Form in die andere hervorrufen, festzustellen, wie weit dabei innere und wieweit äussere Momente mitwirken, sie zu sichten und den Einfluss eines jeden möglichst rein für sich zu bestimmen.
>
> August Weismann (1872: III)

The aim of this study is to contribute towards solving the "mystery of mysteries" (Darwin 1859: 1)[1]: the origin of new species or more precisely the process of diversification in the course of evolution. Almost 150 years after Darwin's statement, the plethora of existing opinions and partial answers to this problem render the situation more confusing and more complicated than ever, despite a multitude of new data. Given the immense complexity of the underlying question this confusion is perhaps inevitable, and it is probably unreasonable to expect simple answers.

However, a considerable amount of the apparent intractability of the problem of speciation is due to the inconsistent use (or rather abuse) of concepts. The very same term may, in extreme cases, convey as many meanings and hypotheses as there are people employing it. A good and relevant example in the context of this study is the so-called 'founder effect'. Consequently, here it is considered an obligatory prerequisite to review and precisely define terms that have been vaguely used in the literature.

Beyond these semantic issues, a more fundamental point is to overcome the sheer accumulation of data, which obviously cannot in itself answer any question relevant to the understanding of speciation. The establishment of a conceptual framework within which observations and experiments can be placed or conducted, and comparisons made, is here regarded as the only possible approach (following Mayr 1988).

---

[1] In contrast to general opinion, this famous sentence was not coined by Darwin. He mentioned "[...] the origin of species – that mystery of mysteries, as it has been called by one of our greatest philosophers." (Darwin 1859: 1), without giving a name. However, in Notebook E, this entry made around December, 1838 is found: "Herschel calls the appearance of new species. the mystery of mysteries. & has grand passage upon problem.! Hurrah. –" (Barrett et al. 1987: 413). Sir John F.W. Herschel again wrote in a letter to Charles Lyell in February, 1836 cited by Charles Babbage: "[...] of course I allude to that mystery of mysteries, the replacement of extinct species by others." (Babbage 1838: 226.)

While the study of complex systems through an investigation of isolated parts thereof is obviously the only feasible and practical approach, the mere addition of the results does not necessarily add up to an accurate picture of the whole system, as observed by Mayr:

> “Systems at each hierarchical level have two properties. They act as wholes (as though they were a homogeneous entity), and their characteristics cannot be deduced (even in theory) from the most complete knowledge of the components, taken separately or in other combinations. In other words, when such a system is assembled from its components, new characteristics of the whole emerge that could not have been predicted from a knowledge of the constituents.” (1988: 15)

If the study of speciation is to be conducted according to this systemic approach, a major task will be to seek model systems that are simple enough to dissect and analyse the factors determining the dynamics of the whole system without losing the ability to put the results back into the overall context.

> “Die Natur antwortet nicht, wenn sie nicht gefragt wird.“[2] (Popper 1934, cited after Popper 1989: 225)

This basic insight prompted one of Popper’s central verdicts:

> "*Es gibt keine reinen* Beobachtungen: sie sind von Theorien durchsetzt und werden von Problemen und von Theorien geleitet." (Popper 1968, cited after Popper 1989: 76).

Consequently, the precise formulation of questions or hypotheses, which can be approached by studying a suitable model system, should precede any attempt to tackle complex problems in evolutionary biology, and indeed all scientific disciplines. This aim is adhered to in this study, which may not necessarily provide definite answers to all questions introduced below, but rather seeks to establish the Hawai'ian cave planthoppers as a suitable model system in the sense outlined above for research on genetic change, speciation, and adaptation.

---

[2] “[...] nature does not give an answer unless pressed for it.” (Popper 1959: 280)

1.1 Theoretical framework

1.1.1 Genetic change, adaptation, and radiation

Research on speciation is on the rise, and the discussion of theories or hypotheses is becoming increasingly vivid (see e.g. Barton 2001, Coyne & Orr 2004). However, speciation is frequently debated without much reflection, not to mention consent on the units involved in this process, i.e. species (Hey et al. 2003). The overlap in the scientific community of those discussing species concepts, and those working on speciation, is rather limited, resulting in widespread confusion and misconceptions. A more general approach, which avoids entering the contentious issue of species, is to focus on genetic change within populations. Here, a major aim is to understand under which circumstances co-adapted gene complexes can be broken up and reassembled, or to phrase it in Wrightean terms, how (adaptive) peak shifts occur (Wright 1931, 1932, 1937, 1988).

Nevertheless, the objects of this study are species or subspecies, and the terms are used in the sense of Mayr (1940, 1942; for subspecies Mayr & Ashlock 1991). Mayr's Biological Species Concept (BSC), earlier also known as Isolation Concept, is the concept explicitly or implicitly used by the vast majority of evolutionary biologists outside the realm of taxonomy (Avise 2000). Following Mayr, species are real entities in nature (at least if applied to bisexually reproducing organisms). They are characterized by the exclusive ability of their members to maintain genetic exchange, i.e. they are reproductively isolated relative to other species. On a more general level, Biological Species may be regarded as "individuals" (for discussion of the 'species-as-individual'-concept see Löther 1972, Hull 1976, Ghiselin 1988) in the sense of being the hierarchical level above the organism, with systemic properties extending beyond those gained by the mere addition of its constituents (so-called 'bio-systems').

According to Mayr (1942, 1963), the multiplication of species is largely dependent on extrinsic factors, basically geographic separation followed by genetic drift resulting in genetic incompatibility (reproductive isolation) as a by-product of independent evolution. Implicitly, this classical view of allopatric speciation contains the notion of adaptive differences between species as a consequence of the variations in the environment, which in the case of geographical separation are always present to a varying degree; the sole exception being Mayr's (1954) theory of founder effects and genetic revolutions. In accordance with this view of adaptive speciation, almost all radiations have, at least implicitly, been regarded as adaptive radiations (Schluter 2000; for a discussion of non-adaptive radiation see Gould 1984, Gittenberger 1991, 2004, Sudhaus 2004).

While the BSC is the most widely accepted species concept, its applicability has always been a contentious issue even among its supporters. A necessary distinction must be made between the concept of the BSC, as briefly sketched above, and the criteria used in practice to recognise biological species (Mayr & Ashlock 1991). Rarely can the only criterion directly arising from the concept as such – the inability to successfully reproduce between individuals of non-conspecific taxa – be applied in nature. The methodological problems inherent to this approach prohibit any employment on organisms that are not easily observable in their natural environment. In the case of allopatric populations, the criterion of reproductive isolation is not applicable at all. Consequently, circumstantial evidence has to be used to estimate the presence and degree of reproductive isolation in the vast majority of studies. The criteria to judge how the available data fit the assumption of the existence of biological species are, however, vaguely defined. Morphological characters are widely used, and a certain degree of discontinuous dissimilarity is usually taken to as an indication of reproductive incompatibility, as e.g. elaborated by Remane (1968) in his proposal for a 'statistic species criterion' (Wessel & Hoch 1999). The exact amount of difference necessary to accept the hypothesis of a biological species is essentially self-defined by an individual researcher, which in turn makes it exceedingly difficult to compare the results of any two treatments of species – especially in allopatric situations – by different authors.

In recognition of this problem, an effort has been made in this study to employ an objective criterion to evaluate hypotheses on the species-status of (allopatric) populations. In the approach followed here, which seems especially suitable for the situation encountered in the Hawai'ian model system, earlier attempts to make use of morphometric data by a statistic criterion (Mayr et al. 1953, Remane 1968) have been extended and formalized (Wessel & Hoch 1999).

The importance of small populations in the formation of species[3] has been discussed since speciation by geographic isolation was proposed as the major process leading to the origin of new species[4] (Wagner 1868, 1870, 1889, see

---

[3] "Die Bildung einer wirklichen Varietät, welche Herr Darwin bekanntlich als 'beginnende Art' betrachtet, wird der Natur nur da gelingen, wo wenige Individuen die begrenzenden Schranken ihres Standortes überschreitend sich von ihren Artgenossen auf lange Zeit räumlich absondern können." (Wagner 1868: 20)

[4] "Das Darwin'sche Buch gibt uns keinen bestimmten Aufschluss weder über die äussere Ursache, welche zu einer Steigerung der gewöhnlichen individuellen Variabilität, also zur beginnenden Zuchtwahl den ersten Anstoss gibt, noch über die Bedingung, welche neben einem gewissen Vortheil in der Concurrenz des Lebens die Erhaltung der neuen Merkmale nothwendig macht. Diese Bedingung erfüllt nach meiner Überzeugung allein die freiwillige oder passive Wanderung der Organismen und die von den orographischen Verhältnissen wesentlich abhängi-

review in Mayr 1982: 562 ff.). Weismann (1872, 1902) probably was the first to emphasize the effect of the random sampling of genetic variation present in an entire population by founder individuals[5], and thus, the first to outline the principle of a founder effect, without formally naming it. The classical founder effect concept was developed by Mayr (see Fig. 1, 1954, 1963, see also Futuyma 2006). The main factor for the transforming effect in his model is the reduced and arbitrary sample of the total genetic variation in the population of origin carried by the founders, and the consequently increased homozygosity even in alleles that are rare in the entire population. Subsequently, the altered genetic environment could cause so-called genetic revolutions, i.e. a break-up and reorganization of co-adapted gene complexes (Mayr 1954).

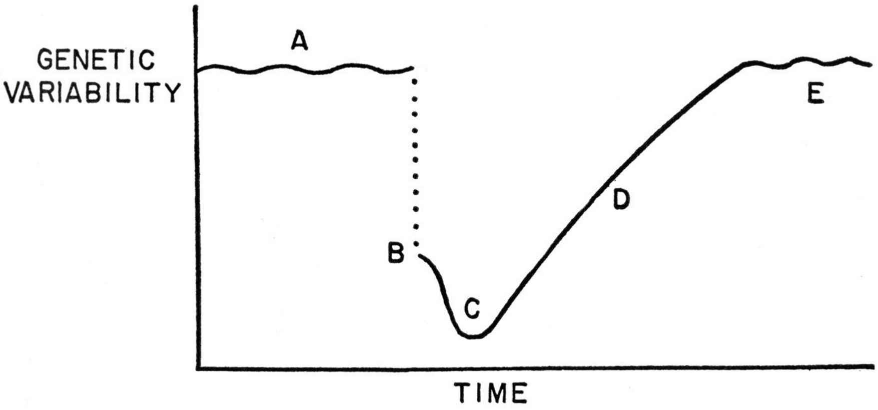


Figure 1. Change of genetic variability in a natural population passing a genetic bottleneck (From Mayr 1954: 174).

---

ge Bildung isolirter Colonien, welche unter günstigen Umständen die Heimat einer neuen Species begründen." (Wagner 1868: 4)

[5] "[...] ob Isolirung allein für sich schon zur Bildung neuer Formen führen kann, oder vielleicht sogar führen muss, wäre jetzt zunächst zu untersuchen. [...] in der That [kann] unter günstigen Umständen die einzelne Variation einer Art zur Stammmutter einer Lokalvariätet werden, falls sie auf isolirtes Gebiet geräth. Gesetzt eine Insel hätte noch keine Tagfalter, und es würde nun eines Tages ein normales befruchtetes Weibchen einer Art vom Festland aus durch Stürme dorthin getrieben, fände geeignete Lebensbedingungen dort vor, legte ihre Eier ab und würde so zur Gründerin einer Kolonie, so läge in der Verhinderung steter Kreuzung dieser Kolonie mit der festländischen Stammart an und für sich noch kein Grund dafür, dass die Kolonie zu einer Varietät sich umbilden sollte. Gesetzt nun aber, die betreffende Gründerin der Kolonie wiche in irgend einer bedeutungslosen Kleinigkeit der Zeichnung, wie sie durch Germinalselektion entstehen kann, von der Stammart ab, so würde sie diese Variation auf einen Theil ihrer Brut vererben, und es würde damit die Möglichkeit gegeben sein, dass auf der Insel eine Varietät sich festsetzte, die das Mittel aus den Charakteren der überlebenden Nachkommen sein müsste. Je mehr die Abweichung unter den ersten Nachkommen der Stammmutter überwöge, und je stärker diese abweichende Variationsrichtung wäre, um so grösser wäre auch die Aussicht, dass sie sich weiter fortsetzte und als eine erkennbare Abweichung von der Zeichnung der Stammart erhielte. Ich habe das damals die Wirkung der Isolirung durch Amixie genannt, d. h. durch die blosse Verhinderung der Kreuzung mit den Artgenossen des Stammgebietes." [Accentuations by the author] (Weismann 1902, II, pp. 320-321; see also Weismann 1872)

Mayr’s concept has been widely discussed and accepted, although, only for singular events, and it is largely considered to be of no general importance for the majority of evolutionary processes leading to diversification; see e.g. the textbooks by Futuyma (1998) and Strickberger (2000).

Three major criticisms have been leveled at the founder effect concept (see e.g. Barton & Charlesworth 1984): (i) Genetic studies have revealed the extraordinary carrying capacity for genetic variability by just a few individuals of a species. Nei et al. (1975), for instance, have calculated from allozyme frequencies that a single gravid female can carry about 65% of the total variability present in the parent population. In order to fulfil the requirements of the Mayr’s model, the number of founding individuals therefore must be exceedingly small and, moreover, persist at this level for several generations (MacArthur & Wilson 1967, Barton & Charlesworth 1984). (ii) As the founding population is subject to strong selection, a peak-shift is improbable in alleles that are directly influencing fitness. (iii) Finally, it is hardly possible to distinguish the impact of population bottlenecks – in small founder populations – from the effect of isolation, environmental differences, and genetic drift in moderately sized populations (Barton & Charlesworth 1984). However, as succinctly pointed out by Mayr:

> "The real problem of speciation is not how to produce difference but rather to escape from the cohesion of the gene complex". (1963: 518)

In recognition of this problem, Hampton L. Carson (1968, 1975, extended by Templeton 1980, Carson & Templeton 1984) developed a founder effect concept, which is much more explicit in explaining the mechanism of a successful shift of the balanced genotype in founder populations. Carson’s model focuses not only on the founder event itself, but considers the population development and structure before as well as after the event.

Accepting Carson's ‘founder flush’ concept, we expect to find a strong increase of variability during the process of rapid population growth (the ‘founder flush’, Fig. 2b→c, Fig. 3a→c) after a founder event (Fig. 2a) and the corresponding bottleneck (Fig. 2b, Fig. 3a). This increase in variation is the result of relaxed selection, especially on sexual traits. With further population growth and the accompanying increase in population density, strong selection is resumed (Fig. 2c, symbolized by the arrow, Fig. 3b→c) and the population collapses (Fig. 2c→d). The break-up of some co-adapted gene complexes in the founder flush phase and random processes can cause the state of some characters in the now stabilized population to differ significantly from those of the parental population (Fig. 2d) (Carson & Templeton 1984).

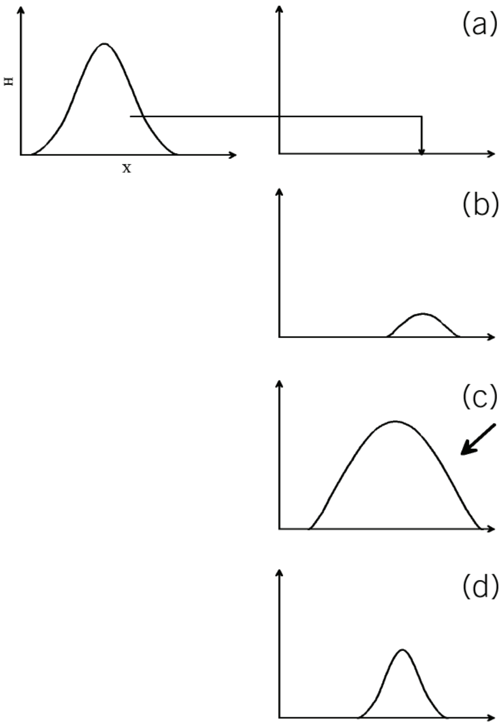


Figure 2. Development of variability in a parameter (x) in a founder population as proposed by the 'founder flush' concept (H = frequency; see text for further explanations).

As illustrated in Fig. 3, the proposed population collapse is not a decrease in the census population size, but rather a collapse of the effective population size after strong sexual selection has resumed and random mating is replaced once more by assortative mating (Fig. 3b→d). Consequently, Carson's concept can only be tested using a natural population with an undisturbed mating system. Moreover, the failure to recognize this requirement has resulted in the repeated failure of attempts to test it in the laboratory (see e.g. Moya et al. 1995, Rundle et al. 1998, but compare Powell 1978, Dodd & Powell 1985, Meffert & Bryant 1991 and, for review, Carson 2003, Kaneshiro 2006, Ritchie 2007, Simoes et al. 2008).

An ideal model system to test founder effect concepts must be simple enough to distinguish between the influence of all factors involved. Based on natural populations, it should contain repeated events ('natural experiments') under similar conditions, and it must be possible to assay all relevant biotic and abiotic factors.

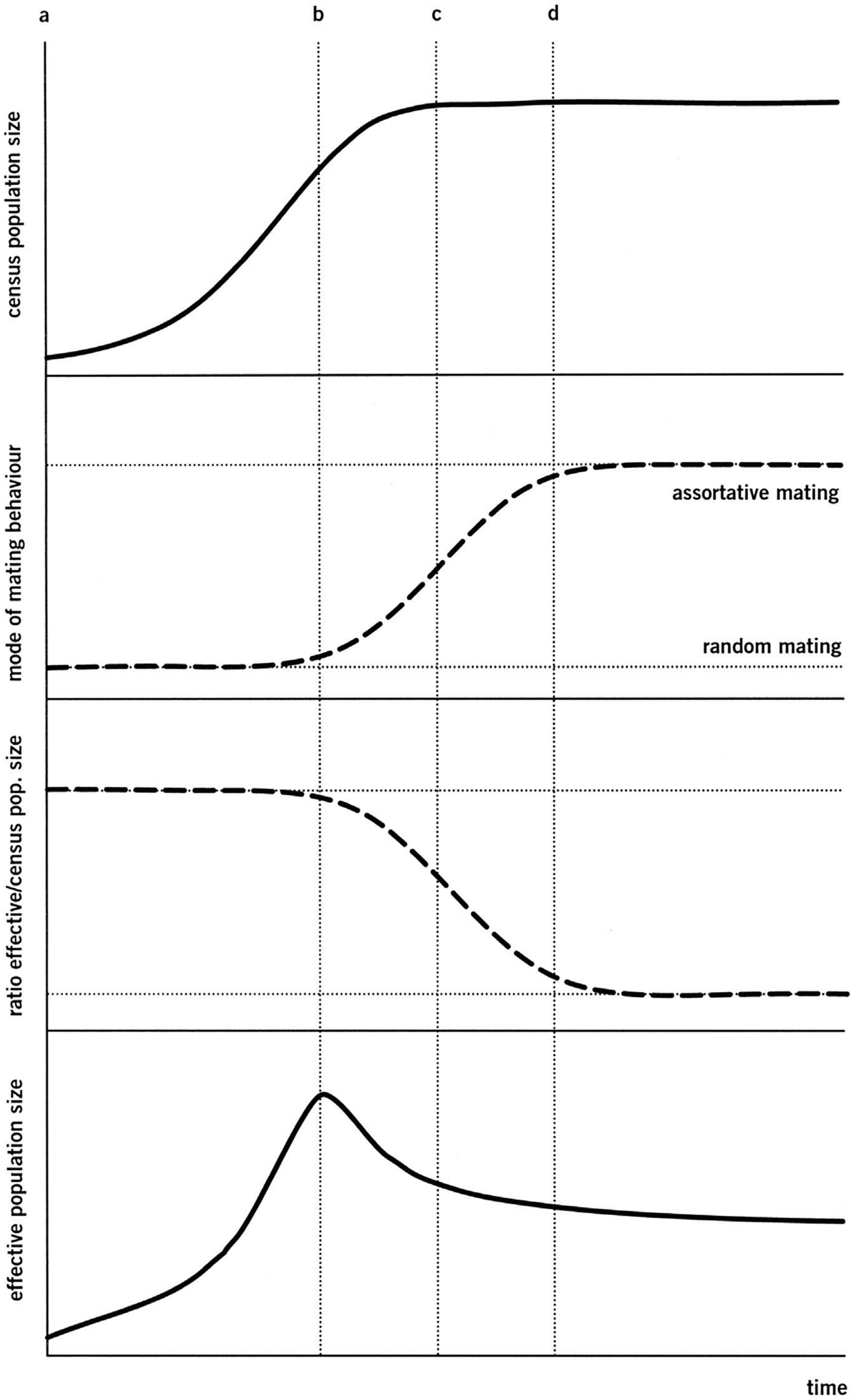


Figure 3. Development of effective population size in relation to census population size in a founder population as proposed by the 'founder flush' concept (see text for further explanations).

1.1.2 Acoustic behaviour and biosystematics

> And now, my friend, what adorable wisdom, what consummate art and skill are displayed in the admirable contrivance and complex structure of this wonderful, this unparalleld apparatus! The Great Creator has placed in these insects an organ for producing and emitting sounds, which in the intricacy of its construction seems to resemble that which he has given to man, and the larger animals, for receiving them.[6]
>
> William Kirby & William Spence (1817)

Behaviour in general is regarded as a pacemaker of evolution (Mayr 1974), as behavioural incompatibilities form the major premating barrier in species with specific courtship behaviour. In this respect, acoustic behaviour (specific song patterns) is particularly effective, and acoustic signals have long been recognized as playing a fundamental role in species recognition in a wide range of animal groups (Darwin 1871; for general reviews see e.g. Tembrock 1959, 1971, 1982/83, 1996, 2005). In recent years, the involvement of acoustic communication in speciation has received increased attention, as exemplified by studies on anurans (Littlejohn & Watson 1985, Gerhardt 1994, Gerhardt & Huber 2002, Hoskin et al. 2005), birds (Seddon & Tobias 2007, Brambilla et al. 2008, Toews & Irwin 2008), and various groups of insects: cicadas (Moore 1993, Marshall & Cooley 2000, Sueur & Aubin 2004, Popple et al. 2008); crickets (Otte 1989, Benedix & Howard 1991, Mendelson & Shaw 2005, 2006); grasshoppers (Butlin 1989, Butlin & Ritchie 1991, Bridle & Butlin, 2002). Acoustic signals can also play a role in the completion of allopatric speciation processes through reinforcement upon secondary contact, as some of these studies have revealed. Reinforcement has long been regarded as a major factor in the origin of reproductive isolation (Dobzhansky 1940). This concept has been a subject of contentious debate (Butlin 1989, 1995, Howard 1993, Noor 1993, Servedio & Noor 2003), which is now largely settled in its favour (see Ortiz-Barrientos et al. 2004).

Insects are the group with the most diverse range of acoustic communication, both in terms of signal producing organs and also the number of acoustically communicating taxa (Haskell 1961, Busnel 1963, Drosopoulos & Claridge 2006). While acoustically communicating insects are usually conceived as producers of air-borne sounds, many groups are known to use low-frequency substrate vibrations for communication, and especially (dueting)-mate attraction and inducement:

---

[6] Kirby & Spence 1817: p. 408, concerning the tymbal organ of cicadas.

Orthoptera (Busnel et al. 1955, Morris 1980), Mantophasmatodea (Eberhard & Picker 2008), Blattodea (Roth & Hartmann 1967), Plecoptera (Rupprecht 1968, Stewart et al. 1988, Stewart 1997, 2001, Stewart & Sandberg 2006), Psocoptera (Pearman 1928), Homoptera (Cocroft & McNett 2006, Strübing 2006, Strübing & Drosopoulos 2006, Tishechkin 2006, Kanmiya 2006a), Heteroptera (Gogala 1985, 2006, Cokl & Virant-Doberlet 2003, Cokl et al. 2006, Lazzari et al. 2006), Coleorrhyncha (Hoch et al. 2006b and unpublished data), Neuroptera (Henry 1979, 1982, 2006), Coleoptera (Slobodchikoff & Spangler 1979, Zachariassen 1977, Hirschberger 2001, Wessel 2006), Diptera (Mook & Bruggeman 1968, Boake & Poulson 1997, Kanmiya 2006b), Trichoptera (Ivanov & Rupprecht 1992), and Hymenoptera (Michelsen et al. 1986, Furrer & Kirchner 1990, Hrncir et al. 2006).

The Homoptera are best known for the sound producing cicadas (Cicadidae), and the song of the Mediterranean cicada was indeed already mentioned by Aristotle (based on translation by Balme 1992, see also Meyer 1855). Despite the early notoriety of these penetrating animal sounds, the mechanism of its production was disputed until the late 19th century. While an involvement of the tymbal organ was suspected since its early (repeated and independent) descriptions by Casserius (1600), Pontedera (1718), Felici (1724), Laurenti (in Zanotti 1731), and finally and best known Réaumur (1741, see also Lepori 1869), an alternative explanation was proposed by Landois (1867, 1872, 1874, see also Brauer 1868), who assumed that the sound was produced by pressing air through stigmata (so-called "Schrill-Stigmen"). Based on experimental evidence, Mayer (1877) could finally show, that the tymbal organ in combination with abdominal air sacs is the sole sound producing organ in cicadas.

Acoustic communication in smaller auchenorrhynchans was first discovered and described by Ossiannilsson (1949: Fulgoromorpha: Delphacidae, Cixiidae; Cicadomorpha: Cercopidae, Cicadellida, Ulopidae), though the responsible structure in the first two abdominal segments was noted earlier (Eggers 1937). In contrast to the large singing cicadas, these groups do not produce air-borne sounds, but use substrate borne vibration for communication (Ichikawa 1976, Strübing 1977b, Traue 1978, Michelsen et al. 1982). The morphology of the sound (vibration) producing organ in these auchenorrhynchans is similar to that of the tymbal organ of the Cicadidae and was regarded as a likely homologue (Eggers 1937, Ossiannilsson 1949), with some modifications in structure and function (see e.g. Mitomi et al. 1984 for Delphacidae). Consequently, the presence of a tymbal had long been considered an autapomorphy for the 'Auchenorrhyncha' (Fulgoromorpha and Cicadomorpha, including cicadas; Hennig 1981). Nevertheless, this view has been challenged by recent cladistic analyses combining morphological and molecular data (Bourgoin & Campbell 2002). However, the recent demonstration of the presence of a simple tymbal organ in the Coleorrhyncha (Hoch et al. 2006b) suggests that the ancestral species of at least four Hemipteran subgroups (Heteroptera, Coleorrhyncha, Cicadomorpha, Fulgoromorpha) may have already used tymbal-like structures to produce vibrational signals. This organ underwent independent refinement in the different hemipteran lineages and provided the morphological basis for the evolution of complex courtship patterns (Hoch et al. 2006b, and unpublished data).

In planthoppers, and generally in small fulgoromorphans, vibrational signals have a low frequency between 100 and 2000 Hz, with a dominant frequency between 100 and 500 Hz (de Vrijer 1984). Characteristically, the host plant provides the substrate for signal transmission (Ichikawa 1976, Bell 1980, Michelsen et al. 1982, Cocroft et al. 2006, Casas et al. 2007). In these animals, the acoustic behaviour plays an important role in mating (Strübing 1958, 1977a, Claridge 1983, 1985, 1990). The signals are crucial for species-specific recognition (Claridge 1990), and have led to the discovery of 'cryptic acoustic species' (Henry 1994), which are morphologically indistinguishable (Claridge & Reynolds 1973, Strübing 1983). Species-specificity in acoustic signals has been observed for several fulgoromorphan groups, e.g. leafhoppers (Claridge & Reynolds 1973, Claridge & Nixon 1986, Claridge 1993), planthoppers (Strübing & Hasse 1975, Booji 1982, den Bieman 1986, de Vrijer 1986, Claridge et al. 1985a, 1988), and treehoppers (Rodriguez et al. 2004).

The potential value of behaviour as a character (-suite) in phylogenetic reconstruction has been recognized for a long time; see e.g. the classical study by Heinroth (1911) on the behaviour of Anatidae. However, the problems associated with the homologization of behavioural characters, particularly of acoustic behaviour, are a significant obstacle in their application in phylogenetic analyses (see e.g. the studies by Bretagnolle 1995, McCracken & Sheldon 1997, Price & Lanyon 2002, Thomassen & Povel 2006, and reviews by Tembrock 1960, 1989, Meissner 1976, DeQueiroz & Wimberger 1993). The widespread species-specificity of acoustic signals in many animal groups, as mentioned above for some fulgoromorphan taxa, render them ideal for biosystematic-taxonomic studies on the species level and below (see Drosopoulos 1985, de Winter & Rollenhagen 1990, and Claridge et al. 1985b).

1.1.3 The evolution of troglobites

The origin of troglobites has fascinated evolutionary biologists since Darwin (1859: 177-178) remarked on their curious and strong modification. However, Darwin did not forward a 'Darwinistic' explanation for their evolution[7], which was subsequently supplied by Weismann (1886)[8].

Troglobite evolution, i.e. the process leading to different, sometimes closely related species, which are highly adapted to life in subterranean spaces, comprises three somewhat independent phenomena and problems:
(i) initial cladogenesis of a cave species, or the origin of a cave dwelling biospecies from an epigean ancestor, which is basically the problem of isolation, or rather separation, of a cave population from its epigean relatives;
(ii) subsequent anagenetic transformation, which comprises the dynamics and driving forces of cave adaptation, the often so-called 'regressive evolution' or 'reductive evolutionary trend', and, in some cases,
(iii) subterranean – presumably non-adaptive – radiation.

---

[7] "As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse." (Darwin 1859: 177)

[8] "Sobald nun aber bei einem solchen Höhleneinwanderer die Fähigkeit erreicht ist, ohne Hülfe der Augen sich hinlänglich Nahrung zu verschaffen, so muss auch ein Rückbildungsprozess der Augen beginnen, denn sobald dieselben nicht mehr notwendig sind zur Existenz der Thiere, sobald stehen sie nicht mehr unter dem Einfluss der Naturzüchtung, denn nun kommt ja nichts mehr darauf an, ob die Augen ein wenig besser oder ein wenig schlechter sind. Jetzt wird also keine Auslese mehr stattfinden zwischen den Individuen mit besseren und denen mit schlechteren Augen, sondern beide werden gleich viel Aussicht haben, erhalten zu bleiben und sich fortzupflanzen. Es wird also von nun an eine Kreuzung stattfinden von Individuen mit besseren und von solchen mit schlechteren Augen, und das Resultat davon kann nur eine allgemeine Verschlechterung der Augen sein. Möglicherweise hilft dabei noch der Umstand mit, dass kleinere und verkümmerte Augen jetzt sogar ein Vortheil sein können, insofern dadurch andere, für das Thier jetzt wichtigere Organe, wie die Spür- und Geruchsorgane, sich um so kräftiger entwickeln können. Aber auch ohne dies wird das Auge, sobald es nicht mehr durch Naturzüchtung auf der Höhe seiner Organisation erhalten wird, nothwendig von ihr herabsinken müssen, langsam, sehr langsam sogar, besonders im Beginn des Prozesses, aber unaufhaltsam." (Weismann 1886: 16-17)
[As soon as such a cave immigrant has developed the ability to obtain food without the help of eyes a reduction of the eyes must commence, since as soon as the same are no longer necessary for the animals' existence, they are not influenced anymore by natural selection, because now it does not matter whether the eyes are a little worse or a little better. Now, no more selection will take place between individuals with better and those with worse eyes, but both will have an equal chance to be preserved and reproduce. Individuals with better and those with worse eyes will cross from now on, and the result can only be a general degradation of the eyes. Possibly this is helped by the circumstance that smaller and stunted eyes can even present an advantage, since this allows other organs such as sensory and olfactory organs, which are more important for the animal now, to develop more strongly. Even without such effect, though, the lack of natural selection maintaining the eye's high level of organization will necessarily lead to its degradation, slowly or even very slowly, especially at the beginning of this process, but inexorably.]

A widely accepted concept aiming to explain the first point, that is the speciation event giving rise to a cave-dwelling and reproductively isolated bio-species, was developed by Thomas Barr in the 1960s, commonly known as the Climatic Relict Hypothesis (CRH):

> "Troglobites have evolved from colonies of troglophiles which became isolated in caves through extinction of surface populations of the troglophiles" (Barr 1968: 96).

According to Barr, the evolution of troglobites is a two-step process: at first, it involves a preliminary, troglophilic stage without apparent troglomorphies or a disruption of gene flow between cave-dwelling and epigean populations. Following this initial cave colonization, the cave dwellers become geographically separated, and thus, genetically isolated due to the extinction of parental epigean populations (supposedly caused by climatic change), at least in the geographical region of the cave. Over time, reproductive isolation will inevitably follow as a side effect of genetic change by drift and natural selection.

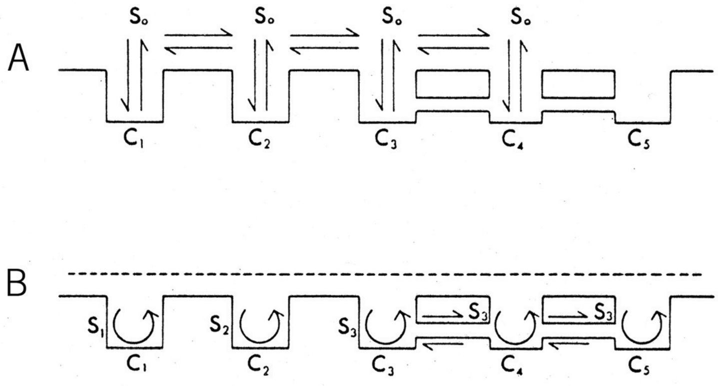


Figure 4. Gene flow (A) in a troglophilic species S_0 and (B) in its descendants S_1-S_3 following extinction of S_0 in epigean environments. C_1-C_5 are caves; C_3, C_4, and C_5 are connected by subterranenan channels, but C_1 and C_2 are isolated from C_3-C_5. C_5, originally unoccupied by S_0, is subsequently colonized by S_3 via subterranean channels (From Barr 1967a: 487).

Support and evidence for this concept was gained from the observed relict distribution of most troglobites known at that time, which were almost exclusively confined to temperate regions. Glaciation during the ice ages was suggested as the most important factor for the change of surface conditions (Barr 1968, Sbordoni 1982, Barr & Holsinger 1985).

This hypothesis remained without alternatives until the early 1970s, when Francis G. Howarth discovered the Hawai'ian cave ecosystems (Howarth 1972). Among other taxa, these caves host highly troglomorphic planthoppers, that are parapatrically distributed with respect to their close epigean relatives, and without the slightest hint of extinction of the sibling epigean species at any time in the past, i.e. they are non-relictual troglobionts. Consequently, Howarth (1981, 1986, 1987) formulated the Adaptive Shift Hypothesis (ASH):

> "[...] potential food resource provides the driving force for the [...] evolution of cave species. Troglomorphic populations [...] evolve from pre-adapted habitual accidentals which [...] establish temporary populations in marginal underground habitats. Once an adaptive shift occurs, allowing a reproducing population to establish itself underground, then it is both the effects of strong new selection pressures and the release from previously strong selection pressures that bring about [...] troglomorphy" (Howarth 1986: 155).

While the exploitation of a large new habitat with new food resources may be the driving force in the evolution of troglobites according to the ASH, a major challenge for survival underground is probably the ability to locate mates and reproduce in the dark. A change in mating behaviour might thus have been the most important adaptive shift necessary for a successful colonization of caves, and would almost inevitably lead to reproductive isolation of the incipient cavernicolous species. The Hawai'ian cave planthoppers provide a striking example for this process, and hence, played a pivotal role in the formation of the adaptive shift hypothesis (Howarth 1986, Howarth & Hoch 2005).

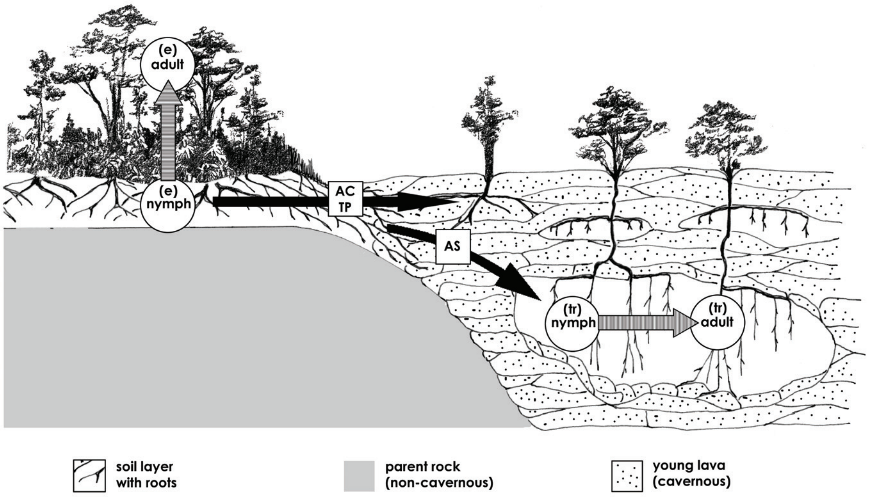
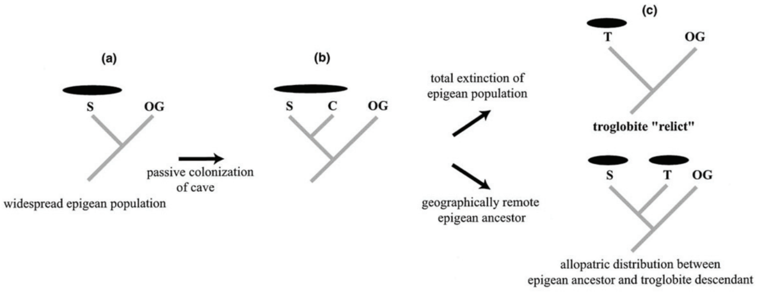


Figure 5. Diagrammatic view of an adaptive shift from surface to underground environments by a cixiid planthopper. AC, accidental; AS, adaptive shift; (e), epigean; TP, troglophile; (tr), troglobite. (From Howarth & Hoch 2005: 20)

The process is illustrated in Fig. 5: Root-feeding planthopper nymphs living in the soil layer, and thus pre-adapted for a shift towards life underground, colonize the caves of young lava flows through the so-called ‘mesocavernous system’ and establish a reproducing cave population.

A principal acceptance of the ASH does not necessarily invalidate the CRH, especially not where the precondition for the CRH, i.e. cave populations or species with a relict distribution, is given. However, a recent relict distribution is not sufficient evidence to unconditionally accept the CRH, given the alternative present in the ASH[9]. The predictions arising from both hypotheses (Fig. 6) must be tested for every single system, such as the Australian cave planthoppers (Wessel et al. 2004, 2007).

Climatic relict



Adaptive shift

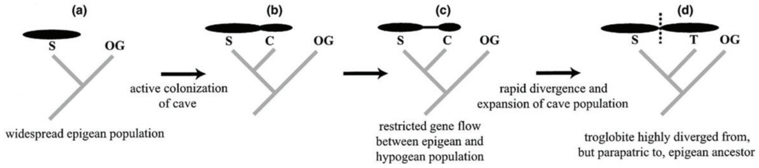


Figure 6. Phylogenetic predictions of speciation by the Climatic Relict Hypothesis and the Adaptive Shift Hypothesis. OG, outgroup; S, surface; C, cave; T, troglobite. Ellipses represent geographic distribution of populations. (Combined from Rivera et al. 2002: 2-3)

---

[9] “The evidence suggests that troglobites evolve from preadapted habitual visitors or accidentals in the cave rather than from well-adapted troglophiles. The former group requires an adaptive shift in order to fully exploit the cave resources. This adaptive shift may lead to the evolution of a troglobitic lifestyle. Well-adapted troglophiles on the other hand tend to remain opportunistic exploiters of the cave environment.
Some temperate troglobites may fit the scenario of isolation by changing climates (Barr, 1968). However, many species including those in the tropics probably do not. I postulate that adaptive shifts led to the colonization of caves and evolution of troglobites, including most of those in temperate caves, but that the complex geological history of the continents including glaciations has obscured the early history and obfuscated the earlier distribution and the evolution of troglobites there.” (Howarth 1981a: 540)

For the CRH, we expect the closest epigean relatives to be allopatrically distributed compared to the cave species, while the ASH predicts a parapatric distribution of cave and epigean species, which are necessarily sister groups (adelphotaxa) (Fig. 6). Conclusive evidence for a decision between both hypotheses may be gained from a molecular phylogeny in conjunction with a sound knowledge of the geographic distribution of both, cave and epigean taxa. However, the last requirement is often problematic, as the sampling of epigean relatives for some cave species is frequently insufficient. For some groups, no epigean relatives are known at all, and it is only through intensive, directed search efforts that this obstacle may be overcome (see e.g. Stone 2004).

Once a population has shifted towards a cavernicolous mode of living, the second problem of troglobite evolution – subsequent anagenetic transformation, or the dynamics of regressive evolution or reductive trends – arises. A basic assumption since Weismann (1886) has been a correlation between the degree of troglomorphy of a taxon and its residence time in caves. Cave adaptation is accordingly described as an orthogenetic, time-dependent process, which is an overall slow, gradual adaptation towards a stage of 'absolute troglomorphy'; see e.g. Wilkens (1986), for review see Barr (1968) and Howarth (1987). Traditional explanations for the mechanisms of this process includes (i) the accumulation of neutral mutations, (ii) pleiotropic effects, and (iii) natural selection for energy economy (Sket 1986, Culver 1982, for review Jeffery 2008). However, the CRH (Barr 1968) and ASH (Howarth 1986) both, contain some notion of a founder effect: Barr with an explicit quotation of Mayr's genetic revolution (Fig. 7), and Howarth with reference to the Carson model of founder effects (compare p. 17).

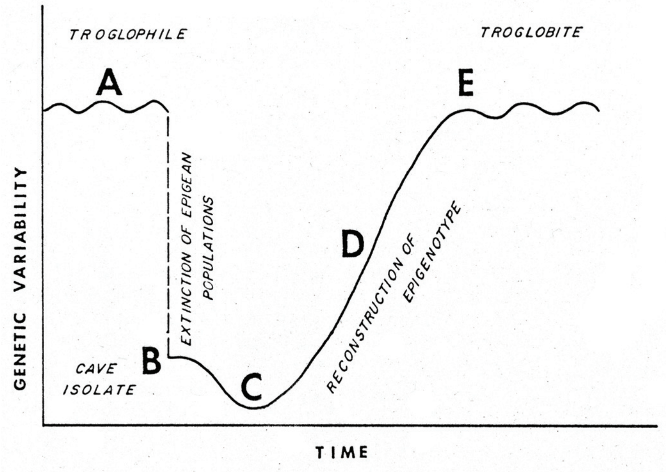


Figure 7. Changes in genetic variability during troglobite speciation (From Barr 1986: 88; adapted from Mayr 1963).

The process of cave adaptation is influenced by several parameters – such as availability of food, population density, microclimate of the caves, and other biotic and abiotic factors of the cave ecosystem –, which make comparisons even between closely-related species exceedingly difficult, and generalisations even more so. Nevertheless, an excellent opportunity to test the assumption of gradual and increased troglomorphy over time can be found in the Hawai'ian cave planthoppers: a morphological comparison has shown the existence of at least seven independent evolutionary lineages, living in caves of comparable ecological conditions, originated from closely-related endemic epigean species on three islands of different age (Hoch & Howarth 1999). These authors, as well as subsequent studies, could find no evidence at all for a correlation between the degree of troglomorphy and the maximum time passed since cave colonization, and ambiguous support for a correlation between the degree of troglomorphy and the physical conditions (food resources) in the caves (see Wessel et al. 2004, 2007).

The third and final complex of troglobite evolution – subterranean radiation – has rarely been investigated and even less discussed, as only a very few suitable model systems are known (Barr et al. 1960, Sbordoni 1982, Barr & Holsinger 1985). Two necessary conditions for the study of intra-cave speciation and radiation are (i) an exclusively troglobiontic mode of living, lacking the possibility of surface dispersal between caves, and (ii) the availability of data on the distribution of cave populations and their age, i.e. the duration of their separation from each other. The Hawai'ian cave planthoppers represent a model system that fulfills these requirements, as this study aims to demonstrate.

1.2 The model system – Hawai'i and its cave-dwelling planthoppers

1.2.1 The Hawai'ian Archipelago

New land open to colonization is conducive to speciation.
Elwood C. Zimmerman (1948a: 122)

The Hawai'i islands have long been recognized for their exceptional potential to conduct evolutionary studies, which has earned them the attribute "natural laboratory of evolution" (see e.g. Simon et al. 1984, Wagner & Funk 1995, Roderick & Gillespie 1998). Research on islands and insular biogeography in general has contributed enourmously to our knowledge of the process of evolution, as reflected in a respective remark by Hampton L. Carson on Hawai'i:

> "The patterns of population structure of island organisms are very different from most of the vast populations familiar to the continental biologist. Island populations in the Pacific lead us to consider the genetic and ecological nature of small, mobile metapopulations such as those that colonize newly emerged islands. The colonists may in turn have descendants that continue to evolve by entering new niches and serially colonizing new lava flows as well as new islets emerging by volcanic action above the surface of the ocean." (Carson 1996: 15).

Islands have clearly defined geographical boundaries, which set a natural framework for looking at patterns of evolution. An extra dimension is added by the fact that data on the historical geology of islands can suggest hypotheses on the evolution of species inhabiting them by allowing a direct timing of speciation events (see e.g. Fleischer et al. 1998, Price & Clague 2002, Price & Elliott-Fisk 2004).

Among all oceanic islands, the Hawai'ian archipelago is characterized by two unique features: (i) it is the most remote island group of the world, being nowhere closer than 3,800 km to the next larger land mass (N America), and (ii) the islands of the Hawai'ian chain are arranged in a series of decreasing (and well-known) age from west to east (Plate I; Clague & Jarrard 1973, Clague & Dalrymple 1975, 1987, Clague 1996). The unique arrangement of the Hawai'ian chain is the result of volcanic outpourings over a stationary thermal plume (a so-called 'hot spot'; Wilson 1963a, 1963b, Morgan 1972, see also Steinberger & O'Connell 1998, and Tarduno et al. 2003) that, in conjunction with the movement of the

Pacific plate over it in a north-western direction, is responsible for creating all the islands in the Hawai'ian archipelago as well as the Emperor seamounts (McDougal 1979; reviewed in Carson & Clague 1995). The activity of the plume started 75-80 mya, and the rate and direction of the Pacific plate movement changed about 43 mya, which accounts for the bend in the chain (Clague & Jarrard 1973). The larger part of the entire Hawai'ian-Emperor chain is below sea level. The sinking of older islands is caused by the cooling and subsidence of the lithospheric plate with increasing distance from the East Pacific Rise (Detrick & Crough 1978).

This simple basic pattern is complicated by the possibility of island integration, i.e. some islands may not have their origin at the present Hawai'ian hot spot. Necker island, for example, became integrated with the Hawai'ian chain as recently as 10 mya, and if its summit was above sea level when it entered the chain, the mixing of Hawai'ian and non-Hawai'ian biotas might have been a biogeographic consequence of island integration (Rotondo et al. 1981). However, with an age of about 75 my, the basement of Necker is old (Clague & Dalrymple 1975), and the 10 my old summit is a result of the renewed volcanic activity as the island passed the Hawai'ian hot spot (Funkhouser et al. 1968, Dalrymple et al. 1974, reviewed in Rotondo et al. 1981)

The pattern of decreasing geological age towards the southeast also holds true within the large island of Hawai'i (Plate II). Hawai'i Island is composed of at least seven volcanoes, five of which are still above sea level today. Of these five volcanoes, the three northern ones are not active any more, and have a highly eroded surface, while one of the two volcanoes in the south, Mauna Loa, is not active at present, but might potentially erupt again. In contrast, Kilauea in the southeastern corner of the island is considered to be the most active volcano on earth. Eruptions in the Pu'u O'o crater have persisted since 1986 until the present, making it a favourite 'model volcano' for volcanologists worldwide (Decker et al. 1987).

The active volcanism on Hawai'i Island causes unique landscape dynamics in the affected areas, e.g. 40% of the entire surface area of the Mauna Loa System, and 90% of the Kilauea System, were replaced within the last 1,000 years (Holcomb 1987, Lockwood & Lipman 1987). The destruction of habitats has also been a creative process as new ecological licences were formed. Habitat fragmentation in the surface biota by new lavastreams resulted in segregated populations that were isolated in "'islands' of climax forest ranging from a few acres to many square miles in extent surrounded by great ares of barren lava flow 'deserts'" (Zimmerman 1948a: 130), the so-called 'kipukas' of the native Hawaiians. The continuous presence of such volcanic activity prompted the assumption of its significant influence on population structure triggering and promoting diversification, and thus, led to the suggestion of a potential model system to study accelerated evolution (Carson et al. 1990). The classical studies by Carson (see Carson & Kaneshiro 1976 for a review) on drosophilids and recent studies on spiders (Vandergast et al. 2004) have provided evidence in support of the unique character of this model system.

Beyond the geological peculiarities of Hawai'i, some general observations on island faunas are valid here as well:

> "Sehr merkwürdige Thatsachen bietet in dieser Beziehung der Vergleich der Inselfaunen mit den Ländern der zunächst liegenden Continente. Mit der grössern oder geringern Ausdehnung der dazwischen liegenden Meeresarme, welche beide trennen, wächst fast überall im entsprechenden Verhältniss die relative Verschiedenheit des Thierreichs nicht nur hinsichtlich der Arten, sondern auch hinsichtlich der Gattungen."[10] (Wagner 1868: 13)

Moritz Wagner's remark on the relationship between geographic distance and endemism hints at the suitability of islands, with endemic species to study the role of isolation as a direct cause for speciation (Weismann 1902: 318). The above mentioned extraordinary geographic isolation of the Hawai'ian archipelago (see also Plate I, inset) led to a so-called 'disharmonic fauna' (Zimmerman 1948a, Gressitt 1971) and an extremely high rate of endemism[11]. In the introduction of "Insects of Hawai'i", the first comprehensive synopsis of the Hawai'ian biogeography and evolution, Elwood C. Zimmerman wrote:

> "It has been shown that upon these oceanic islands of Hawaii there has been developed an array of endemic organisms characterized by certain features which mark the Hawaiian biota as one of the most distinct in the world. The extreme isolation of the archipelago has resulted in great restriction upon the types of organisms which have succeeded in reaching it and becoming established. We have estimated the number of ancestral immigrants and have found that only a relatively few individuals have given rise to the extensively developed groups of genera and species now existing here." (Zimmerman 1948a: 121)

The most conspicuous 'faunistic disharmony' on Hawai'i is certainly the complete lack of native amphibians and terrestrial mammals with the exception of two bat species (one of which is extinct now). Terrestrial reptiles are also possibly

---

[10] Rather curious facts emerge from a comparison of island faunas and the countries of the surrounding continents. The relative distinctiveness of the animals not only at the species but also at the genus level is correlated with the larger or smaller width of sea separating the two [faunas].

[11] For problems in usage and semantics of the term 'endemism' see Anderson (1994); according to the Oxford English Dictionary "*spec.* of a plant or animal species, the state or condition of being indigenous only in a specified area. [...] first use by DeCandolle." (Burchfield 1972: 943).

not native to Hawai'i and may have been introduced by the first Polynesians colonising the islands (Cox 1999, Ziegler 2002).

A significant bias, with respect to the presence and speciosity of single groups, is also observed among invertebrates. While the native fauna of Hawai'i lacked 21 of the 35 higher taxa (‚orders') of insects (at least 15 of which are now represented by immigrant species), some groups have radiated in an extraordinary way (Zimmerman 1948a, 1958). Only 10% of dipteran families occur on Hawai'i, for example, but with an estimated 1,000 species (Kaneshiro 1993), it harbours a third of the world's entire *Drosophila* fauna. A general characteristic of the Hawai'ian fauna is the almost complete endemism at the species level in terrestrial groups (native taxa only). According to recent estimates, the degree of endemism for terrestrial molluscs and arthropods is 99% (Eldredge & Miller 1995, 1997, Miller & Eldredge 1996).

A species restricted (i.e. endemic) to Hawai'i, or to one of the Hawai'ian islands, is a result of speciation on the islands, as their low age and volcanic origin precludes relict occurrences of taxa. Much of the species diversity on Hawai'i originated through radiation processes. The most striking example are probably the drosophilids mentioned above. Even though the Hawai'ian *Drosophila* is regarded as one of the most thoroughly studied cases of adaptive radiation (Coyne & Orr 2004), the total number of species in this radiation remains speculative. While 511 taxa are already named (Hardy 1965, Hardy & Kaneshiro 1981), another 300 have been collected and await description (Kaneshiro et al. 1995). Additionally, at least 20 species have been introduced in historic times (Kaneshiro et al. 1995). Nevertheless, the islands' drosophilids remain an excellent model for testing central concepts of evolutionary biologists, such as sexual selection as a factor in speciation (Ringo 1977, Kaneshiro 1983, Coyne & Orr 1989).

The remoteness of the Hawai'ian archipelago leads to the expectation that its fauna is the result of comparatively few colonisations with subsequent adaptive radiation, and founder effects may have been an important initial factor. This view is not unchallenged though. The founder principle in the context of the origin of island faunas has been critically discussed, e.g. by MacArthur and Wilson (1967: 155-156):

> "[...] islands that are colonized by a given species are probably colonized by multiple propagules. [...] If the true immigration rate is high enough for as few as several sets of propagules to arrive per generation time, a large fraction of the total genetic variation of the mother population can be inserted into the founder population, in turn reducing random effects to a low level. [...] evolution due to genetic sampling error is an omnipresent possibility but one easily reduced to relative insignificance by small increases in propagule size, immigration rate, or selection pressure."

However, the situation on Hawai'i suggests that very few colonizations resulted in the outstanding diversity observed. The approximately 5,000 described endemic insect species stem from about 250-400 successful colonizations (Zimmerman 1948a, Howarth 1982a, 1990)[12]. The many cases of adaptive radiation may have been triggered by the existence of free ecological licences for the first colonizers:

> "Any area in which one can pass within a few miles on a single mountain mass from a seaside semidesert to a rain forest receiving over 50 feet of rain in a year, or from lush, steaming tropical jungle to a perpetual, subpolar desert (mean minimum July-August temperature at 13,000 feet of 0°C or less) where snow on occasion lies on the ground the entire year at nearly 14,000 feet, and which has such a spectacular, rugged topography clothed with dense vegetation containing about 2,000 known native higher plants making one of the most distinctive botanical provinces of the world, cannot escape having an unusual range of ecological conditions. The remarkable thing is that so many different types of ecological niches are available in such limited areas." (Zimmerman 1948a: 178)

The study of the evolution of Hawai'ian insects has had an enormous impact on ideas about evolution, as exemplified by a long list of phenomena and concepts, whose conception has been significantly influenced by case studies from the islands: founder events and isolation, hybridization, sexual selection, habitat shifts, host switching, and co-speciation (reviewed in Roderick & Gillespie 1998).

---

[12] "About 400 colonizers gave rise to over 5,000 endemic species of arthropods, with probably at least as many more undescribed species awaiting study. This dearth of knowledge of the total fauna makes it difficult to assess their conservation status and formulate conservation programs for native arthropods. Over 3,200 alien species of arthropods have been purposefully or inadvertently introduced by human activities. Possibly 2,500 of these are established residents." (Howarth 1990: 4)

1.2.2 Hawai'ian cave ecosystems

Caves provide ideal conditions for the study of evolutionary patterns and processes. Their stable environment, the simple communities encountered in caves, particularly in the interior 'dark zone', and the island-like isolation of cave dwellers, greatly reduce the number of parameters that need to be considered (see e.g. studies by Culver 1970a, 1970b). While a vast and ever-growing amount of literature on cave organisms and their evolution exists (see Wilkens et al. 2000, Culver & White 2004), a detailed study of terrestrial caves under a holistic and synthetic approach, comparable to the benchmark study by R. Riedl (1966) on marine caves, is still a desiteratum in modern biospeleology. However, caves provide natural 'experimental designs' that can be used for testing hypotheses on e.g. adaptation and genetic change in small and isolated populations. Therefore, respective studies on cave organisms will contribute to a better understanding of the relative importance of different evolutionary forces in speciation. Caves and their fauna are mostly employed as model systems for evolutionary change associated with striking habitat change, i.e. invasion of – and evolution into – the caves, while this study is rather focused on the evolutionary processes occuring within caves after successful colonisation.

The vast majority of caves are found in limestone, and particularly karst areas, and almost all studies on cave faunas have been conducted in karst caves (Vandel 1964, Barr 1966, Poulson & White 1969), e.g. the classical studies in the Mammoth Cave, Kentucky (Barr 1967, Barr & Kuehne 1971). In contrast, lava tube caves are a comparatively rare phenomenon, as their formation not only requires magmatic activity, but is also dependent on lava composition and temperature. These requirements are seldom met. Generally, lava tubes are formed by exterior encrustation of a lava flow through cooling of its surface, while the lava continues to flow below (Plate III a,b); the resulting tube structure depends on the chemical and physical characteristics of the respective lava (Greeley 1971, 1972, Peterson & Swanson 1974, Peterson et al. 1994, Dragoni et al. 1995, Kauahikaua et al. 1998). When the flow of lava ceases after an eruption, an interior cavity with a diameter from a few centimeters up to several meters remains, and can extend throughout the whole length of the lava flow, i.e. several dozen kilometers (the longest known lava tube, Kazamura cave on Hawai'i Island, has a documented length of 59.3 kilometers with a vertical extent of 1,098 m; Allred & Allred 1997). The cave usually traces all branches and mergers of the lava flow, and may consequently follow a rather complicated course. Roof intrusions, so-called 'skylights', which either develop during the encrustation process or later through erosion, provide access to the newly formed caves. The cave walls are characterized by a system of cracks and voids (mesocavernous system, Howarth 1983), which probably connect neighbouring lava flows. The extent, to which such a mesocavernous system is formed, depends upon the composition, temperature, and gas content of the lava.

After formation of a lava tube, the very dry and rather inhospitable surface of the lava flow is predominantly colonized by a single pioneer plant species, *Metrosideros polymorpha* Gaudich. (Myrtaceae) (Gaudichaud-Beaupré 1830), the Hawai'ian *'ōhi'a lehua* (Plate III d). This plant can cope with the lack of surface water by extending its roots downwards through the roof of the lava tubes into the cave below, where accumulated water and a high humidity provide the necessary conditions for survival (McDowell 2002). The cave water is rich in nutrients washed out from the lava, and indeed, the subterranean proportion of the plant's biomass (massive root bundles) may actually greatly exceed that found on the tube surface, where small bushes are loosely scattered. The living roots are a potential food resource for plant-sap sucking insects, while the root debris can sustain saprorhizophagous species. The crevices formed through root growth may also allow additional organic matter to get into the cave. However, living roots form the basis of a food web in these caves (Howarth 1986), and thus, the Hawai'ian lava tube faunas are root communities (Stone et al. 2005). In contrast, karst cave faunas usually depend on nutrient input through bats (guano communities) (Gnaspini & Trajano 2000), subterranean rivers, or streams (Poulson & Lavoie 2000, Jasinska & Knott 2000).

The ecological succession on the lava flow surface following the first colonization by *Metrosideros* causes changes within the cave also. Soil formation, which is accelerated by the accumulation of dust through the action of wind, reduces evaporation and leads to the establishment of a water reservoir. The resulting reduction in water stress allows plants to limit root growth to the soil and near-surface lava crevices. Consequently, only a few roots are found in older lava tubes overgrown with forest. The density of rhizophagous species is accordingly low (Hoch & Howarth 1993).

The first cave ecosystems in lava tubes, and at the same time the first tropical caves with a rich terrestrial fauna, were discovered in 1971 by F. G. Howarth on Hawai'i Island (Howarth 1972). The first organisms reported from the Hawai'ian caves include highly troplomorph cixiids (Fulgoromorpha) and several weakly-pigmented aquatic and terrestrial arthropods with reduced or completely absent eyes (Howarth 1972, 1973). Further inventories have revealed a significant diversity with today 43 endemic troglobiont species described: aquatic amphipods (Barnard 1977), terrestrial amphipods (Bousfield & Howarth 1976), springtails (Bellinger & Christiansen 1974, Christiansen & Bellinger 1992), earwigs (Brindle 1980), planthoppers (Fennah 1973a, Hoch & Howarth 1993, 1999), true bugs (Gagne & Howarth 1975a, 1975b), arachnids (Gertsch 1973), crickets (Gurney & Rentz 1978), beetles (Liebherr & Samuelson 1992), pseudoscorpions (Muchmore 1979, 1983, 1989), isopods (Taiti & Howarth 1997, Rivera et al. 2002), and mites (Zacharda 1982). In addition, several species and subspecies of moths, flies, crickets, centipedes, millipedes and pseudococcids (Howarth 1973, Howarth & Mull 1992, Lavoie et al. 2007) still await description. With a total of 143 recorded species (Stone & Howarth 2005, Howarth et al. 2007, and unpublished data; see check list in the appendix), the Hawai'ian lava tubes contain, next to the karst caves of Maros (Sulawesi, Indonesia; 93 species; Deharveng & Bedos 2000) the most diverse cave fauna known.

The Hawai'ian cave ecosystem is a unique model system combining several aspects, that are each of immense interest for evolutionary biology: tropical caves with parapatric distribution of epigean and hypogean species; its location on the most remote island system in the world with an accompanying highly disharmonic fauna; and the specific structure of the Hawai'ian lava tube caves. This study is an attempt to exploit this set of properties to test general hypotheses on the genetic, morphological and behavioural diversification of cave organisms, with particular emphasis on the empirical assessment of founder effect theories.

1.2.3 The cave planthopper *Oliarus polyphemus* Fennah, 1973

> Die wunderbaren Metamorphosen der Insekten, die Mannigfaltigkeit ihrer Ernährungsweise schon im Larvenzustande und besonders ihr sehr verschiedener Grad von Bewegungsfähigkeit machen das Studium der geographischen Vertheilung der Insekten zu einem der wichtigsten Mittel, die Richtigkeit der natürlichen Zuchtwahl zu beweisen und das Gesetz zu erkennen, nach welchem dieselbe auf die Vertheilung der Formen wirkte.
>
> Wagner (1868: 6)

Among the planthoppers (Fulgoromorpha), 53 cave-dwelling species have been described from many parts of the world (Tab. 1), four-fifth of them cixiids including the Hawai'ian *Oliarus* species (Fig. 8; Hoch 1994, Hoch & Wessel 2006). No cave-adapted leafhoppers (Cicadomorpha) are yet known. The degree of adaptation to a subterranean life varies greatly, primarily depending on their habitat in the cave or soil (Fig. 9).

Table 1. Systematic position and geographic distribution of cavernicolous Fulgoromorpha.

Hypochthonellidae	Zimbabwe	China & Fennah 1952
Delphacidae	New Caledonia	Fennah 1980a, Hoch et al. 2006a
Kinnaridae	Mexico	Fennah 1973b
	Jamaica	Fennah 1980b
Meenoplidae	Australia	Fennah 1973b, Hoch 1990, 1993
	New Caledonia	Hoch 1996
	Western Samoa	Hoch & Asche 1988
	Canary Islands	Remane & Hoch 1988, Hoch & Asche 1993
	Cape Verde Islands	Hoch et al. 1999
	Madagascar	(unpublished, in preparation)
Cixiidae	Madagascar	Synave 1953
	Canary Islands	Remane & Hoch 1988, Hoch & Asche 1993
	Azores	Hoch 1991
	Mexico	Fennah 1973b, Hoch 1988
	Hawai'i	Fennah 1973a, Hoch & Howarth 1999
	Galápagos	Hoch & Izquierdo 1996
	Argentina	Remes Lenicov 1992
	Australia	Hoch & Howarth 1989a, 1989b
	New Zealand	Fennah 1975
	Reunion Island	Hoch et al. 2003
	[Balearic Islands]	Racovitza 1907 (unconfirmed record)

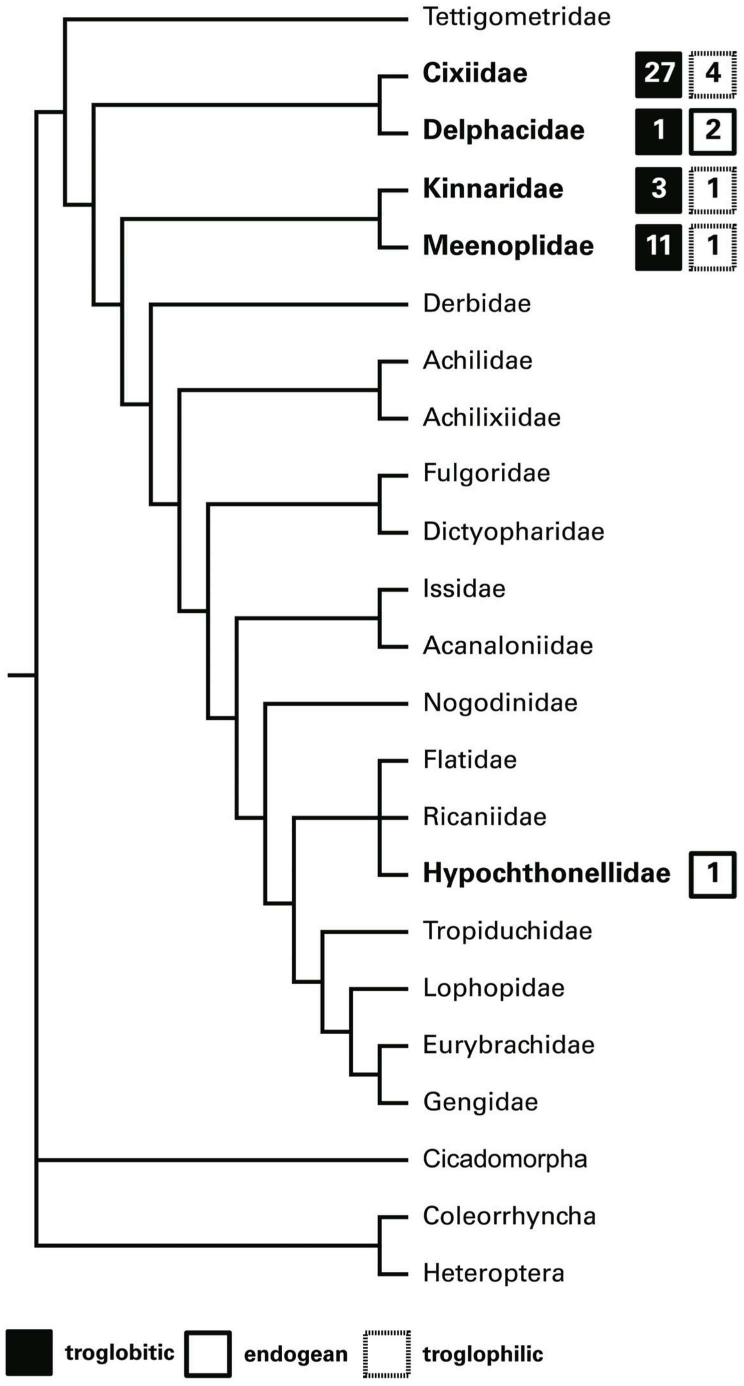


Figure 8. Taxonomic distribution of hypogeic (troglobitic, endogeic, and troglophilic) Fulgoromorpha species. Morphology-based consensus cladogram combined after Asche (1987), Bourgoin (1997), and Emeljanov (1990). Families containing taxa adapted to a subterranean mode of living are highlighted. Boxes show the number of respectively adapted species (From Hoch et al. 2006a).

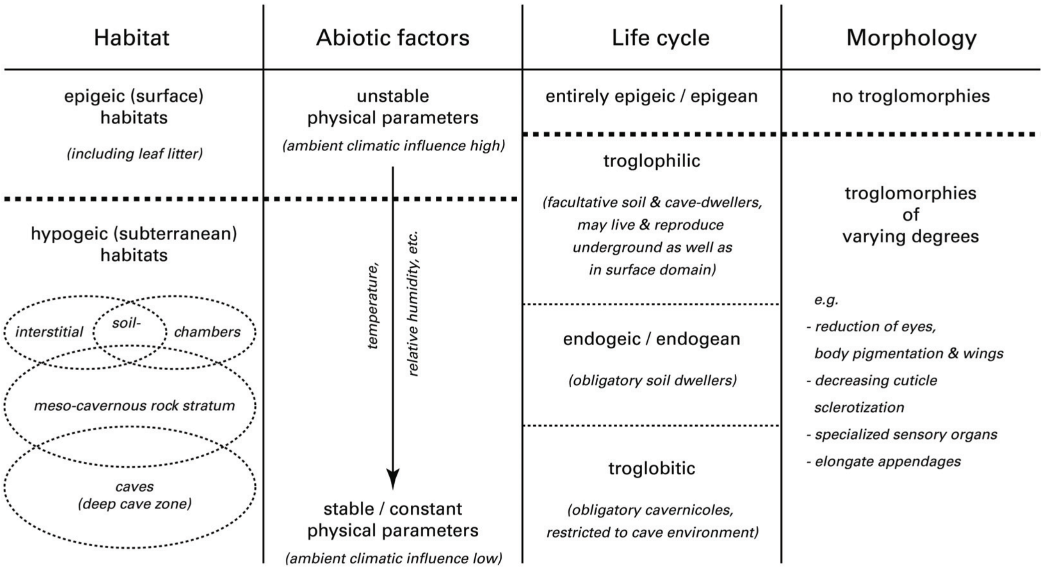


Figure 9. Terminology of interdependence between physical parameters of the habitat and organismic adaptations. (From Hoch et al. 2006a).

In cave planthoppers, the adaptation to similar environments has led to the evolution of a very similar external morphology in different parts of the world. Therefore it represents a striking example of parallel evolution. The morphological modifications of cave planthoppers are characterised by reductive evolutionary trends, as in most obligately cavernicolous animals. Most conspicuous are the reduction and loss of compound eyes and ocelli, tegmina, wings, and bodily pigment (see Fig. 9). It has also been suggested that apparently non-troglomorphic characters have an increased adaptive value in the underground environment, such as e.g. the specialised spine configurations of hind tibiae and tarsi, which may possibly enhance walking on wet or rocky surfaces (Hoch 2002).

The closest epigean relatives of cavernicolous Fulgoromorpha species all have immature stages living close to the soil, e.g., under the dead bark of rotting logs, in leaf litter, or moss, or even within the soil, feeding on roots or perhaps on fungi (Remane & Hoch 1988). This mode of life has been considered an ecological pre-adaptation to a later switch to a permanent (adult) life underground (see also Fig. 5; Hoch 2002, Howarth & Hoch 2005).

With about 80 described epigean taxa (species and subspecies) *Oliarus* (*Nesoliarus* Kirkaldy, 1909) is the most speciose planthopper genus on the Hawai'ian islands (Giffard 1925, Zimmerman 1948, Asche 1997); Nishida (2002) lists 63 species. Based on morphological data, this diversity has been hypothesised to stem from a single colonisation event (Asche 1997, Hoch & Howarth 1993). The first cave-dwelling species of the genus, *Oliarus polyphemus* Fennah, 1973 on Hawai'i Island, and *Oliarus priola* Fennah, 1973 on Maui (Fennah 1973a), were discovered by Howarth (1972). Later, five more troglobitic taxa were discovered on the archipelago (Hoch & Howarth 1999). The, altogether seven, cave-dwelling species owe their origin to several independent colonisation events on three islands (on Molokai, one adaptive shift; on Maui, three adaptive shifts; on Hawai'i Island, at least three adaptive shifts; Hoch & Howarth 1999).

Fennah (1973a) proposed *Oliarus inaequalis* Giffard, 1925 as the sister taxon of *O. polyphemus*. However, this assumption was challenged by Hoch & Howarth (1999), who pointed out several shortcomings in the morphological description of *O. polyphemus*. To date, the epigean sister groups of the cavernicolous taxa remain unknown (Hoch & Howarth 1999).

O. polyphemus (Plate IV a-c) shows the highest degree of character reduction (eyes, wings, pigmentation) associated with a troglobitic habit of all the Hawai'ian cave-dwelling *Oliarus* species. A rather prominent claw on the pretarsus, only found in *O. polyphemus*, may be a possible autapomorphy of the species (Fennah 1973a). *O. polyphemus* has the widest distribution range of all the cavernicolous Hawai'ian *Oliarus* (Plates V & VI), populating all volcano systems on Hawai'i Island except Kohala, and is found in numerous lava tubes from sealevel up to an altitude of ca. 1,200 feet and ranging in age from less than 100 to several thousand years, respectively (Hoch & Howarth 1993). The mesocavernous system, which connects neighbouring lava tubes and streams, might enable inter-cave migration of *O. polyphemus* (and that of all cavernicolous Hawai'ian *Oliarus*), and thus, facilitate the colonisation of new caves (Howarth 1983).

The cavernicolous *Oliarus* are plant-sap suckers (as are all Auchenorrhyncha) and feed on roots growing into the caves, predominantly from the native pioneering plant *Metrosideros polymorpha* (Howarth 1986). Laboratory populations of *O. polyphemus* were maintained on fresh soy bean sprouts, indicating that host plant specificity is largely lacking (Hoch, unpublished data).

All life history data also stem from laboratory observations on *O. polyphemus*. About 4–14 days after fertilisation, the females deposit bundles of up to 10 eggs into wax 'nests' on the roots. From these, the first instar nymphs hatch after 70–74 days, which molt into second instar nymphs after 30–32 more days. The adult stage is reached after five instar stages, and the animals become reproductively active 7–10 days after the last moulting. In the laboratory, adult animals survived a maximum period of 70 days (females) or 122 days (males), respectively, indicating a total life span of about 12 months (Hoch & Howarth 1993).

In field studies on *O. polyphemus* in Pahoa Cave (Kilauea Volcano), a population density of about two animals per square meter root surface was found (Hoch & Howarth 1993). The study site contained about 1,000 roots of ~2 m length with a diameter of ~4 mm, and a maximum of 200 individuals was observed in this section of the cave. The majority of observed animals were large (4th or 5th instar) nymphs, while adults were only rarely found. The nymphs are surrounded by conspicuous wax cocoons, which provide protection against predators and water drops running down along the roots. Young, more sensitive nymphs usually remain close to their place of hatching in sheltered areas, whereas larger nymphs with their larger cocoons also can be found in more exposed areas (Hoch & Howarth 1993). This might explain, why sometimes twice as many large nymphs as small ones were counted. The rarity of adults might be caused by either high mortality during the last instar stage or alternatively immediate migration after the last moulting. Both hypotheses enjoy some support and might be complementary. The last (5th) instar stage is a critical phase with a high risk of predation due to its long duration and the following last moulting, while it is also safer for the adults to hide in the cracks of the mesocavernous system except for feeding and mating (Howarth 1982b). The fast colonisation of new lava tubes such as Kaumana Cave provides additional evidence for migration through the mesocavernous system (Hoch & Howarth 1993).

The first occurence of substrate vibration in cavernicolous planthoppers, widely known in small epigean fulgoromorphans (see 1.1.2), was discovered in *Oliarus polyphemus* (Howarth et al. 1990). The roots, the animals feed from, provide at the same time the substrate for the transmission of their vibrations. In physical terms (and slightly simplified), the roots may be regarded as water-filled tubes, which can carry the vibrations along a distance of several meters without a significant loss in information. The signal is not only transmitted vertically along a single root, but also horizontally across whole root ‘curtains’ (Hoch & Howarth 1993). For *O. polyphemus*, substrate vibration is probably the only possibility to communicate, as the eyes are completely reduced and a chemical communication through pheromones is not known (Hoch & Howarth 1993). This does not preclude possible tactile communication upon direct contact.

The limitation in available communication channels is also evident in observations on the reproductive behaviour of *O. polyphemus* (Hoch & Howarth 1993). If member of both sexes are put together, random encounters always lead to escape reactions, indicating that the animals fail to recognise a potential mating partner or even conspecifics. The escape reaction is only suppressed if an animal starts to communicate through substrate vibration, and the courtship phase commences.

In contrast to all epigean fulgoromorphans studied so far, and also most other insects (Tembrock 1971), the female initiates the courtship song in *O. polyphemus*. The female remains stationary during the courtship phase and 'sings' continuously, while the male tries to locate the female through 'trial and error' movements, occasionally it answers through calling as well. This deviation from 'standard' courtship behaviour in planthoppers might represent an adaptation to subterranean life, as suggested by Hoch & Howarth (1993). They assume that the behavioural modification is a strategy to economise the process of finding a mating partner, which reduces the risk of predation. In almost every instance, calling females accept males able to localise them, indicating that 'singing' activity in females is strongly correlated with their receptivity. Thus, males will by default only react to females willing to mate. An efficient system is deemed of paramount importance for *O. polyphemus*, since few adults are found on roots (see above), where they only dwell for feeding and mating. Nevertheless, substrate vibration cannot function on lava, which is where the adults are assumed to predominantly hide. Predation risk is also highly increased during courtship, as the transmitted signals may also lead potential predators such as spiders efficiently to their prey (see Rovner & Barth 1981). The exclusive initiation of courtship behaviour by receptive females minimises this risk.

Oliarus polyphemus was described as a single widespread species, but comparative analyses of male and female courtship call patterns in 11 populations from lava tubes in the Hualalai, Mauna Loa, and Kilauea volcanic systems revealed a high degree of divergence between them, and the existence of a young complex of 'cryptic acoustic species' has been assumed (Hoch & Howarth 1993, Wessel & Hoch 1999). This finding has prompted speculations about rapid subterranean speciation (Hoch 1999), but data to support this hypothesis are still largely lacking.

1.3 Research aims

The cavernicolous planthopper *Oliarus polyphemus*, with different populations in the lava tubes of Hawai'i Island, has been regarded as a model system for studying rapid speciation (Hoch & Howarth 1993, Hoch 1999, Wessel & Hoch 1999). However, so far, this model system constitutes a promise rather than a reality, i.e. the existing data indicate the potential of the system, while being too sparse to allow a grand exercise in model testing. The major aim of this study has therefore been to develop this promise into a framework of facts, concepts, and (testable) hypotheses.

Consequently, the research program followed here has been structured according to this aim:

1. The search for facts

- GIS (Geographical Information System) approach through creation of detailed maps showing the location of caves in lava flows. This includes obtaining precise estimates of cave ages.
- Compile data from the extensive literature on the complex geological history and makeup of Hawai'i Island – this is essential for any meaningful interpretation of the biological patterns encountered both above and below the ground.
- Description of the biological patterns, mainly by studying the differentation of populations through analyses of their morphology (morphometry), communication signals (ethometry), and molecular genetics (molecular phylogenetics).

2. Concepts and hypotheses

Based on the assumption that the different *O. polyphemus* populations are indeed a product of rapid subterranean differentiation (primary test for the monophyly of the *O. polyphemus* complex), the following questions arise:

- What has been the tempo and mode of dispersal (development and test of different models with morphological and molecular data).
- What has been the tempo and mode of differentiation, or what processes drive divergence (genetic change) – random drift, natural selection, or sexual selection?

- Have founder effects been involved, and which of the different concepts proposed is most appropriate? Can the Hawai'ian model system be employed to test the founder effect hypotheses in nature?
- Is the inter-population differentiation of *O. polyphemus* indicative of speciation? This question is closely linked to the concept here underlying the meaning of the word 'species', or how should species be identified?
- How does the system add to our understanding of the causes of the origin of biological diversity?

2 Material and methods

2.1 Material

2.1.1 Specimens

This study is based on material collected between 1972 and 2000 by F. G. Howarth (Bishop Museum, Honolulu), F. D. Stone (Hawai'i Community College, Hilo, Hawai'i), M. Asche, H. Hoch, and A. Wessel (Museum für Naturkunde, Berlin) (Tab. 2). Specimens were obtained (i) from the systematic sampling of the entire cave fauna in all known (and accessible) cave passages by F. G. Howarth and F. D. Stone (see checklist of Hawai'ian cave animals, Appendix). All material collected during these field trips was preserved in 70-96% ethanol and voucher specimens are deposited in the Hawai'i Biological Survey collection at Bishop Museum, Honolulu (Howarth et al. 2007). A large amount of specimens was also specifically collected (ii) for this project by M. Asche, H. Hoch, and A. Wessel in 1999 and 2000. For genetic analyses, living nymphs (4th and 5th instar) were additionally collected during these campaigns and fixed in 96% ethanol.

The number of specimens sampled was adjusted according to the observed population density in the respective cave or cave section. Generally, a maximum of six specimens was collected during any single visit to a cave in order not to endanger the stability of the ecosystem.

For the location of the collecting sites see Plates V to VII and Results 3.1 (for abbreviations see Tab. 3). Because of requests by the land owners, the policy of the Hawai'ian Volcanoes National Parks and the caves' vulnerability to human disturbance, the precise location of the cave entrances is considered confidential. Certain information for scientific purposes only is available upon request from the author and the office of The Nature Conservancy of Hawai'i.

2.1.2 Song recordings

The vibrational signals were recorded in 1989 and 1995 by H. Hoch and in 1999 and 2000 by A. Wessel, comprising in total about 50 hours of taped recordings. For measurements and statistical analyses, signals of 53 individuals from 15 caves could be analysed, and from eight caves recordings of both sexes were available (see Tab. 4).

2.2 Methods

2.2.1 Cave exploration, sampling, mapping, and age determination

The existence of lavatubes on Hawai'i Island has long been known. In prehistoric times (i.e. for Hawai'i before Captain Cook's first visit in 1778) the caves were used for burials and were considered taboo (*kapu*). Since the discovery and exploration of the cave ecosystems in July, 1971 (Howarth 1972) – in the course of the International Biological Programme, Hawai'i Subprogramme – the caves are systematically explored through the Hawai'i Biological Survey (Howarth et al. 2007). In order to protect the sensitive ecosystems and the burial sites, the cave entrances have not been officially mapped, and the respective data are treated as confidential. Two caves are open to the public as designated tourist caves and can be found on maps, one of these caves (Kaumana Cave) harbours a population of *O. polyphemus*.

Table 2. Specimens available for morphometric (adults) and genetic (nymphs) analyses.

Cave (cave section, cave entrance)	Males	Females	Nymphs
Pahoa Cave	19	23	+
Kaumana Cave	28	15	+
Ainahou Cave (North)	16	12	+
Ainahou Cave (Main)	9	6	+
Ainahou Cave (Mo'o)	4	1	–
Paradise Park Cave	17	11	–
MacKenzie Park Cave	12	15	+
Lanikai Cave	8	11	+
Kazumura Cave (Sepulcher)	17	9	+
DocBellou Cave	6	6	+
Charcoal-Calabash Cave	6	3	+
Kazumura Cave (Main)	8	1	+
John Martin's Cave	15	4	+
Pink Pistillaria Cave	3	0	+
Pink Pistillaria Cave (sp. 2)	2 (#278, #282)	0	–
Carson's Cave	2	2	+
Bird Park Cave [locus typicus]	6	1	+
Blair Cave	3	5	+
Surprise Cave	3	1	+
Stainback Highway Cave #12	5	0	+
Bob's Cave	(1)	0	+
Shick's Cave	(2)	0	+
$N^{(adults)} = 315$	189	126	

Table 3. Abbreviations for cave and cave entrance names[1] (see Plates V-VII).

AM	Ainahou Cave, Main Entrance
AN	Ainahou Cave, North Entrance
Bl	Blair's Cave
Bo	Kazumura Cave, Bob's Entrance
Ca	Carson's Cave
CC	Charcoal Cave / Calabash Cave
DB	DocBellou Cave
JM	John Martin's Cave
K	Kaumana Cave
KM	Kazumura Cave, Main Entrance
L	Lanikai Cave
MK	MacKenzie Park Cave
Pi	PinkPistillaria Cave
P	Pahoa Cave
PP	Paradise Park Cave
Se	Kazumura Cave, Sepulcher Entrance
Sh	Kazumura Cave, Shick's Entrance
SH	Stainback Highway Cave #14
Su	Surprise Cave
T	Thurston Cave

Table 4. Measured vibrational signals ('calls') available for statistical analyses.

Cave	Males		Females	
(cave section, cave entrance)	Individuals	Measured calls	Individuals	Measured calls
Pahoa Cave	4	17	4	51
Kaumana Cave	7	44	3	53
Ainahou Cave	3	15	2	10
Paradise Park Cave	2	7	2	10
MacKenzie Park Cave	2	10	2	30
Lanikai Cave	1	5	2	10
Kazumura Cave (Sepulcher)	1	5	1	5
DocBellou Cave	1	5	2	10
Charcoal Cave	2	10	0	0
Calabash Cave	1	5	0	0
John Martin's Cave	1	8	0	0
Pink Pistillaria Cave	4	22	0	0
Bird Park (locus typicus)	2	12	0	0
Blair Cave	0	0	2	22
Surprise Cave	1	16	0	0
O. hevaheva (epigean)	1	3	0	0
N = 53 / 385	33	184	20	201

---

[1] Most of these names are not "official", but rather informal terms in order to facilitate communication among the scientific community. For several caves or cave entrances, respectively, more than one term can be found in the literature (reports, lists etc.).

Populations of *O. polyphemus* are known from 27 caves, 19 of which could be sampled for this study. In the course of these explorations, nymphs were collected for the genetic analyses (see 2.1.1) and, if abundant, also adults and 5th instar nymphs for bioacoustics. Other cave organisms were determined *in situ* and their occurrence was recorded.

The position of the cave entrances as well as that of skylights was determined with a Global Positioning System (GPS) device (Garmin GPS 12XL, 12 channels). If possible, several independent measurements were taken on different dates, and the coordinates were averaged.

The values were mapped onto a topographical map (DeLorme 1999: 1:84,000, WGS84) using a GPS grid. The map was then digitised and re-scaled, and the dots were then transferred onto a (also digitised) geological map (Wolfe & Morris 1996: 1:100,000, Universal Transverse Mercator Projection). In all cases, it was possible to assign the positions unambiguously to a dated lava flow within the error probability (see Plates V & VI). The course of the ca. 60 km long Kazumura master tube was mapped using data from Allred & Allred (1997), and the course of Carson Cave could be charted for about 3.7 km using own measurements.

2.2.2 Morphology (morphometry)

For the morphometric analyses, individuals from 22 populations were studied (Tab. 2). Nine parameters (Tab. 5) were measured using a measuring ocular with an Olympus SZH 10 at 50-fold magnification (accuracy ±10 μm). In the analyses, these measurements were complemented by four indices computed from six of the measured parameters (see also Wessel & Hoch 1999 and for details Wessel 1997).

Table 5. Morphometric parameters and indices used in the statistical analyses (parameters 01-13).

01	Tegmina length	
02	Tegmina width	
03	Pronotum length	
04	Mesonotum length	
05	Mesonotum width	
06	Head width	
07	Vertex width	
08	Length of middle tibia	
09	Length of rear tibia	
Indices		
10	Wing proportion	= wing length:wing width
11	Relative wing length	= wing length:mesonotum width
12	Relative length of rear tibia	= length of rear tibia:mesonotum width
13	Head proportion	= vertex width:head width

2.2.3 Acoustic recording and analyses

For the sound recordings, adults and 5th instar nymphs were taken to the laboratory and kept under controlled conditions closely resembling those of their natural habitat (complete darkness, constant temperature about 18°C). Adults were kept individually on roots of *Metrosideros* or fresh sprouts of soybeans, as a substitute; the nymphs were separated following final moulting (for details see Howarth 1979 and Hoch & Howarth 1993).

For recording of vibrational signals, a male and female (if available) from the same population were placed together onto the substrate. The natural substrate (living *Metrosideros* roots) was substituted by fresh *Metrosideros* leaves or small pieces of balsawood. Light exposition of the recording area was considerably reduced; although, enough light was retained to observe the animals and record their behaviour.

The vibrational signals were received with a magneto-dynamic induction converter system ('MD-system' sensu Strübing & Rollenhagen 1988) and amplified approximately 1,000 times in the process. The signals were tape-recorded either with a Philips D 6920 MK2 or a Sony TC-D5M (on Sony UX Position Chrome 60 or TDK SA 60 tapes, both IEC II/Type II, High Bias 70 μs EQ) or with a Digital Audio Tape Recorder Sony TCD-D8 (on TDK DA-RXG DAT-tapes, sampling rate 48 kHz).

For time pattern measurements, signals were digitised using Mac Lab/4s (ADInstruments) running on a Power Macintosh 7600/132 with a sampling rate of 44 kHz. Measurements were taken using Chart v3.5.4./s with an accuracy of ±0.15 ms. The data were then transferred to Microsoft Excel. For archival storage, the recordings were digitised under studio standards (sampling frequency 96 kHz, 16 bits) using Avisoft-SASLab Pro v. 3.0-4.40 (software by R. Specht, 1991-2007, Germany, distributed by www.avisoft.de). Spectrographic analyses were performed with Avisoft-SASLab Pro and PRAAT v. 4.3.14 (software by P. Boersma & D. Weenink, 2001-2005, The Netherlands, distributed by www.praat.org).

Ten time pattern parameters of single calls (composed of more or less homogenous pulse trains, see Fig. 10) were taken (Tab. 6). After omission of the first and last three pulses of the call, the parameters 17 to 23 were included in the analysis as parameters 24 to 30 in order to assess intraindividual variability (Tab. 6, see also Wessel & Hoch 1999, for details Wessel 1997).

Table 6. Song parameters measured and used in the statistical analyses (parameters 14-30).

14	Number of pulses per call
15	Call duration
16	Duration of the following pause
17;24	Longest inter-pulse interval (IPI)
18;25	Shortest IPI
19;26	Mean value of the duration of the IPIs
20;27	Variation range of the IPI durations
21;28	Standard deviation of the IPI durations
22;29	Ascent of the linear regression above the sequel of IPI durations
23;30	Intersection of the linear regression with the ordinate

2.2.4 Statistical analyses

Statistical analyses were performed with SPSS v. 11.5.1 for Windows (SPSS Inc.). Only cases with complete parameter sets were included for population comparisons. For the specific parameters of the different analyses see Results 3.2, the statistical treatment of the DNA sequence data is described in Methods 2.2.5.

2.2.5 Molecular genetics and sequence analyses

DNA extraction: DNA was purified from whole nymphs (4th and 5th instar larvae) with DNeasy Tissue kits from Qiagen using the standard protocol in the DNeasy Tissue Kit Handbook. Final DNA concentration was estimated from agarose gel bands.

DNA amplification: Polymerase chain reaction (PCR) was used to amplify two mitochondrial gene fragments with universal primers, a region of 710 basepairs at the 5'-end of the cytochrome oxidase subunit I gene (COI) (primers LCO1490 & HCO 2198, Folmer et al. 1994) and a ~550 bp region of the 16S ribosomal gene (primers 16Sar & 16Sbr, Palumbi et al. 1996). PCR was performed in 25 μl volumes containing 1X Taq buffer, 1.5 mM $MgCl_2$, 200 μM each dNTP, 1-2.5 U Taq polymerase, ca. 100 nM DNA and ddH_2O up to volume on a Perkin Elmer GeneAmp 2400 thermocycler. After an initial denaturation step of 3 min. at 94°C, cycling conditions were 35 cycles of 1 min each at 94°C, 45°C (COI), or 53°C (16S) and 72°C, with a final elongation step of 5 min. PCR products were purified with QiaQuick PCR purification kits (Qiagen) following the standard QiaQuick PCR purification protocol.

Sequencing: Both strands of both genes were cycle sequenced with the original PCR primers using ABI Prism BigDye™ terminator chemistry and visualised on an ABI Prism 377 automated DNA sequencer. The resulting sequence electropherograms of both strands were corrected manually for misreads and merged into one sequence file using BioEdit Version 5.0.1 (Hall 1999), which was generally used to store and manage sequences.

Alignment: COI sequences were aligned manually and checked by translating the DNA sequences into amino acids in DAMBE 4.0.75 (Xia & Xie 2001) using the genetic code for invertebrate mitochondrial DNA. The ribosomal DNA sequences were aligned with Clustal v. X 1.8.1 for Windows (Thompson et al. 1997) using default settings. The resulting alignment was corrected manually.

Data exploration: MEGA 3 (Kumar et al. 2004) was employed to calculate pairwise distances and nucleotide composition.

To determine the best substitution model (Cunningham et al. 1998), hierarchical likelihood ratio tests (Posada & Crandall 2001) were carried out with MrModeltest 2.2 (Nylander 2004) and PAUP*4.0b10 (Swofford 2003) for Macintosh. The parameters specified by the selected models (Tab. 7) were used for further analyses where applicable.

Table 7. Selected models and parameters specified for phylogenetic analysis (using hLRTs).

	Model selected	-lnL	Base frequencies				Gamma distribution
			A	C	G	T	shape parameter
COI	GTR+G	2003.6532	0.3516	0.1828	0.1373	0.3282	0.2844
16S	GTR+G	972.5927	0.3188	0.0776	0.1638	0.4398	0.0

Phylogenetic analysis: Different reconstruction methods were used to derive phylogenies as this allows the consistency of phylogenetic estimation to be evaluated (Avise 1994). Phylogenetic trees were reconstructed using distance (neighbor joining (NJ), Saitou & Nei 1987) and maximum parsimony (MP, Fitch 1971) methods as implemented in PAUP*, and Bayesian inference (BI, Huelsenbeck et al. 2001) using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). NJ analyses were conducted using the random initial seed option to break ties. As suggested by running the sequence sets through MrModeltest (see above), the models of Kimura (1981) – COI – and Tamura & Nei (1993) – 16S – were used to correct for multiple substitutions. The robustness of inferences was assessed through bootstrap resampling (1,000 replicates) (Felsenstein 1985). In the MP analyses, the heuristic search algorithm was employed with 10 random additions of taxa and tree bisection–reconstruction (TBR) branch swapping. The random addition of sequences increases the effectiveness of heuristic searches as it decreases the risk of finding local optima only (Maddison 1991). Gaps were treated as fifth base. All other settings were left at default values. Support for nodes was estimated by bootstrap resampling (1,000 replicates) with one random addition per replicate. BI offers the advantage of providing values indicating statistical support for nodes. In all analyses, four independent chains were run for 1,000,000 generations, and every 100th tree was sampled. The burnin value was determined in preliminary runs, and was consequently set at 4,000 (COI) and 5,000 (16S). The general time reversible model (GTR, Rodríguez et al. 1990) of sequence evolution with among-site rate variation gamma distributed – the gamma shape parameter as estimated by MrModeltest – was employed. In addition, the COI data set was run with among-site rate variation set to codon position site specificity.

A minimum spanning COI network was generated using DNA Sequence Polymorphism (DnaSP), v. 4.50.2 (Rozas et al. 2003) with parameters set to "missing/gaps not considered" and "invariable sites included" and TCS v. 1.21 (Clement et al. 2000), which employs the method of Templeton et al. (1992) with a connection limit (parsimony criterion) of 94%.

Outgroups and rooting: *Pentastiridius pachyceps* (Cixiidae, GenBank acc. no. AF158030, v. AF158030-1) (COI), two Australian species of *Oliarus* and a Australian cave-dwelling *Solonaima* (16S rRNA) were used as outgroups to root the phylogenies.

3 Results

> Trotzdem darf man die Betrachtung des rationellen Zusammenhangs der Erscheinungen nicht übersehen. Was helfen alle Details, alle Speziesreitereien, wenn man nicht die Übersicht des Ganzen gewinnt!
> Und das ist nicht schwer, wenn man zuvor gründlich Details geritten hat.[1]
>
> Friedrich Rolle, um 1850

3.1 Position and age of caves

The position of the explored caves (entrances are marked) and the extent of the respective lava flows are shown on the map in Plate V. The lava flows were identified following the geological map of Hawai'i by Wolfe & Morris (1996) and are colour-coded according to their age. The courses of the Kazumura master tube and Carson Cave were added (see Methods 2.2.1). The GIS (Geographical Information System[2]) based on the merger of two digitised maps can be freely combined with other digital image data. For demonstration, the lava flows were mapped onto a satellite image following transformation with a respective contortion algorithm (Plate VI). This allows multiple correlations of lava flow position, for instance, with recent vegetation cover, land use patterns, and human settlements. GIS employment also enabled the exact determination of the age of the respective cave systems in all cases (see Tab. 8). The coordinates and exact altitude of cave entrances are treated confidentially (see Methods 2.2.1).

3.2 Bioacoustics and morphology

3.2.1 Qualitative differentiation

Single calls of animals of all populations consist of more or less homogenous trains of double pulses. Differences between populations are primarily quantitative with respect to absolute call length, mean pulse number, mean length of interpulse interval (IPI), and changes in the modulation of interpulse intervals among pulse trains.

---

[1] Cited after Martin & Uschmann 1968: 17.

[2] "A computer system for capturing, storing, checking, integrating, manipulating, analysing and displaying data related to positions on the Earth's surface. Typically, a Geographical Information System (or Spatial Information System) is used for handling maps of one kind or another. These might be represented as several different layers where each layer holds data about a particular kind of feature. Each feature is linked to a position on the graphical image of a map." (Patterson & Gittings 1996)

Table 8. Volcanic system, age and altitude of the explored caves.

Volcanic system*	Cave (section)	Age** in years	Altitude in feet***
Hualalai	PinkPistillaria Cave	5,000 – 10,000	2,200
Mauna Loa	Lanikai Cave	101 (in 1907)	800
	Kaumana Cave	127 (in 1881)	950
	Stainback Highway Cave #12	750 – 1,000	1,250
Kilauea	Calabash/Charcoal Cave	750 – 1,000	2,650
	Ainahou Cave	230 – 750	3,000
	Surprise Cave	38 (in 1970)	3,000
	Bird Park Cave	750 – 1,000	4,000
	Blair's Cave	230 – 750	2,900
	Bob's Cave	230 – 750	2,600
	Shick's Cave	230 – 750	2,600
	Carson's Cave	230 – 750	2,250
	Kazumura Cave (Main)	230 – 750	1,350
	John Martin's Cave	230 – 750	1,100
	DocBellou Cave	230 – 750	1,050
	Kazumura Cave (Sepulcher)	230 – 750	1,150
	Paradise Park Cave	230 – 750	250
	Pahoa Cave	230 – 750	550
	MacKenzie Park Cave	218 (in 1790)	50
* see Plate II		**lava flows, according to Wolfe & Morris 1996	***at cave entrance, rounded

The animals from Pink Pistillaria Cave form an exception: analyses of new recordings of males from Pink Pistillaria Cave have confirmed the earlier assumption (Hoch & Howarth 1993) of the existence of two *qualitatively* very different call patterns (Fig. 10). While the calls of some individuals show the usual homogenous pulse trains, the calls of the remaining animals are split into shorter pulse trains with a higher pulse frequency separated by pauses or pulse trains with a lower pulse frequency. This is the only documented case of single calls consisting of pulse trains with a different but constant frequency. It also represents a higher level of complexity if contrasted with all the other observed signals. An analogous case on the level of song structure is the occurrence of a regular duet structure in animals from the MacKenzie Park Cave population (Wessel 1997).

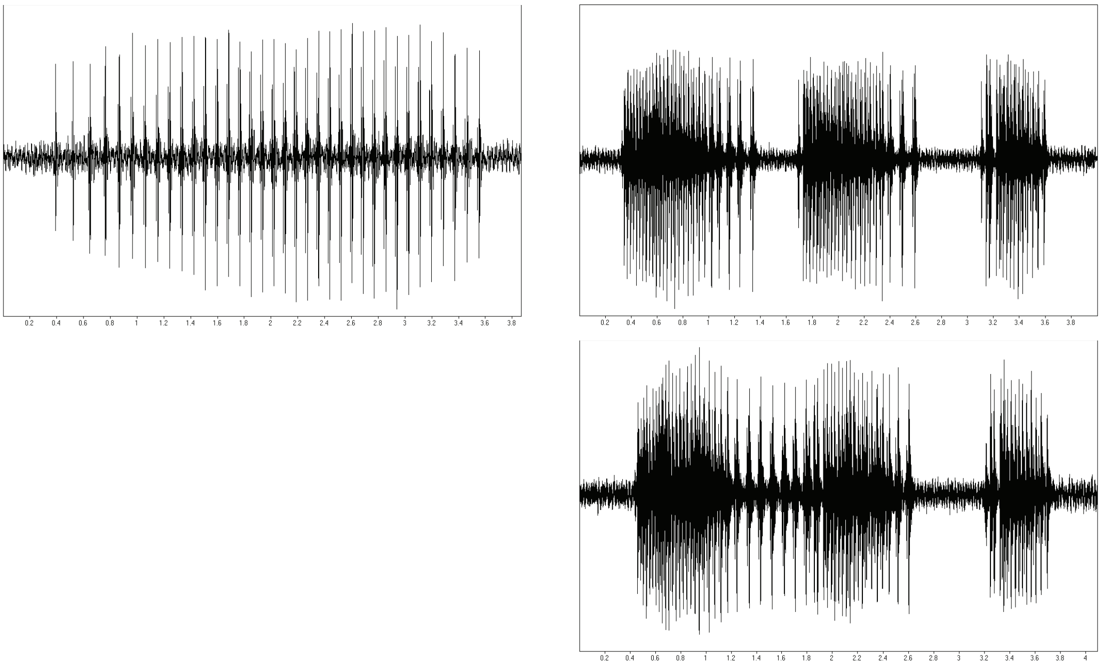


Figure 10. Oszillogramms of single calls of two different males from Pink Pistillaria Cave, at the right side two calls from one individual.

The different call patterns of the Pink Pistillaria Cave animals are specific for the tested individuals and transitions were never observed. Consequently, it is assumed here that two sympatric populations occur in Pink Pistillaria Cave, and the acoustic as well as morphometric data of the respective individuals have been treated separately in the following analyses (Pink Pistillaria 1 & 2). The separation of the Pink Pistillaria dataset also explains the phenomenon of an extraordinary range of variation or even bimodality in most morphological and acoustic parameters observed in earlier analyses (Wessel 1997). Following the separation of individuals in the analysis, an average or sub-average range of variation was found for all parameters (Fig. 11).

3.2.2 Quantitative differentiation

A sufficient set of measured parameters for statistical analyses was available for 18 (morphometry) and 12 (acoustics) populations, respectively (Tab. 2, 4 & 10). An analysis of variance (ANOVA) reveals a significant or highly significant differentiation in all measured parameters between all cave populations. Due to the pronounced sexual dimorphism (see Wessel 1997), there is less overlap between populations in the studied parameters if sexes are analysed separately. The populations are more clearly differentiated by acoustic than by morphological parameters (for F values see Tab. 9)

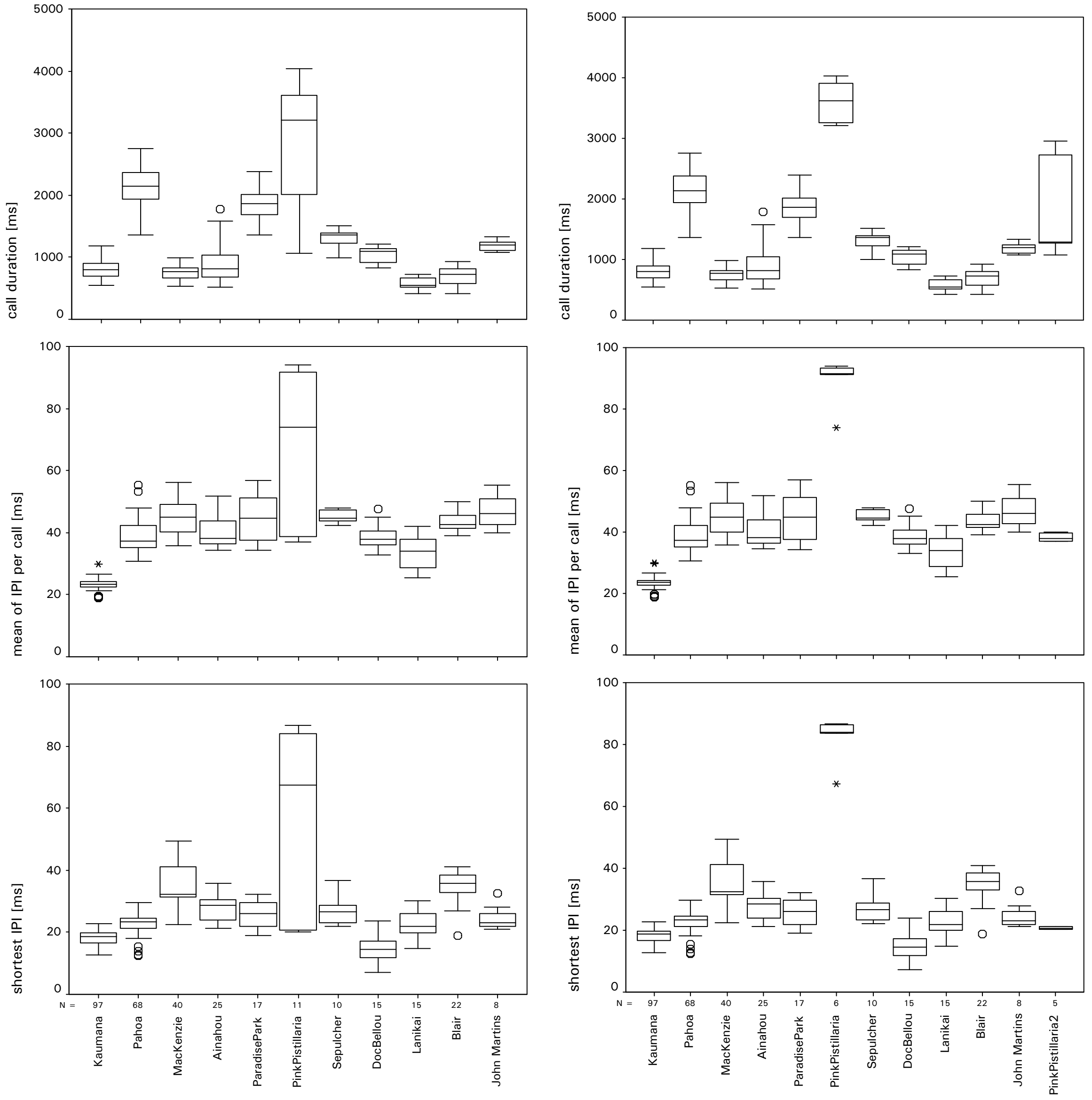


Figure 11. Variation in song parameters in different cave populations (boxplot graphs); on the left side the individuals from Pink Pistillaria Cave were analyzed together, on the right side they were analyzed separately based on qualitative differences in call pattern (see text for explanation).

Table 9. Differentiation of single parameters between cave populations as yielded by ANOVA tested both for each sex separately and combined. F values with levels of statistical significance are shown.

	All	Males	Females
Morphology	2.189**– 15.823*** N=313	3.743***– 14.036*** N=188	2,059*– 10.489*** N=125
Call pattern	26.725***– 141.519*** N=330	11.633***– 210.383*** N=129	17.687***– 248.358*** N=201

In two single call parameters (males), a non-overlap between one of the two Pink Pistillaria Cave populations and all other populations was observed. In one of these parameters the Kaumana Cave animals also showed a gap in measurement range to all other caves (Fig. 12).

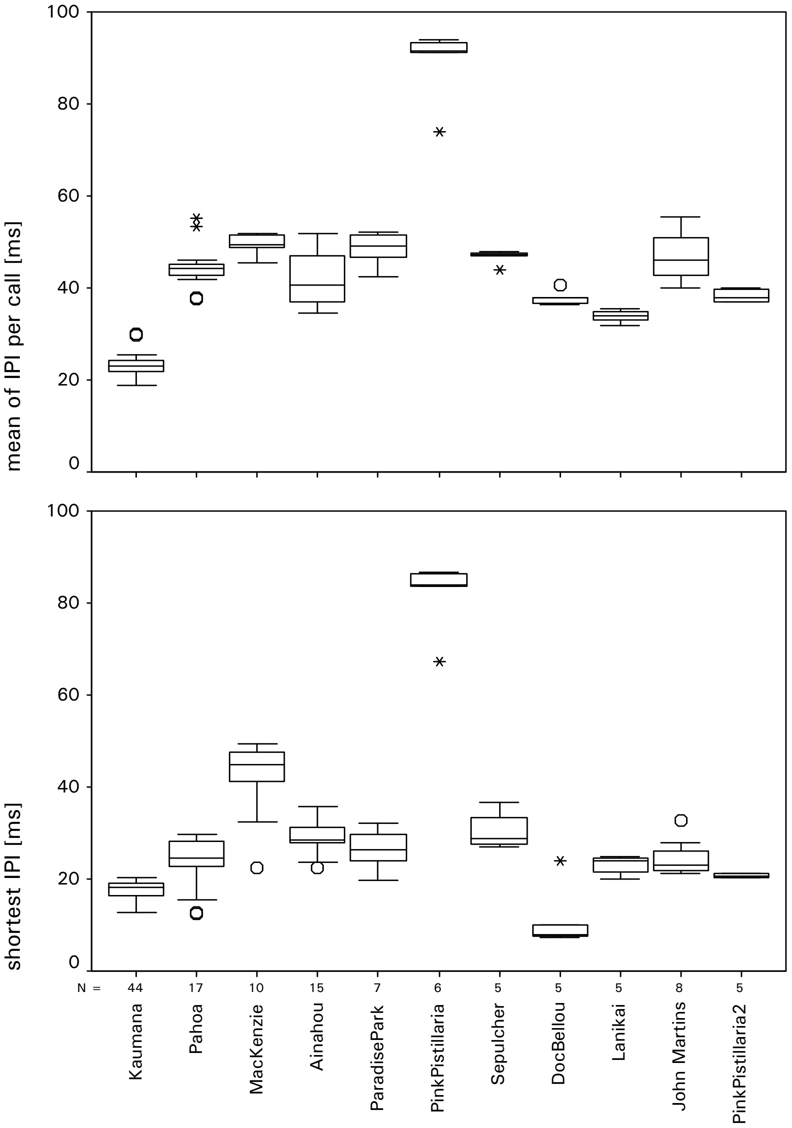


Figure 12. Variation in song parameters in different cave populations (boxplot graphs).

Discriminant analyses were conducted using all measured morphological and acoustic parameters for 18 populations (Tab. 10). Individuals from the Kaumana Cave population were 100% correctly classified by acoustic parameters. The individuals of both Pink Pistillaria Cave populations could also be 100% correctly classified by morphological parameters, i.e. they were discriminated both from all other cave populations and from each other. For the Lanikai Cave population this is possible for the acoustic parameters analysed separately by sex, and for male morphology parameters, for the Carson Cave animals for the morphological parameters analysed separately by sex. The populations of Paradise Park Cave, MacKenzie Park Cave, Kazumura Cave/Sepulcher Entrance, Kazumura Cave/Main entrance, DocBellou Cave, John Martins Cave, Bird Park Cave, Blairs Cave, Surprise Cave, and Stainback Highway Cave were 100% correctly classified for at least one character complex in one sex.

Table 10. Results of discriminant analyses for the differentiation of populations by morphology and song pattern, tested both for each sex separately and combined. The numbers refer to the percent of correctly classified individuals (cases), at the bottom the number of calculated discriminant functions and F values of the first discriminant function are shown.

	Morphology			Song pattern		
	All	Males	Females	All	Males	Females
N =	315	188	127	331	130	201
Pahoa	50	31.6	60.9	78.3	88.9	92.2
Kaumana	69.8	82.1	80	**100**	**100**	**100**
Ainahou	39.6	27.6	57.9	60	53.3	60
Paradise Park	53.6	70.6	54.5	76.5	**100**	90
MacKenzie Park	70.4	66.7	73.3	70	**100**	90
Lanikai	63.2	**100**	81.8	73.3	**100**	**100**
Sepulcher	23.1	23.5	55.6	90	80	**100**
DocBellou	41.7	33.3	66.7	86.7	80	**100**
Calabash	66.7	83.3	66.7	-	-	-
Kazumura/Main	66.7	37.5	**100**	-	-	-
John Martins	26.3	46.7	**100**	75	**100**	-
PinkPistillaria 1	**100**	**100**	-	**100**	**100**	-
PinkPistillaria 2	**100**	**100**	-	80	80	-
Carson’s	75	**100**	**100**	-	-	-
Bird Park	57.1	66.7	**100**	-	-	-
Blair	50	66.7	**100**	51.6	-	86.4
Surprise	50	33.3	**100**	-	-	-
Stainback Hwy.	80	**100**	-	-	-	-
correct classified	52.7	55.6	69.8	81.9	90.8	92.4
n-functions	14	14	14	12	11	8
eigenvalue of 1. function	2.526	3.857	15.264	13.95	35.92	12.915

3.2.3 Trends in quantitative trait differentiation

Correlation analyses were conducted in order to uncover statistically significant patterns of population differentiation. No significant relationships were found when the means and medians of both morphological and acoustics parameters were correlated with the distance between caves, the distance to a hypothetical center of origin, cave age, or cave altitude (see Figs. 13 & 14).

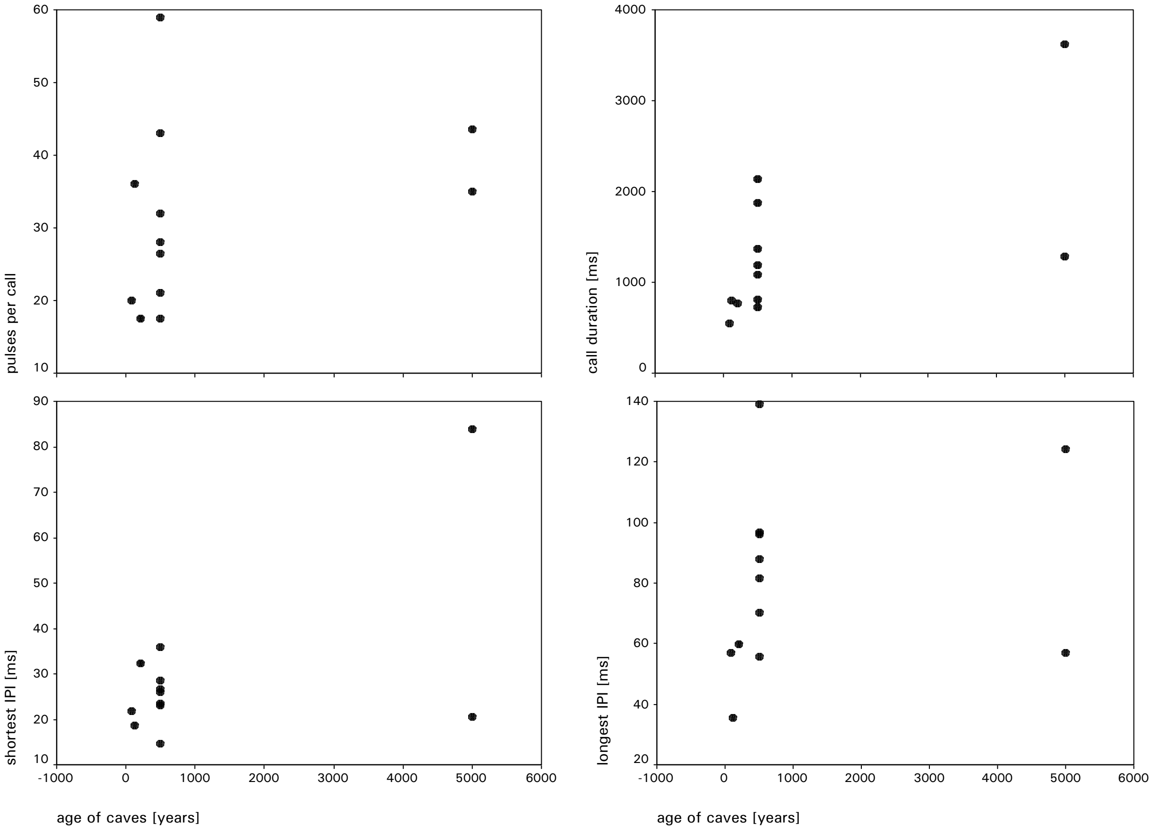


Figure 13. Scatterplots of the relationships between median of song parameters and the cave age.

A potential relationship between character variability and population age was tested by plotting variance against cave age (Figs. 15 & 16). Confidence for correlation was tested using Kendalls τ (Marascuilo & McSweeney 1977, Bortz et al. 1990) and correlation strength using Spearmans ρ (Marascuilo & Serlin 1988, Siegel & Castellan 1988, Bortz et al. 1990).

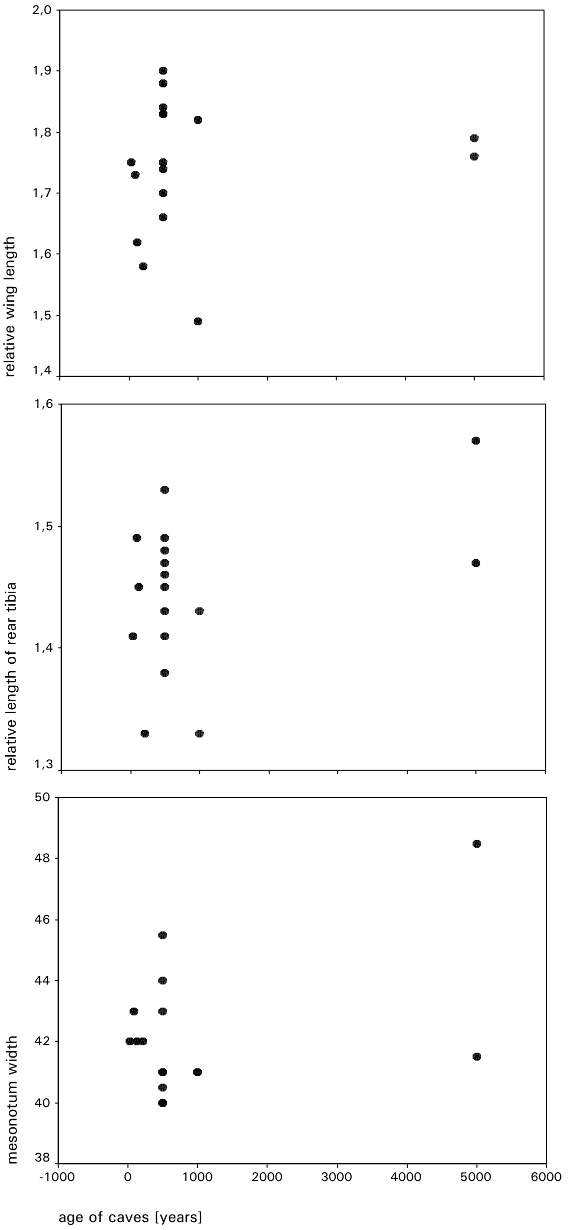


Figure 14. Scatterplots of the relationships between median of morphological parameters and the cave age.

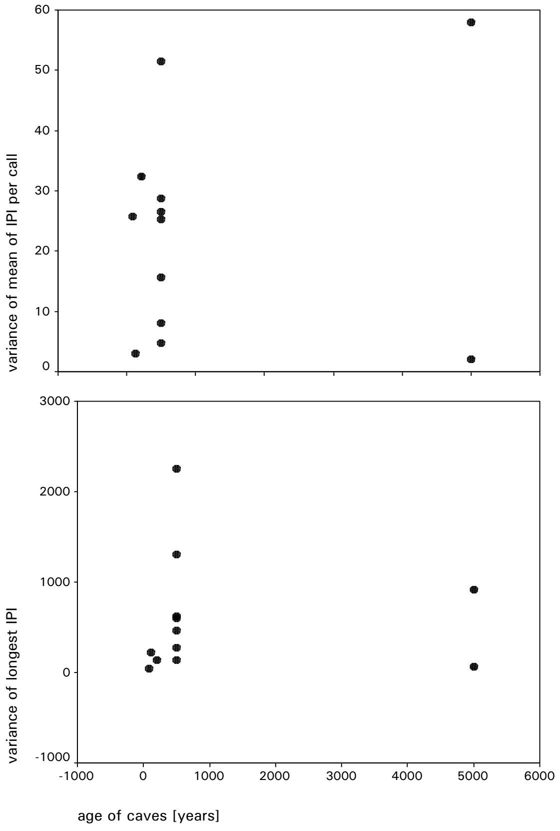


Figure 15. Scatterplots of the relationships between the variance of song characters with cave age.

None or a non-significant negative correlation was found for the acoustic parameters, while 9 out of 14 morphological characters showed a significant or highly significant negative correlation to cave age, two characters a non-significant negative correlation, two more none at all, and one a weak positive correlation (see Tab. 11).

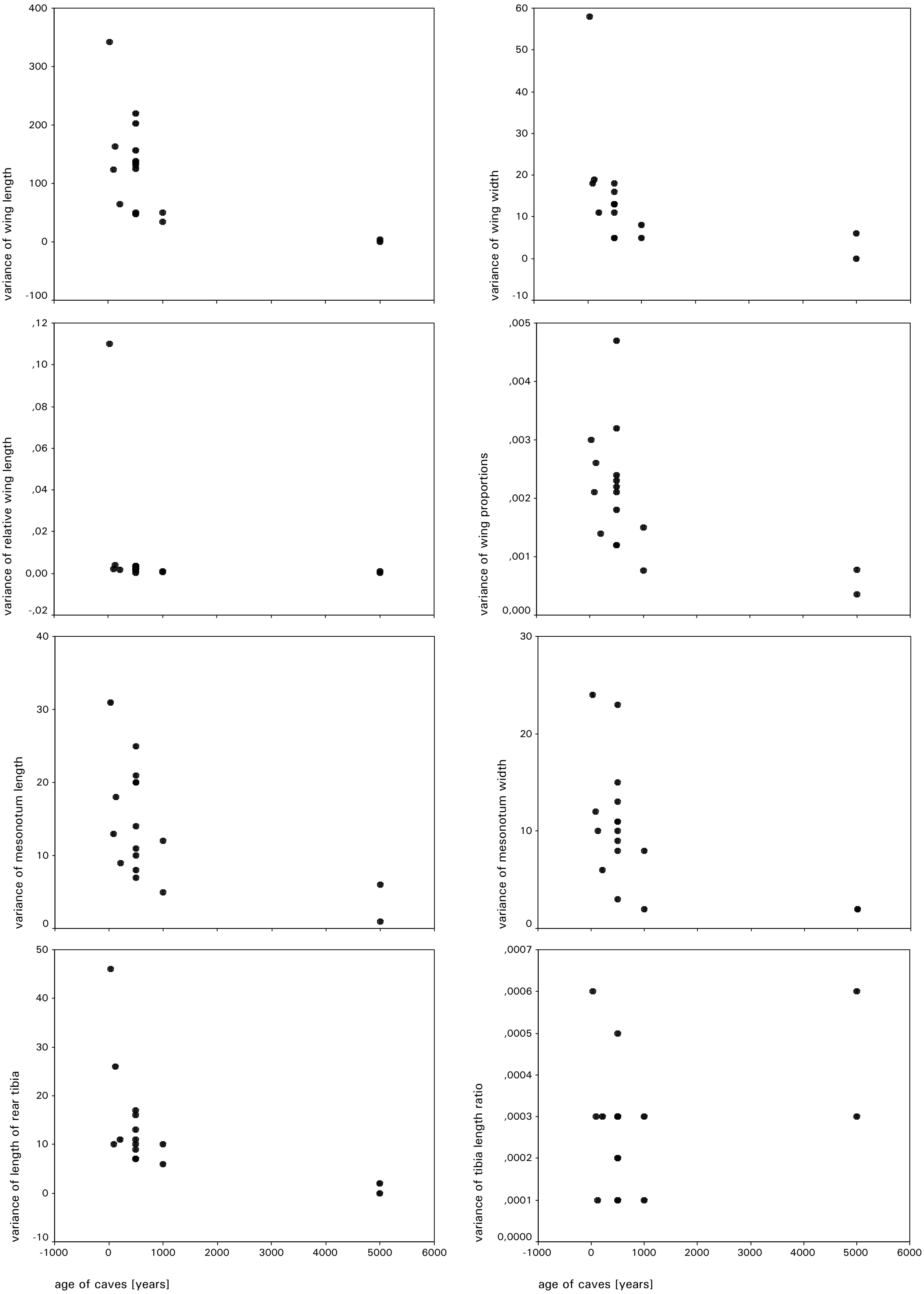


Figure 16. Scatterplot of the relationships between the variance of morphological characters with cave age.

Table 11. Correlation between the variance and mean of morphological parameters and cave age (Correlation coefficients and significances).

Parameter	Variance / Age (all)				Mean / Age (all)	
	Kendall's ▯		Spearman's ▯			
	Correlation Coefficient	Significance (2-tailed)	Correlation Coefficient	Significance (1-tailed)	Correlation Coefficient	Significance (2-tailed)
Tegmina length	-0.530	0.006**	-0.643	0.003**	0.329	0.197
Tegmina width	-0.632	0.001**	-0.742	0.0***	0.298	0.245
Mesonotum length	-0.452	0.019*	-0.578	0.008**	-0.042	0.874
Mesonotum width	-0.514	0.009**	-0.620	0.004**	-0.099	0.704
Pronotum length	0.044	0.821	0.079	0.382	0.154	0.556
Head width	-0.159	0.417	-0.192	0.23	-0.339	0.183
Vertex width	-0.452	0.019*	-0.56	0.01*	0.071	0.786
Length of middle tibia	-0.412	0.034*	-0.48	0.026*	-0.007	0.980
Length of rear tibia	-0.605	0.002**	-0.706	0.001**	0.106	0.686
Tegmina proportions	-0.480	0.013*	-0.588	0.007**	0.204	0.433
Rel. tegmina length	-0.574	0.003**	-0.693	0.001**	0.242	0.349
Rel. length of rear tibia	-0.143	0.469	-0.19	0.233	0.165	0.528
Ratio of tibia length	0.0	1.0	0.003	0.49	-0.003	0.992
Head proportions	0.248	0.206	0.306	0.116	0.448	0.072

3.3 Genetic differentiation and phylogeny

In the genetic analysis of the two mitochondrial gene fragments, 11 haplotypes (A-L) in 20 individuals from 14 caves were found for COI and 8 haplotypes in 13 individuals from 13 caves for 16S. Only in one case two different haplotypes were observed in one cave (COI). Pairwise distances (p-distance) for both genes are summarised in Tables 12 and 13.

For COI, the maximum genetic distance found in *O. polyphemus* is 4.2% between individuals from Lanikai Cave and Kaumana Cave. The distance between Lanikai Cave and Pink Pistillaria Cave is 1.9%. The genetic distance of the dominating haplotype (D, see next paragraph) to Kaumana Cave is 1.4%, to Stainback Hyw Cave 0.6% and to Surprise Cave less than 0.1%. The distance between *O. lorettae* and an *O. polyphemus* population ranges from 1.7% (haplotype D and Surprise Cave) to 4.4% (Lanikai Cave), while the distance of the *O. spec.* is between 6.2% (Stainback Hyw. Cave) and 7.0% (Lanikai Cave).

	1	2	3	4	5	6	7	8	9	10	11
1	0.000										
2	0.017	0.000									
3	0.014	0.031	0.000								
4	0.000	0.017	0.014	0.000							
5	0.000	0.017	0.014	0.000	0.000						
6	0.014	0.028	0.022	0.014	0.014	0.000					
7	0.014	0.028	0.022	0.014	0.014	0.000	0.000				
8	0.033	0.044	0.036	0.033	0.033	0.042	0.042	0.000			
9	0.014	0.025	0.022	0.014	0.014	0.022	0.022	0.019	0.000		
10	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	
11	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
12	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
13	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
14	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
15	0.011	0.028	0.019	0.011	0.011	0.025	0.025	0.039	0.025	0.011	0.011
16	0.006	0.017	0.019	0.006	0.006	0.019	0.019	0.033	0.019	0.006	0.006
17	0.006	0.022	0.019	0.006	0.006	0.019	0.019	0.039	0.019	0.006	0.006
18	0.014	0.028	0.022	0.014	0.014	0.000	0.000	0.042	0.022	0.014	0.014
19	0.063	0.062	0.064	0.066	0.066	0.066	0.066	0.070	0.064	0.066	0.066
20	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
21	0.000	0.017	0.014	0.000	0.000	0.014	0.014	0.033	0.014	0.000	0.000
22	0.003	0.019	0.017	0.003	0.003	0.017	0.017	0.031	0.017	0.003	0.003
23	0.222	0.219	0.219	0.222	0.222	0.217	0.217	0.222	0.217	0.222	0.222

	12	13	14	15	16	17	18	19	20	21	22
12	0.000										
13	0.000	0.000									
14	0.000	0.000	0.000								
15	0.011	0.011	0.011	0.000							
16	0.006	0.006	0.006	0.017	0.000						
17	0.006	0.006	0.006	0.017	0.011	0.000					
18	0.014	0.014	0.014	0.025	0.019	0.019	0.000				
19	0.066	0.066	0.066	0.062	0.069	0.062	0.066	0.000			
20	0.000	0.000	0.000	0.011	0.006	0.006	0.014	0.236	0.000		
21	0.000	0.000	0.000	0.011	0.006	0.006	0.014	0.236	0.000	0.000	
22	0.003	0.003	0.003	0.014	0.003	0.008	0.017	0.236	0.003	0.003	0.000
23	0.222	0.222	0.222	0.231	0.225	0.225	0.217	0.311	0.222	0.222	0.222

Table 12 (page 63). Pairwise distances for COI. 1, Ainahou Cave (#3); 2, *O. lorettae*; 3, Pahoa Cave; 4, Surprise Cave; 5, Bird Park Cave ; 6, Kaumana Cave (#1) ; 7, Kaumana Cave (#3) ; 8, Lanikai Cave ; 9, Pink Pistillaria Cave ; 10, DocBellou Cave ; 11, Kazumura Cave (Sepulcher Entrance); 12, Carson's Cave (downflow); 13, Ainahou Cave (#2); 14, Ainahou Cave (#1); 15, Calabash Cave; 16, Shick's Cave; 17, Stainback Highway Cave; 18, Kaumana Cave (#2); 19, *O. spec.* (epigean); 20, Bob's Cave; 21, DocBellou Cave; 22, Carson's Cave; 23, *Solonaima pholetor/stonei*.

Table 13. Pairwise distances for 16S. 1, Kazumura Cave (Main Entrance); 2, Paradise Park Cave; 3, John Martin's Cave; 4, Surprise Cave; 5, Ainahou Cave (#3); 6, Carson's Cave (downflow); 7, Stainback Highway Cave; 8, Bird Park Cave; 9, Lanikai Cave; 10, Bob's Cave; 11, Shick's Cave; 12, Pink Pistillaria Cave; 13, Kaumana Cave; 14, *O. spec.* (epigean); 15, *O. filicicola* (epigean); 16, *Pentastiridius spec.*

	1	2	3	4	5	6	7	8	9	10	11
1	0.000										
2	0.000	0.000									
3	0.000	0.000	0.000								
4	0.000	0.000	0.000	0.000							
5	0.000	0.000	0.000	0.000	0.000						
6	0.000	0.000	0.000	0.000	0.000	0.000					
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000				
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
9	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.000		
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000
12	0.013	0.013	0.013	0.013	0.013	0.013	0.013	0.013	0.013	0.013	0.013
13	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006	0.006
14	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.019	0.013	0.019	0.019
15	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.016	0.023	0.023
16	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.126	0.123	0.126	0.126

	12	13	14	15	16
12	0.000				
13	0.013	0.000			
14	0.026	0.019	0.000		
15	0.019	0.023	0.016	0.000	
16	0.129	0.129	0.129	0.123	0.000

For 16S, the maximum distances found in *O. polyphemus* is 1.3% between Pink Pistillaria and the remaining populations, and 0.6% between both Lanikai Cave and Kaumana Cave and the remaining populations, except Pink Pistillaria. Distances to the epigean *Oliarus* range from 1.3% (*O. spec.* – Lanikai Cave) to 2.6% (*O. spec.* – Pink Pistillaria Cave), while a distance of 1.6% was observed between the epigean *Oliarus* species.

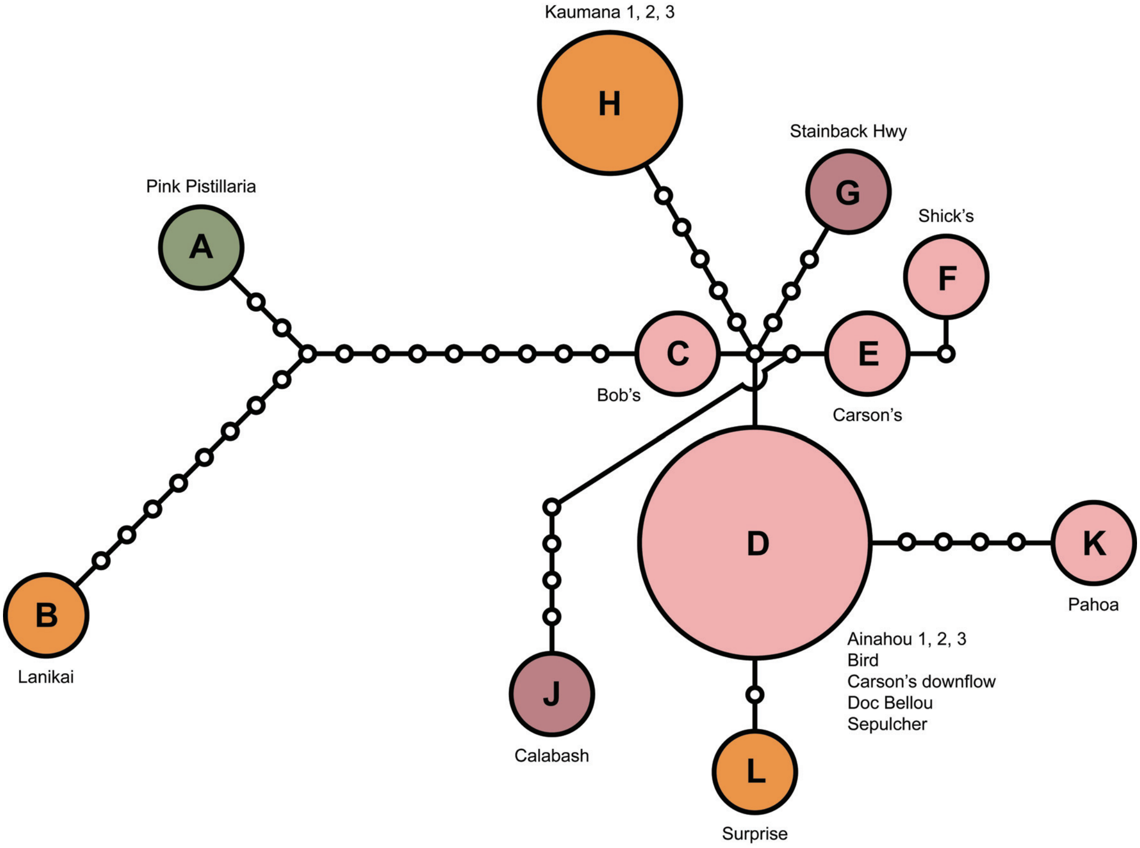


Figure 17. COI haplotype network (for explanation see text).

For COI, a haplotype network was calculated with TCS v. 1.2.1 (Fig. 17) and the geographic distribution of haplotypes is depicted on a schematic map (Fig. 18). In the network, the haplotypes have been arranged roughly according to the geographic position of the caves and are colour coded for cave age. The smaller unfilled circles represent extinct or unsampled haplotypes (see Templeton 2006). Nine haplotypes (A-C & F-L) are each found in only one cave or population. One haplotype (D) is found in seven individuals from five caves, which are situated in a single 200-750 year old lava flow at a maximum distance of 25 km. Only in one cave (Carson's Cave), an additional unique haplotype (E) was found in the upstream section in addition to the widespread haplotype D. In the network, five haplotypes (C-F & K) from a single lava flow are relatively close to each other with a maximum distance of five steps to the dominating haplotype D. The largest distance in the network is found between haplotypes A and B with 12 steps (between each other and between A and C), which corresponds to a relatively isolated geographic position (see Fig. 18).

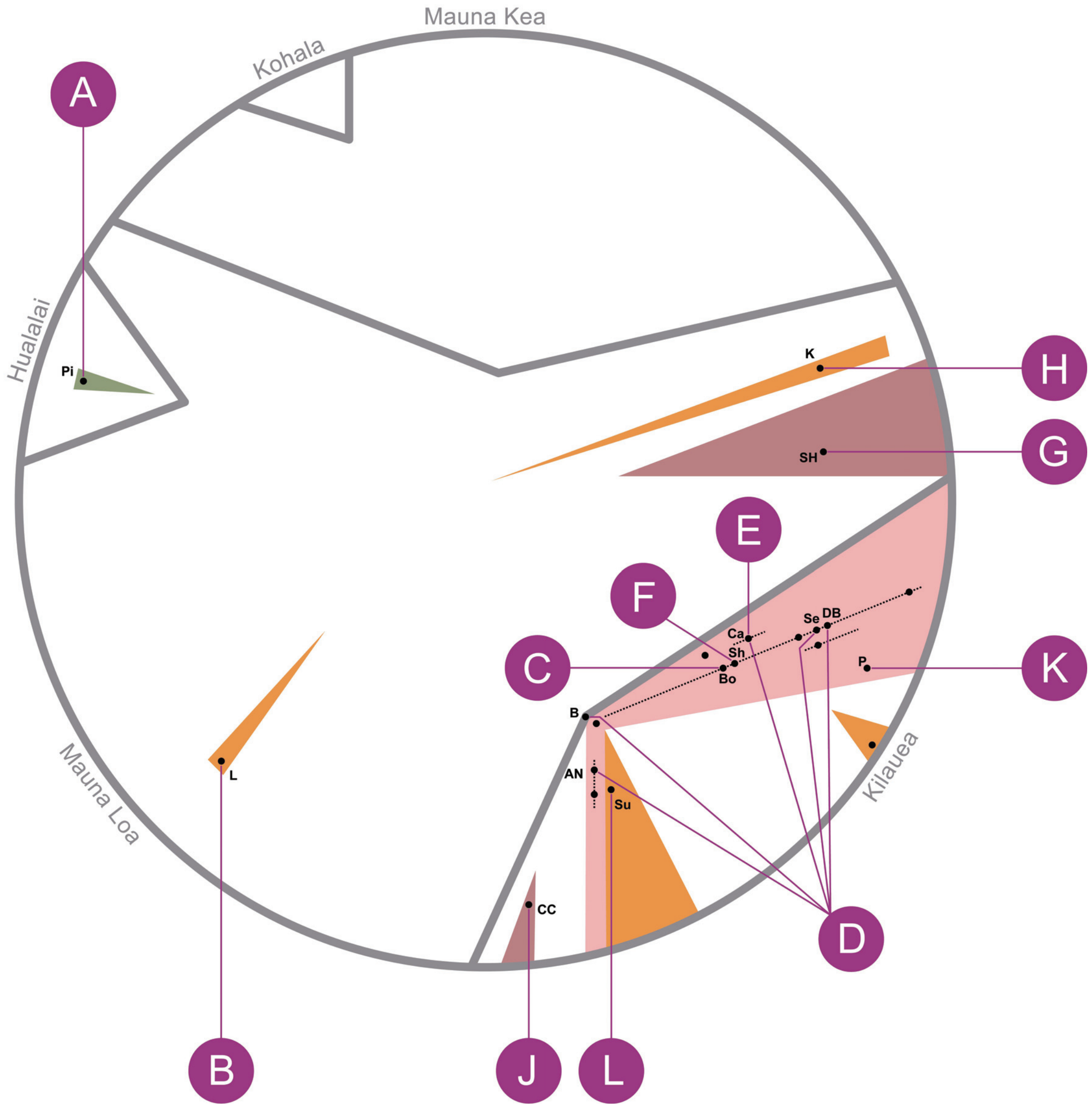


Figure 18. Schematic illustration of the geographic distribution of COI haplotypes.

The phylogenetic analyses were conducted separately for both gene fragments due the rather incomplete overlap between the COI and 16S datasets. Unrooted and rooted NJ topologies and a strict consensus MP tree each for COI and 16S are shown in Figures 19-24. An additional cave species from Hawai'i Island (*Oliarus lorettae* Hoch & Howarth, 1999) was included in the COI analysis. An epigean *Oliarus* species from Hawai'i Island as well as two epigean *Oliarus* species and a troglobitic *Solonaima* species from Australia were used as outgroups. For 16S, two epigean *Oliarus* species from Hawai'i Island and a sequence of a species of *Pentastiridius* (Cixiidae) from GenBank (AF158030-1) were employed as outgroups.

O. polyphemus is recovered as a monophyletic group in all analyses, but the low genetic variability prevents a sufficient resolution within this clade. However, the individuals from Pink Pistillaria Cave and Lanikai Cave are always found in a basal position. Both cave populations appear as sister groups in all COI analyses (with a MP bootstrap value of 84), while they are placed basal (yet unresolved) in the 16S MP consensus tree, in the 16S NJ topology, Lanikai is found basal to all other *O. polyphemus* populations.

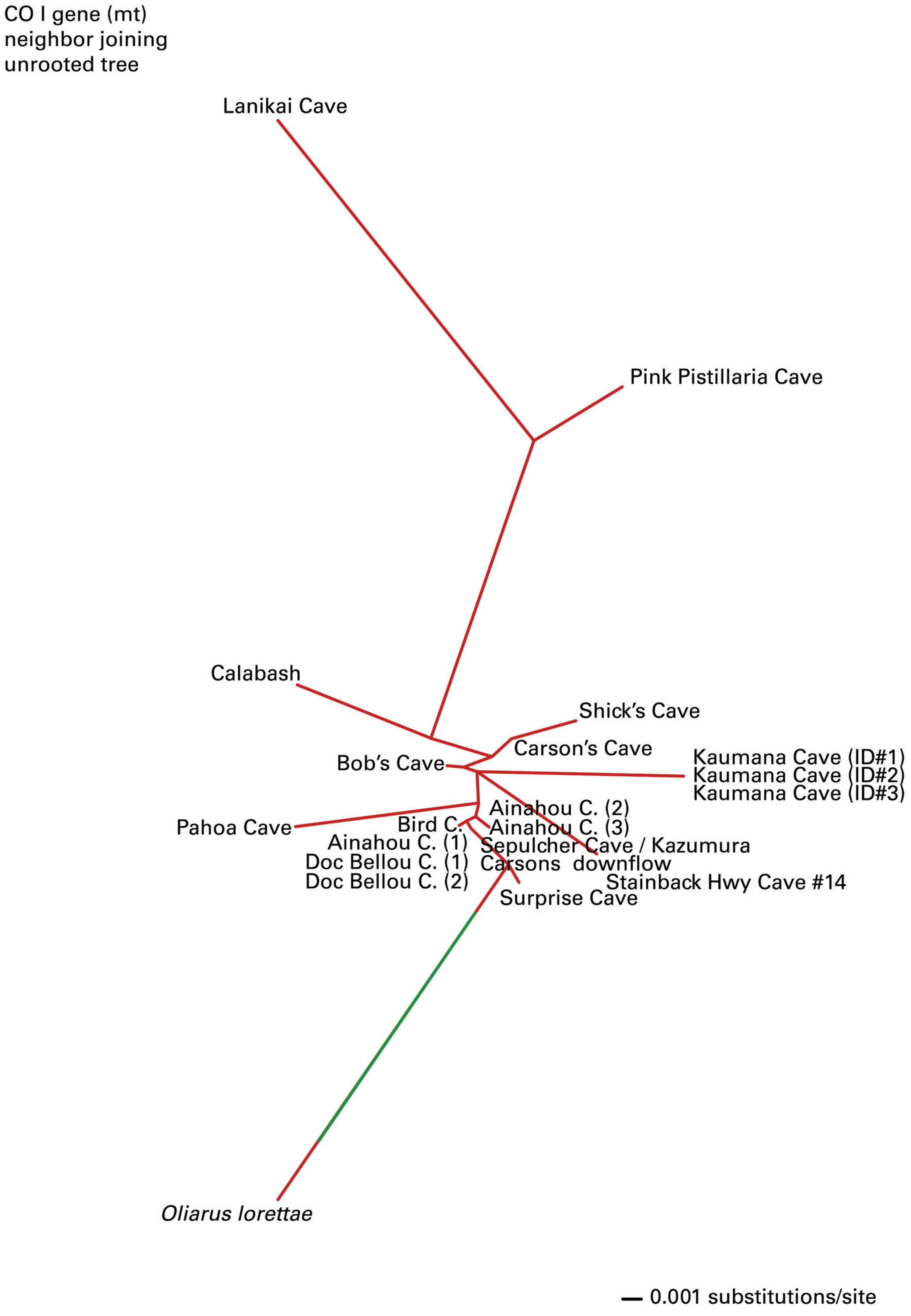


Figure 19. Unrooted Neighbor Joining topology (COI); red lines represent troglobitic lineages, green lines epigean lineage.

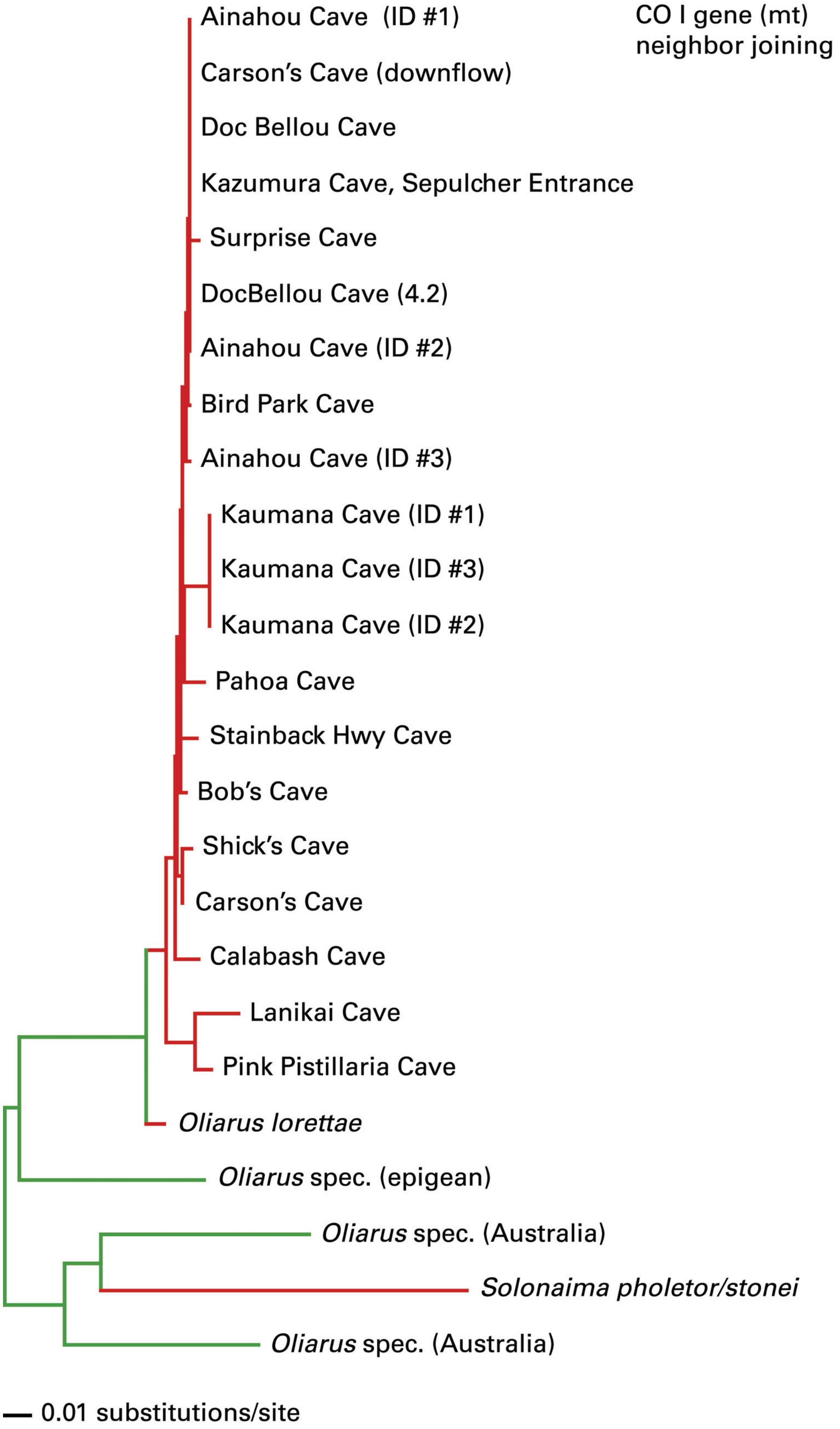


Figure 20. Neighbor Joining phylogram (COI); red lines represent troglobitic lineages, green lines epigean lineages.

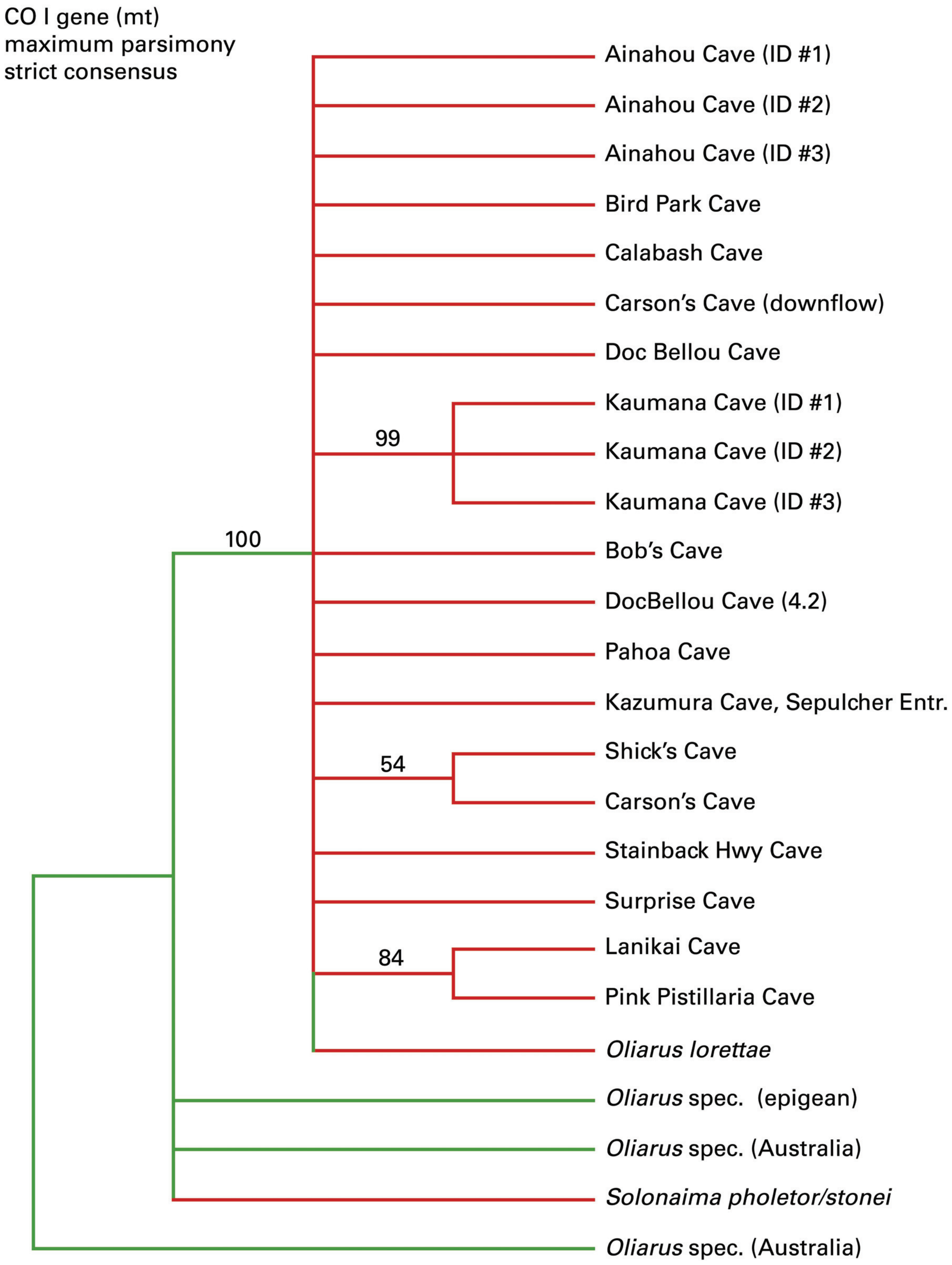


Figure 21. Maximum Parsimony cladogram (COI); red lines represent troglobitic lineages, green lines epigean lineages, numbers on branches are MP bootstrap values.

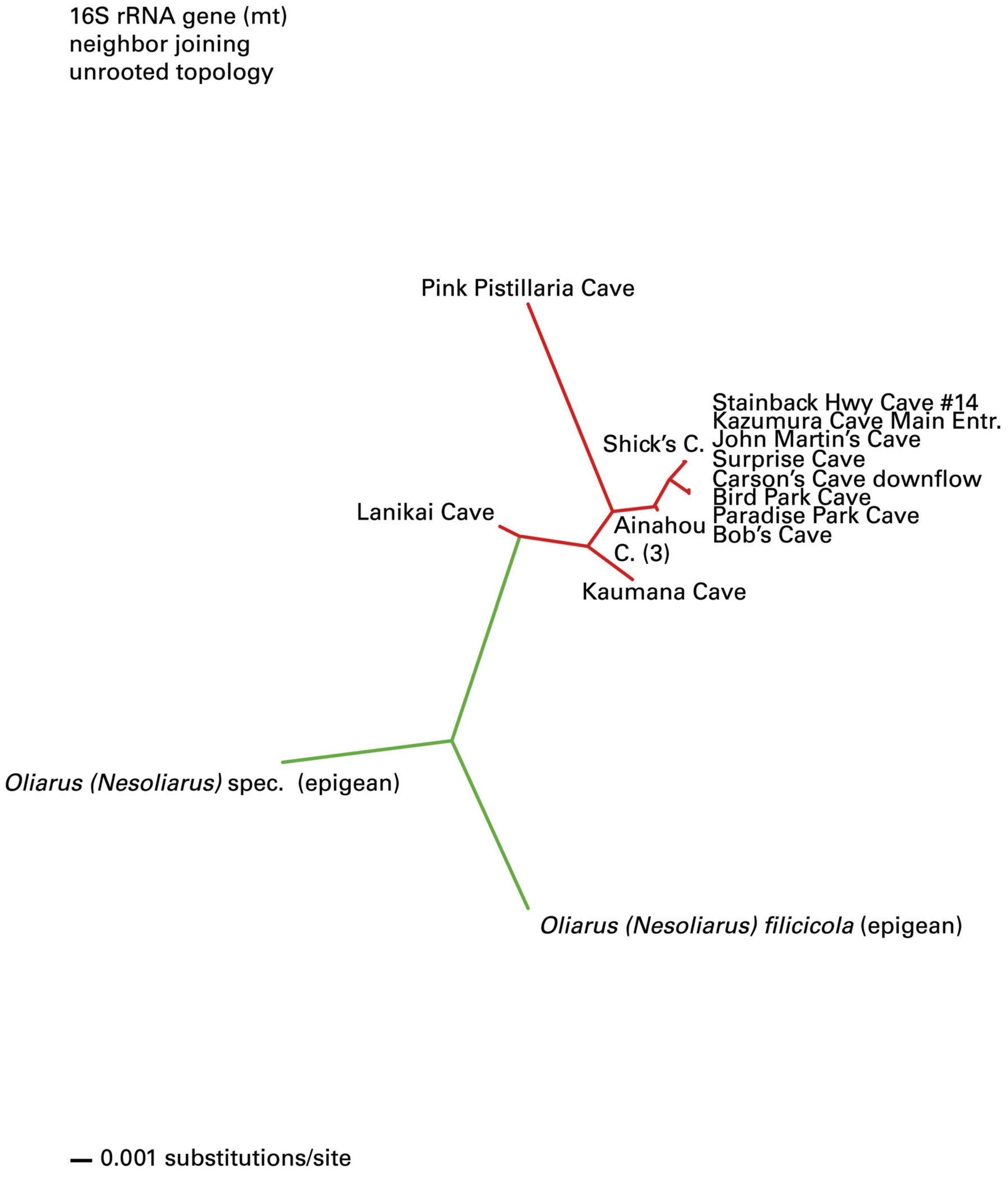


Figure 22. Unrooted Neighbor Joining topology (16S); red lines represent troglobitic lineages, green lines epigean lineages.

Figure 23. Neighbor Joining phylogram (16S); red lines represent troglobitic lineages, green lines epigean Hawai'ian lineages.

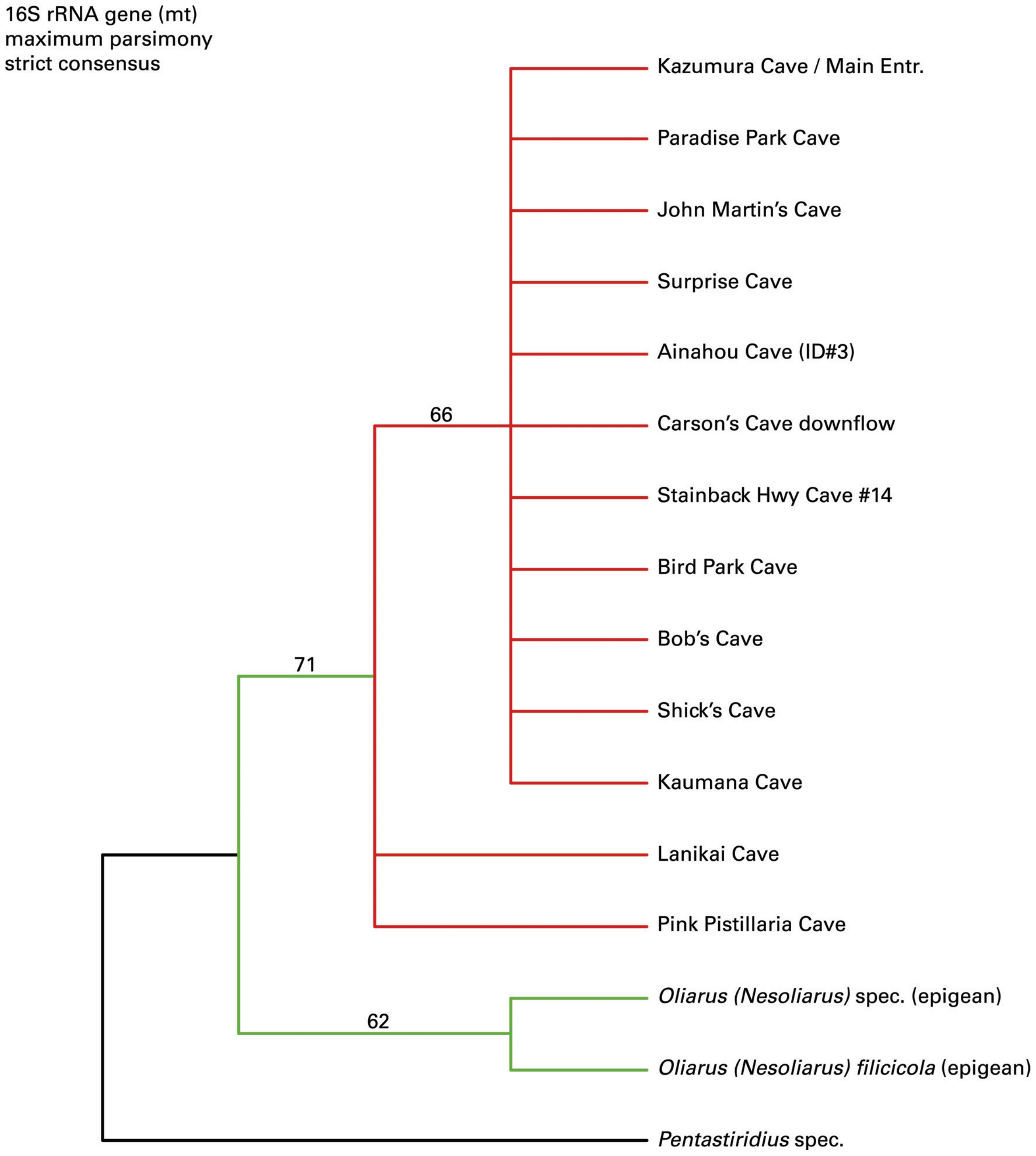


Figure 24. Maximum Parsimony cladogram (16S); red lines represent troglobitic lineages, green lines epigean Hawai'an lineage, numbers on branches are MP bootstrap values.

4 Discussion

> Unser Wissen ist ein kritisches Raten; ein Netz von Hypothesen; ein Gewebe von Vermutungen.[1]
>
> Karl R. Popper (1968)

4.1 Monophyly in *Oliarus polyphemus*

The establishment and usefulness of the *Oliarus polyphemus* complex as a model system crucially depends on its monophyly. With respect to the present study, Ernst Mayr remarked, "Dass auf Grund der Ähnlichkeit der Selektionsdrucke in verschiedenen Höhlen viel Parallelevolution stattfinden muss, ist unvermeidlich, aber manchmal ein Problem für den Taxonomen"[2] (Mayr, pers. comm., letter of February 10th 1998). Parallel evolution or parallelophyly is here used with respect to "phenotypic similarities [which] were independently acquired owing to an inherited ancestral propensity of their lineage to develop these characters" (Mayr & Bock 2002: 179).

On Hawai'i Island alone, caves have been colonized at least three times independently by *Oliarus* lineages. The seven troglobiont *Oliarus* species of the Hawai'ian Archipelago all share similar morphological characters due to the similar selection pressures in their habitat. All known species with the exception of *O. polyphemus* have a very restricted distribution, i.e. they have only been recorded from a single cave or cave system (Hoch & Howarth 1999). What is then the probability that the *O. polyphemus* population complex has arisen from several independent cave colonisations followed by convergent (parallelophyletic) evolution?

The remarkable morphological similarities of the *O. polyphemus* populations serve as first evidence against the polyphyly hypothesis. While the *O. polyphemus* complex and all other cave species can be easily distinguished from each other by habitus and genital morphology, single populations of *O. polyphemus* can only be separated by quantitative (morphometric) characters. There are neither diagnostic qualitative differences nor discontinuities in morphometric characters between populations. In addition, the pattern revealed by the genetic data (relative distances, molecular trees and networks) is congruent with the assumption of a single cave colonization event and subsequent subterranean distribution: geographic

---

[1] Cited after Popper 1989: XXV.

[2] "Widespread parallel evolution in different caves is inevitable given the similar selection pressures; this may pose a problem for the taxonomist, though."

distances are reflected in the genetic distances. The tree and the network, respectively, may be interpreted without conflict to a presumed distribution of the *O. polyphemus* complex originating at the western flank of the Hualalai via the southern slope of the Mauna Loa and the Kilauea, and again, northwards toward the eastern flank of Mauna Loa without exceeding an altitude of 4,000 feet.

Under the alternative hypothesis, i.e. the polyphyly of the species complex, these patterns can only be explained by assuming the existence of an epigean *Oliarus* species which colonized newly formed lava flows in an identical fashion and invaded the caves several times independently. This seems rather unlikely since young lava flows are not suitable habitats for epigean planthoppers and, in addition, the scenario would require a remarkable degree of convergent evolution within an extremely short period of time. Moreover, no epigean candidate species is known to be morphologically similar to *O. polyphemus* and shows a comparable distribution. Further evidence on this point is expected from work in progress on a phylogeny of the Hawai'ian *Oliarus (Nesoliarus)* clade (H. Hoch, unpublished data).

4.2 Populations, species and subspecies – differentiation in *Oliarus polyphemus*

The *O. polyphemus* complex comprises numerous allopatrically and peripatrically distributed populations that differ to a varying degree in their morphology (morphometrics) and ethology (acoustics) in caves of different age. How can this remarkable differentiation be interpreted? What is their biological meaning? How many species are hidden in this complex?

4.2.1 Concepts and criterions of different order

A general discussion on species concepts is not considered necessary here. Following Mayr (1963), biological species are regarded as natural units (bio-systems) reproductively isolated from each other under natural conditions (Biological Species Concept – BSC, see Introduction 1.1.1). It is nevertheless necessary to investigate in which way criteria may be derived from the BSC in order to recognize the existing bio-systems and delineate them against each other. A central aim is to use the criteria thus gained for the formulation of falsifiable hypotheses on the species status of the populations under study.

Problems in the recognisability and delineation, or the non-recognisability, respectively, of units in nature neither question their objective reality nor the underlying concept.

> "The nonarbitrariness of the biological species is the result of this internal cohesion of the gene pool and of the biological causation of the discontinuities between the species." (Mayr 1963: 21)

While a direct criterion of the first order may be derived from this definition, this will rarely be practically applicable:

> "The nonarbitrary criterion of the category species, biologically defined, is that of the interbreeding or noninterbreeding. When confronted with the task of having to assign a taxon to the correct category, the occurence or potentiality of interbreeding is usually only inferred. [...] Whether a given taxon deserves to be placed in the category species is a matter of the total available evidence. [...] Such difficulties are caused by lack of information, by evolutionary intermediacy (speciation incomplete), or by genuine inapplicability of the concept (owing to asexuality, that is, uniparental reproduction)." (Mayr 1963: 21-22)

The major problem concerning objectivity in species recognition and delineation may be traced to the rather limited knowledge regarding the entire system. Consequently, criteria must be employed in order to form falsifiable working hypotheses. Obviously, the criteria and the derived evidence must always be interpreted based on the underlying concept. The observable differences between populations should be discussed and tested with respect to the biological importance for the individuals of these populations.

The distinction between a theoretical and a practical species definition was already emphasised more than a hundred years ago by Ernst Haeckel, who deplored the arbitrary definition of so-called “essential species characters [wesentliche Artmerkmale]” by taxonomists (see Haeckel 1906). According to the BSC, “essential“ species characters or differences in sexually reproducing organisms, must either serve for the reciprocal recognition of individuals as members of the same species or prevent species recognition, or the production of fertile offspring, respectively. These “essential“ characters may not (yet) be recognizable to the taxonomist, though, or prove to be practically inapplicable as e.g. behavioural traits, which cannot be studied in museum specimens. Such cases require the establishment of indirect criteria of a second order, which allow to infer the degree of reproductive isolation. According to Mayr and Ashlock, the practical procedure follows these lines:

> "Whenever the taxonomist encounters two taxonomically distinct allopatric populations, a decision must be made whether to consider them species or subspecies. Various types of evidence are used in making this decision. Adherents of a typological species concept consider degree of difference per se to constitute sufficient rea-

> son for species recognition. Adherents of the biological species concept look for evidence of actual or potential interbreeding. They use degree of morphological difference only to draw inferences on the probability of potential interbreeding." (1991: 100)

Morphological differences are usually crucial for taxonomic practice since most studies are based on the examination of museum specimens. However, in theory, differentiations in any character complex are suitable to infer the reproductive isolation of populations.

If each species constitutes a distinct biological system, significant differences without any overlap in trait expression (referred to as gaps) must be present in at least one character, competence, tolerance, or preference in order to guarantee the integrity of the bio-system. Discontinuities or gaps that delineate species can occur in any character complex characterising the respective organisms. Behavioural or physiological traits may serve this purpose as well as morphological characters.

Reproductive isolation is always associated with a character gap between populations. Conversely, not every gap is causally related to reproductive isolation. Character gaps may be a consequence of reproductive isolation, they may occur due to correlated changes with characters, that are directly involved in reproductive isolation, or they may represent adaptations to environmental changes and thus secondarily induce genetic incompatibility.

In addition, the manifold sources of variation in a single population must not be neglected in the interpretation of interpopulation differentiation. Major well documented types of nongenetic variations are ontogenetic variation (e.g. larval stages, allometric changes in development), ecological variation (habitat variation, variation induced by temperature or light changes, host-determined variation or density-depend variation), polymorphisms like insect castes, and traumatic variation (parasite induced, teratological or postmortem changes). Genetic variation can occur as sexual dimorphism (primary and secondary gender differences, gynandromorphs and intersexes), as reproductively different generations (sexual versus uniparental strains), and as simple continuous as well as discontinuous (polymorphism) variation.

Another important aspect concerns the way populations or groups of individuals, respectively, are separated. In a nondimensional system sensu Mayr (sympatric and synchronous populations, see Mayr 1963), each gap, no matter in which character, signifies the existence of distinct bio-systems (species). Even the mere statistically significant separation of two populations through an analysis of variance in any trait (but for the exceptions listed above) is sufficient evidence for the existence of separate biological systems, i.e. species. However, causally the lack of interbreeding must be due to gaps in other (not analysed) traits.

More difficult is the analysis of allopatric or allochronic populations, where statistically significant differences between populations are just indicative of a current interruption of gene flow, but not necessarily of reproductive isolation. However, a gap in character distribution between allopatric populations, suggests the existence of discrete biological systems, which will, with some probability, exhibit also genetic incompatibilities.

Recently, under the label "DNA barcoding", neutral molecular markers, most commonly a ca. 600 bp fragment of the mitochondrial cytochrome oxidase subunit I gene (Hebert et al. 2003a, b), are used for species delimitation and identification in order to obtain "transparent and reproducible hypotheses" (Fisher & Smith 2008). While various methods have been proposed to assign haplotype clusters to species (Blaxter et al. 2005, Matz & Nielsen 2005, Zhang et al. 2008), all share the use of an arbitrary cut-off point. The simplest approach will use a sequence divergence threshold to distinguish species. For instance, all haplotypes or clusters differing by more than 2% will be regarded as species (Hebert et al. 2003b).

DNA barcoding is basically the application of an indirect criterion of a third order, which is dependent on a mere correlation with the results of the use of first or second order criteria for species delimitation. While phenotypic differences between individuals from different populations allow to make inferences about their biological meaning, i.e. the integrity of the respective systems (species), percentage differences in neutral markers will only yield such insights if used in correlation with phenotypic differentiation. Sequence differences without a (known) biological effect on the behaviour of individuals in a population are calibrated with differences between species, whose limits have been tested through other methods. The species delimitation threshold is thus derived from the known differences between "good species", or recognized subspecies, and then applied to populations of doubtful taxonomic status. The application of this third order criterion is rather problematic, though. Obviously, the calibration of the species delimitation threshold is crucially depending on the correct inference of species status in the reference taxa. This procedure is prone to a tautological reasoning. In addition, the assumption of equal mutation rates in all taxa over longer periods of time (molecular clock) has been largely falsified (Pulquério & Nichols 2007). Even assuming for the sake of simplication that a molecular clock will work in certain groups, and that speciation events are occurring clock-like as well, the time needed for the evolution of reproductive isolation between populations in a specific case will still strongly depend upon the circumstances on the populations' separation, their genetic structure, and accompanying environmental changes. Frequently, cases of both young, yet "good" species that share the same haplotype in neutral markers, and old, widely distributed species, with a pronouced haplotype polymorphism, are encountered.

Theoretically, sequence differences in single genes or gene complexes may be used for species delimitation if these are known to effect the expression of characters responsible for the recognition of mating partners (the SMRS sensu Paterson 1985). Even in this case, though, the sequence differences would just be secondary traits used for inferring differences between species-specific phenotypes where these are not directly accessible, such as e.g. behavioural traits in museum specimens.

Considering these limitations, molecular genetic analyses are nevertheless invaluable tools to gain insights into the history of speciation or species status for single taxa. Conspicuous sequence differences may indicate the existence of cryptic sibling species. Contrariwise, hypotheses about cryptic species gained through the analysis of other characters can be tested and additionally amended by quantitative estimates of gene flow or the duration of isolation (see e.g. Avtzis et al. 2008). Genetic evidence, e.g. for the existence of recent gene flow, can of course also reject hypotheses of species status based on morphological evidence (see e.g. Pérez-Barros et al. 2008).

4.2.2 Species as process – a probabilistic view

The existence of two distinct species can be hypothesised if gaps in character variation emerge from a comparison of allopatric or peripatric populations, or even if merely statistically significant differences are found between sympatric populations. How should statistically significant differences between allopatric populations be interpreted using objective criteria, and which taxonomic conclusions should be drawn?

As evidenced by the following citation, Mayr, Linsley, and Usinger held a deeply sceptical view about the use of statistic criteria which succinctly still reflect current opinion on this point, even though Mayr later partly changed his mind (see Mayr 1963):

> "The mere fact of a (statistically provable) difference between several populations of a species is therefore of no special interest to the taxonomist; he takes it for granted. Even the lowest recognizable taxonomic category (the subspecies) is normally composed of numerous populations that differ 'significantly' in the gene frequencies and in the means of certain variates. What the taxonomist wants to know

> is whether these differences between populations are large enough to justify classification in different taxonomic categories. [...] On the other hand, statistical methods do not usually reveal much about the quality of a difference. They do not permit a decision as to whether or not two allopatric populations belong to the same species, or whether two sympatric variants are individual variants or sympatric species. Reproductive isolation (the species criterion) and morphological differences are not necessarily closely correlated. [...] ... statistics deals with probabilities, not with certainties." (Mayr et al. 1953: 152-153)

The rejection of statistical methods based on the rationale that they "only" rely on probabilities and not on certainties seems a trifle odd if used in respect to phylogenetic analysis, which might also be called outright "analysis of probability". With regard to these views, it seems desirable to briefly touch upon the approach of regarding "species as process" in contrast to a treatment of the species as a static unit – one of the most important conclusions from the synthetic theory of evolution for systematics.

The practical difficulties in systematic or taxonomy, respectively, prompted already Weismann to point out that "typical" species will always only exist for a limited period of time (Weismann 1902, II: 342). As Mayr put it:

> "Evolution is a gradual process and, in general, so is the multiplication of species (except by polyploidy). As a consequence one finds many populations in nature that have progressed only part of the way toward species status. They may have aquired some of the attributes of distinct species and lack others. One or another of the three most characteristic properties of species - reproductive isolation, ecological difference, and morphological distinguishability - is in such cases only incomplete developed." (Mayr 1963: 24)

The first step in speciation is always the evolution of differences, i.e. discontinuities in any character between (spatially and/or temporally) separated populations by genetic drift, natural, or sexual selection. The evolution of isolating mechanisms is a secondary step only, either as a by-product or through reinforcement at secondary contact. The first step is largely a question of how to achieve a change in (or escape from) the co-adapted genotype, or how to shift from one adaptive peak to another in a structured adaptive landscape. This is also the focus of this study. Nevertheless, the taxonomic application of the criteria discussed above will be outlined here as well.

In the first place, taxonomy is an information storage system for the knowledge existing about the phylogenetic relationships of taxa and their status in the evolutionary process. Thus, it may be rather helpful to provide names for taxonomic units below the species level (i.e. subspecies):

> “The study of subspecies played an important role in the period during which the morphological species concept was replaced by biological. [...] Evolutionists also had a great interest in subspecies because subspecies were believed to reflect adaptation to the local environment and to represent incipient species.” (Mayr & Ashlock 1991: 97)

However, there are several different subspecies definitions. Also, the utility of the subspecies category is severely limited, if every specialist uses a personal threshold for the degree of difference necessary to justify naming a subspecies, or if this category is employed excessively for any local population. Consequently, if the category ‚subspecies’ is to be used at all in a meaningful way, both an underlying concept (species-as-process), with clearly defined criteria and an unambiguous definition of the term are indispensable.

According to Mayr and Ashlock, populations should only be ranked as a subspecies “if they differ ‘taxonomically’, that is, by sufficient diagnostic morphological characters” (1991: 44). The remarks made above about the definition of “essential species characters” by a specialist also apply to this procedure. Furthermore, they recommend the use of subspecies “in the sense of ‘allopatric populations of doubtful rank’” (Mayr & Ashlock 1991: 105). In this sense, the category would only be used as a temporary label as long as the limited knowledge of the system does not allow an unambiguous assignation to a taxonomic level. For an information retrieval purpose, the use of a species name would constitute a better working hypothesis, possibly with the addition “species inquirenda“ for the sake of clarity. Later workers may then, upon a more intimate insight into the study system, either maintain the name or synonymise it.

From a species-as-process perspective, those populations with no current gene flow to other populations, and which have consequently acquired (statistically) recognisable differentiation, may be hypothesised to represent incipient species and therefore be categorised and named as subspecies. The interpretation of inter-population differences can be formalised as a Statistic Species Criterion (SSCr), originally proposed by Remane (1968) and expanded upon by Wessel and Hoch (1999). In the simplest case, it will be sufficient to conduct an ANOVA of one character in which the result will be a highly significant ($p<0.001$) rejection for the derivation of samples from one population. Frequently, it will be more sensible to look at several characters at the same time. Mayr and Ashlock about this “variational overlap“:

> "Closely related species are sometimes so variable and their variation is so overlapping that no single character seems to have absolute diagnostic value. A combination of characters usually permits the correct assignment of all seemingly intermediate species." (1991: 93-94)

This also makes sense from an organismic perspective, since every genotype represents a system of co-adapted gene complexes, and variations are correlated with each other within certain limits, i.e. they will simultaneously be apparent in several morphological (structural) as well as ecological and reproductive traits. In studies on sibling species, for instance, several differences are usually discovered with time (see Mayr 1963). A discriminant analysis may be used for comparisons of multiple characters or character complexes in more than two populations. If all members (100% of cases) that are a priori assigned to a pre-defined group (a natural population) will correctly classified to this group, in at least one sex after the analysis, the population can be hypothesised to represent an incipient species here as well and be named as a subspecies.

The assignation of a population to the taxonomic category subspecies is an hypothesis on the probability that the population has embarked – as an incipient species – onto the path of speciation. If this statement shall serve as a proper (i.e. falsifiable) working hypothesis for further biosystematic work, it is of utmost importance to combine it with the actual statistic data and a clear description of methods.

While simple in theory, the successful application of the SSCr in practise requires the consideration of several factors. For a start, a sufficient amount of material for a sound statistic analysis is crucial. The remark already made by August Weismann and critically directed at some of his contemporaries, that the easiness with which one can ‘make’ a new species increases if the number of specimens available decreases (Weismann 1902, II: 342), still holds true. While it is important to have sufficiently many specimens of every local population studied, a complete coverage of samples from the entire geographic range of the species or species complex, respectively, is equally crucial. The geographic pattern of differentiation or discontinuities is, similarly to the degree of separation, pivotal for the interpretation of the statistic analyses. If geographic sampling coverage proves insufficient and the differences between the studied populations correlate with the geographic distance between them, the existence of a widely distributed species with clinal variation between populations should be assumed. This hypothesis will of course also be preferred in the case of continuous trends in character variation if there is complete or sufficient geographic sampling coverage. The erection of subspecies taxa makes no sense in these cases. Mayr and Ashlock state about that:

> "Where variation is clinal in continuously distributed populations, no particular benefit accrues from splitting the continuum into several subspecies unless there are pronounced steps in the cline or there is a great difference among the endpoints.

> Furthermore, only subspecies that are isolates are incipient species, whereas subspecies that are part of a continuum are not." (Mayr & Ashlock 1991: 97)

As a conclusion of this discussion, the question of the methodological status of the SSCr remains to be posed. Is it a theory on its own or a theory-independent method? Following the arguments of Mayr and Bock, taxonomic rankings by SSCr are singular theoretical statements (= historical-narrative explanations) about groups of organisms based on the evolutionary theory of speciation and are subject to empirical testing (see Mayr & Bock 2002: 186).

4.2.3 Taxonomy

What is the situation then, if the criteria hitherto discussed are now applied to the studied populations of the *Oliarus polyphemus* complex? In two cases, viz. one of two populations from Pink Pistillaria Cave and the Kaumana Cave population, there is a non-overlap in at least one character in at least one sex with all other populations. Consequently, we assume species status for both populations. In both cases this hypothesis rises additional questions or problems.

Two sympatric populations are found in Pink Pistillaria Cave. Is this a case of two sibling species? If so, are these a product of sympatric speciation or rather the secondary contact of two populations that differentiated in allopatry? The co-existence of two very similar species in one cave system rises the problem of exclusion. According to the ‘competitive exclusion principle’[3] (Hardin 1960), two species cannot coexist in the same space and at the same time if they form identical ecological niches[4]. Either there are sufficient differences between the ecological tolerances and preferences of the two species to allow them to form distinct ecological niches and use distinct microhabitats, or one species will eventually become extinct. Here, the existing data do not allow to answer this problem conclusively. Two alternative cladogenetic hypotheses are conceivable as shown in Fig. 25 (a & b). The two Pink Pistillaria populations could either be sister groups or one of both could belong to the unresolved *O. polyphemus* „remainder“-clade. The second interpretation does not seem very probable since the COI gene trees show the Lanikai Cave population as sister group of one of the Pink Pistillaria populations or even basal to all other *O. polyphemus* populations. In addition, the discriminant analysis classifies the males of the Lanikai population morphologically 100% cor-

---

[3] Also known as Gause’s principle (see Gause 1934).

[4] Hutchinson (1958) defined, or redefined incorporating some features of older concepts (see MacArthur 1968), the ecological niche as point or section in a n-dimensional space. In this infinite-dimensional space each measurable feature of the environment was given one coordinate, the region, in which the fitness of an individual was positive, was called that individual's niche.

rectly and both (separately) males and females 100% correctly with respect to bioacoustics. Without preferring one to the cladogenetic alternatives, the species status is hypothesised for both populations in Pink Pistillaria Cave (*Oliarus* spp. n. 1 and 2) and for the Lanikai Cave population (*Oliarus* sp. n. 3).

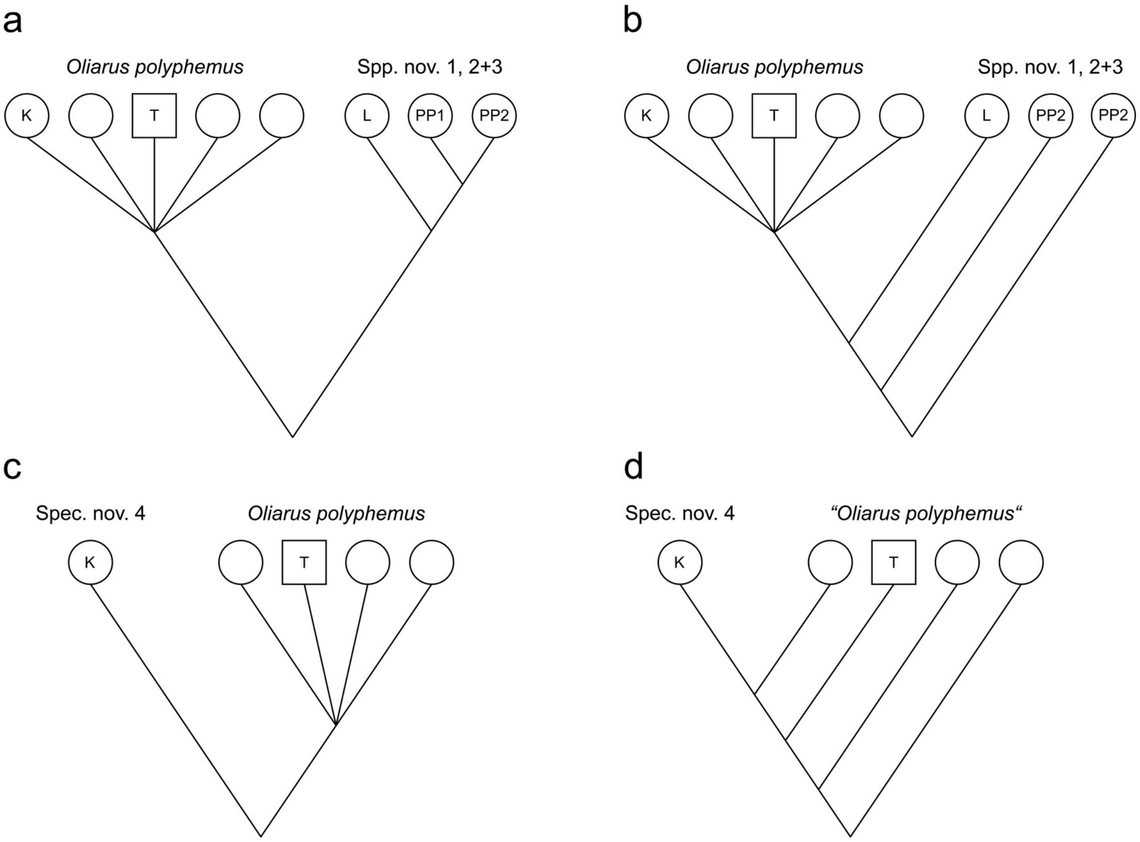


Figure 25. Alternative hypotheses for the cladogenetic development of the *O. polyphemus* complex, see text for discussion.

All other *O. polyphemus* ("remainder") populations including the distinct species in Kaumana Cave are probably a monophyletic group as suggested by the genetic analyses. Yet, this raises a different taxonomic issue. A new taxon originates in evolution, according to the theory of phylogenetic systematics sensu Hennig (1950), by the splitting of the parental lineage into two daughter lineages, giving rise to two new sister groups. The splitting of the parental lineage is considered to be the end of the parental taxon and, at the same time, the origin of the two sister groups as two new taxa. The cladograms in Figs. 25c and 25d show two theoretically conceivable alternatives, which will either render *O. polyphemus* (with the type locality (T) Bird Park Cave) as monophyletic if the Kaumana Cave population should be basal to the entire clade, or paraphyletic if it should occupy a terminal position within the clade.

Is this uncertainty, immanent in the data, sufficient cause not to elevate the Kaumana Cave population to species status or to split the “remainder“ clade into additional species? The theoretically simple and also logical assumption of diversification through purely dichotomous cladification meets with many obstacles in practice, particularly in cases of peripatric speciation[5], founder events, and extremely fast speciation. This led Mayr to a fundamental criticism of Hennig’s basic assumption[6]. Given that the complex of populations considered here is probably the result of a very recent, fast, and still continuing differentiation, where one population has already crossed the threshold of non-overlap in the variation of one character, species status is hypothesised for the Kaumana population (*Oliarus* sp. n. 4).

The variation between all populations is not correlated with geographic distance or showing a cline for any character examined. Among the remaining 14, the members of eleven populations are correctly assigned at 100% to their respective population by discriminant analyses, in at least one character complex and in at least one sex. These are here hypothesised as new subspecies of *O. polyphemus* (ssp. 1-10) and - the population from the locus typicus - as *Oliarus polyphemus polyphemus*. Two of the three populations (in Calabash Cave and Pahoa Cave) that fail to be highly significantly separated by any character complex are geographically isolated and show a more than average distance from the dominant haplotype in the network (shared by five other populations). Thus, these populations are recognised as subspecies as well (*Oliarus polyphemus* ssp. 12+13). The reasons for the low degree of phenotypic differentiation can probably be traced to the specific type of differentiation (compare 4.5). The single remaining population from Ainahou Cave cannot be discriminated by any means and shares its haplotype with the population from the locus typicus. Consequently, it is here regarded as belonging to *Oliarus polyphemus polyphemus* as well.

---

[5] "Peripatric speciation by primary isolation: Here a new population is founded outside the continuous species range by a single colonist (a fertilized female) or a small founder group and remains isolated long enough to acquire the genetic basis for reproductive isolation." (Mayr & Ashlock 1991: 89)

[6] "However, there exists an alternate for the origin of new taxa, which is of great importance for the evaluation of cladification. In this process, best designated as *budding*, the new lineage 'buds off' (=separates) from the parental line, enters a new niche or adaptive zone and establishes a new group that frequently diverges rather quickly (and sometimes drastically) from the parental lineage which continues to exist virtually unchanged. [...] What is important is that this new higher taxon has emancipated itself ecologically from the parental lineage and is now an independent evolutionary/ecological entity. The budding off of a new lineage is of no influence on the continued existence of the essentially unchanged parental taxon." (Mayr & Bock 2002: 186)

4.3 Distribution and dispersal in *Oliarus polyphemus s.l.*

4.3.1 Emigrants and founders

A conclusive answer to the larger question for the driving forces of the rapid differentiation between populations depends on obtaining clarity on a number of associated points, i.e. their distribution as well as mechanisms of dispersal and the probable degree of isolation or separation[7], respectively, between those populations.

Quite certainly, only a small part of all existing *O. polyphemus s.l.* populations is accessible and known. It seems fair to assume that populations will occur in most of the suitable cave habitats in the area ranging from Hualalai via the southern slope of Mauna Loa and Kilauea to the eastern slope of Mauna Kea from sea level up to an altitude of about 4,000 feet. Thus, on a macro-scale, distribution is very likely rather continuous. However, detail studies of some areas, such as Kazumura Main tube and its tributaries, have revealed that suitable habitats show a rather patchy distribution on a micro-scale. Consequently, this is also true for the individual populations, particularly since not all suitable habitats have actually been found to harbour populations of *O. polyphemus*.

A special problem associated with the cave habitats is the cycle of ecological succession, which will inevitably lead to the loss of habitat suitable for cave planthoppers with time (see 1.2.2). From the perspective of the entire population, it would rather make sense to have target-oriented (e)migration into newly formed habitats. An example of an "emigration model" is shown in Fig. 26A. Even the migration of just a part of the population into a new habitat would result in a largely constant gene pool, i.e. young caves could also harbour "old" populations.

The available data on the autecology of cave planthoppers do not support the possibility of any target-oriented colonisation of new habitats, though. No mechanism that might enable a directional navigation in the permanent darkness of the caves is yet known. Individuals should seek to remain in the close vicinity of their food resource, which usually consists of narrowly confined root patches (the "rich root room" in Pahoa Cave is one of the few remarkable exceptions). Own observations suggest that individuals, which loose the contact to their roots perform random search movements. This can either with a certain probability lead to success or alternatively even increase disorientation – the individual found furthest from a visible suitable foot source was found at a distance of ca. 60 m. This suggests not only that colonisations of new habitats are facilitated exclusively by

---

[7] We use here "separation" as the appropriate term for "isolation by external barriers" following Sudhaus and Rehfeld (1992).

such “lost animals“, but also indicates that selection should favour “sessility“ of the animals.

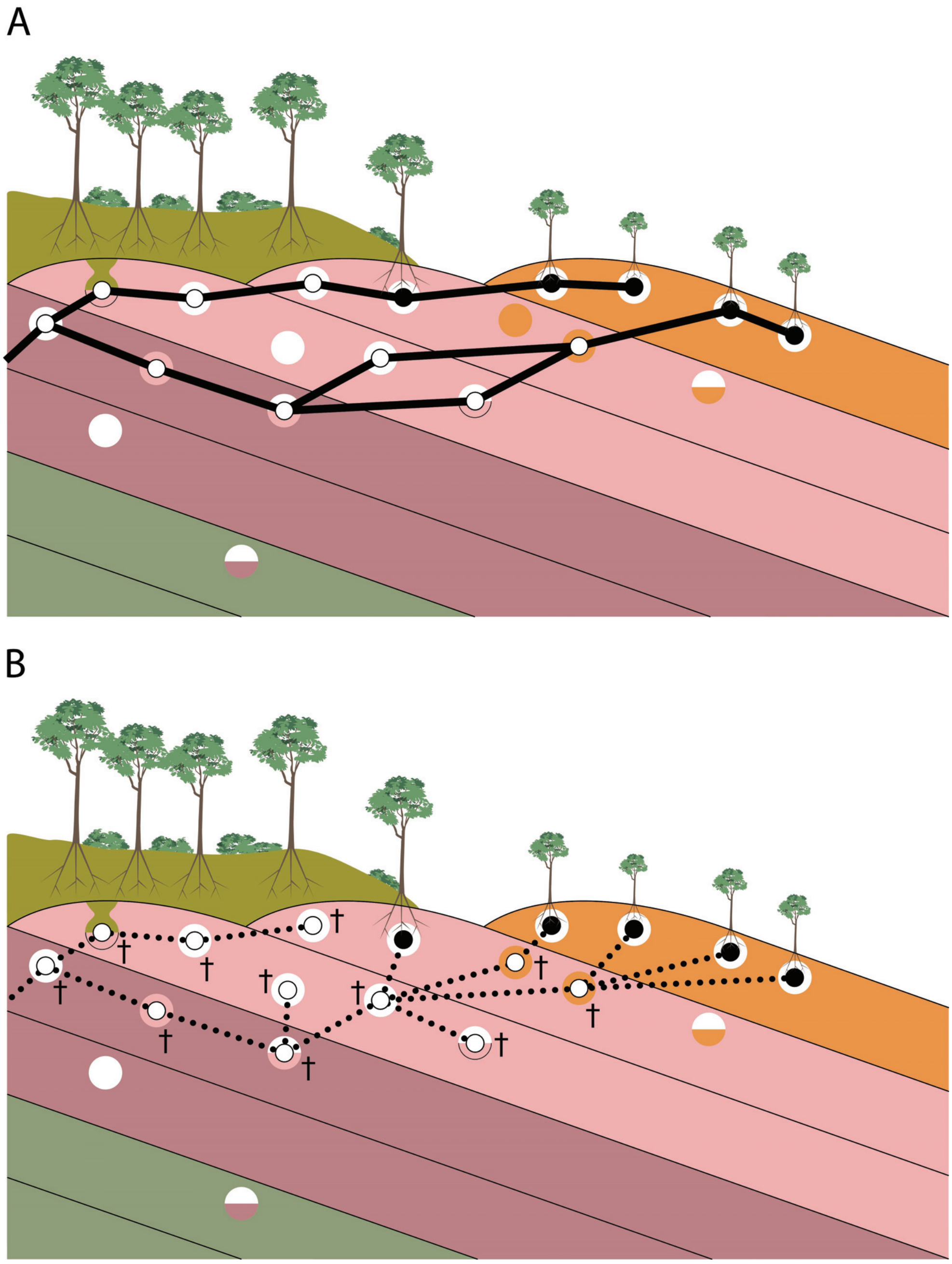


Figure 26. Schematic representation of the “emigration model” (A) and the “founder model” (B) of dispersal in *O. polyphemus s.l.*. Filled (black) dots represent extant populations, empty (white) dots extinct ones; continuous lines stand for the (e)migration of the population, or considerable parts of it, dotted lines for the random dispersal of founder individuals; see text for further explanation.

However, how can this reasoning be reconciled with the maintenance of the high degree of principal dispersability, which is deemed responsible for the wide distribution of *O. polyphemus s.l.*? One possible answer may be derived from the plausible assumption that all individuals of a newly founded population are the descendants of such "wandering" ancestors and that respective prepositions are additionally fixed through founder effects or bottlenecks.

Thus, the apparent migration or emigration of the animals should rather be interpreted as "random individual dispersal" as shown in Fig. 26B. Single founder individuals randomly colonise new habitats, and some then succeed in establishing a new population. The migration rate from the source population to a new habitat is influenced by various factors, which in turn may effect each other. The probability of a founder reaching a new habitat is depending upon the size of this habitat, the frequency of "wandering" individuals, distance between old and new habitat, population size and density of the source population, and the individual mobility of the animals. The probability of a founder establishing a new population is depending upon its ressource demands and free ecological licences, and most importantly, whether it can find a mating partner or is by any chance a female carrying fertilised egg cells.

The average dispersal rate can be estimated at 10 m per year based on the colonisation date of Surprise Cave, the youngest of all caves studied, and the distance to the next possible source. Under the assumption of "random individual dispersal", this does not imply a continued increase of colonised habitats by 10 m/a, but rather that a distance of, for instance, 100 m from a source population to a new habitat will on average be covered once every ten years by a successful founder. If this assumption holds true, it would create ideal conditions for a continued series of founder events, which may then serve as a model to explain the observed degree of differentiation.

Whether such founder events can play a role in speciation processes depends among other things on the degree of separation of the new population. Exactly 140 years ago Moritz Wagner called "die Migration der Organismen und deren Coloniebildung die nothwendige Bedingung der natürlichen Zuchtwahl"[8] (Wagner 1868, after Weismann 1872, p. 1) and, as an antithesis to natural selection, even expanded this later into a "theory of separation [Separationstheorie]" (Wagner 1870, 1872). Dixon and Gulick later assented to his opinion that (spatial) isolation is an essential precondition for change in species, and Romanes considered the various forms of spatial isolation as the single species-forming mechanism (after Weismann 1902: 319). Weismann states on this topic:

---

[8] "the migration of organisms and their formation of colonies the necessary precondition of natural selection"

> "So liegt die Vermuthung nahe, die Darwin zuerst auf die Entwicklungslehre hinführte, dass die Verhinderung der steten Kreuzung einer isolirten Kolonie mit den Artgenossen des ursprünglichen Wohngebietes die Bildung neuer endemischer Arten begünstige, [...]"[9] (Weismann 1902, II: 318)

As Weismann nevertheless points out, the concept of an isolated area is relative, even though the degree of isolation may be absolute within the respective time frame of observation. It is therefore essential, to have an idea about the time frame (duration) of the processes, for which an isolation is considered indispensable.

The recognition of the importance of geographic separation in speciation culminated with the establishment of allopatric speciation as a core part of the new synthetic theory of evolution by Mayr (1942, 1963). While the basic idea was circulated for the better part of a century already, as evidenced by the citations above, it remained for Mayr to integrate the findings of systematics, genetics, and ecology into a comprehensive theoretical framework, that remains essentially undisputed at its core, even though the exclusive absoluteness of allopatric speciation as the sole model of speciation certainly is not.

Finally, it should be mentioned that recently the incorporation of realistic types of population structure into speciation models has led to surprising results. Church and Taylor, for instance, could show that "the simulation also shows that speciation in subdivided populations occurs most rapidly when subpopulations are not strictly allopatric" (2002: 1859), and a model of divergence with zero gene flow was rejected in an empirical study with a coalescent-based analysis in cave salamanders (Niemiller et al. 2008, see also Nosil 2008)

4.3.2 Space for time – pattern and process

The peculiarity and uniqueness of the *O. polyphemus* complex as a model system particularly results from the fact that it essentially consists of what may well be naturally occurring replicates of an evolutionary experiment at different time horizons. Hence, the single isolated populations are different stages of an evolutionary transformation, which occur contemporaneously in close spatial proximity.

---

[9] "There is some support for the assumption, which initially led Darwin towards the theory of descent, that the prevention of continuous cross breeding between an isolated colony and the conspecifics in their former geographic range ferments the formation of new endemic species, [...]."

For the study and description of succession processes, this “space-for-time approach” is an old concept in ecology (Johnson 1979, Pickett at al. 1992). The classic studies in vegetation succession (Cowles 1899, Dachnowski 1912, 1926, Cooper 1923, 1931, 1939, Billings 1938, Oosting 1942, Crocker & Major 1955) already used a space-for-time substitution method to reconstruct a chronosequence, a method, which has been critical reviewed and to some extent rejected by Johnson and Miyanishi (2008). Consequently, such an approach should not be employed without due consideration for the methodology or be used for the easy generation of general conclusions.

A dependence of early primary succession on environmental variables such as temperature has also been shown for the epigean ecosystems of Hawai’i Island (Anderson-Teixeira et al. 2008). In comparison, the cave ecosystems have an important advantage in their simplicity, which greatly limits the number of influencing factors and their mutual dependency. While the sequence of cave colonisation by troglobiont species may potentially exercise a strong influence on the structure of the respective ecosystem, this influence is deemed to be rather limited with respect to the evolution of *O. polyphemus* as a primary consumer.

4.4 Moving peaks – founder effect, (non-)adaptation, and genetic change in *Oliarus polyphemus s.l.*

> I do, however, continue to wonder whether the Mayrian viewpoint might still hold some validity, and might now be subject to overly curt and confident dismissal.[10]
>
> Stephen J. Gould (2002)

4.4.1 The pattern

The following patterns have to be summarised and interpreted in order to achieve an understanding of the underlying evolutionary process: on Hawai’i Island, populations of the widespread and strongly troglomorphic *Oliarus polyphemus* are found in young caves (cave ecosystems) with a gradual age from 38 to about 1,000 years (except for Pink Pistillaria Cave with an age of ca. 8,000 years). Genetic data reveal this population complex to be monophyletic, dispersal over the study area has occurred subterranean within the last 10,000 years subsequently to a single evolutionary transformation to a troglobitic way of life. The populations studied here show a sufficiently high degree of differentiation in mor-

---

[10] Gould (2002:797-798) concerning the importance of speciation in small, peripherally isolated populations.

phology and, even more pronounced, in behaviour to justify hypotheses of subspecies status in thirteen cases or even distinct species status in four instances. The average values of phenotypic differentiation do neither correlate with the geographic distance between caves nor is there a clinal distribution. None of the morphological or ethological differences can in any way be interpreted as an adaptation to possible differences in habitat. Character variability is negatively correlated to cave age, this correlation is highly significantly for the morphological characters and barely significant with respect to the acoustic parameters. The observed distribution is probably caused by random individual dispersal, where single or very few individuals act as founders of new populations. These colonies are separated from each other, and the maximum age for the gene pool of the populations in a cave is limited by the age of the cave.

4.4.2 The process – founder effects

There is general agreement that a founder event will have an effect on evolution, particularly if it involves the extreme case of the establishment of a new population by a single fertilised female. Nevertheless, the mechanism, and the factors influencing the process, are far from being agreed upon.

First, the establishment of a new population by a founder involves genetic random sampling of some gene complexes from a larger gene pool, which will certainly result in an overrepresentation of rare alleles and, with a high probability, also in their fixation. Secondly, a colonisation will always be accompanied by a certain amount of change in environmental conditions. Even in very simple and extremely similar habitats, such as the cave habitats of Hawai'i, the founder and its descendants are subjected to completely different conditions in at least one respect: the complete lack of conspecifics. How can then a transformation and, thus, differentiation of populations be triggered if no adaptive reaction to a different (abiotic) environment is to be expected?

The classical interpretation of a founder effect sensu Mayr (see 1.1.1) attributes changes to the extreme genetic bottleneck following random genetic sampling by the founder and a subsequent genetic revolution in a changed genetic environment. Mayr's concept was a first important step towards a naturalistic population genetics, which allowed "organismic naturalists" to maintain their stand against "reductionistic geneticists" (Mayr 1984). Mayr's rather pointed statements culminated in the legendary "beanbag allegation":

> "The emphasis of the early population genetics was on the frequency of genes and on the control of this frequency by mutation, selection, and random events. Each gene was essentially treated as an independent unit favored or discriminated against [...]. [...] this period was one of gross oversimplification. Evolutionary change was essentially presented as an input or output of genes, as the adding of certain beans to a beanbag and the withdrawing of others." (Mayr 1959: 2)

Contrary to prevailing expectations of selection acting independently at each locus, newly developed concepts assumed that the selective value of genes can only be realised within the organismic context. Interaction effects in co-adapted gene complexes and during ontogeny began to be considered, "selection of genes" was complemented by "selection for genes" (Sober 1984). Generally, it can be said that this was the beginning of the tentative and still ongoing penetration of system thinking at the population level.

Hampton L. Carson, a student of Dobzhansky, was one of the most important theoretic workers in the field, even though the significance of his work has not (yet) been universally recognised. His most important contribution in this context was the establishment of the role of sexual selection in the evolution of populations.

> "At the time of reproduction, the genetic uniqueness of each individual, whether female or male, is thus put to the final test of Darwinian fitness. Each deme thus has its own genetic elite, made up of those individuals that leave more offspring than others. Full appreciation of the fitness-maximizing role of sexual selection in local populations has been held back by theories and experimental designs that ascribe many of these same behavioral attributes to a wholly different function, namely, premating, intergroup sexual isolation. I propose a return to the original Darwinian view. Thus the genetically based reproductive isolation often observed between species is simply an incidental outcome stemming ultimately from the process of selection, natural or sexual or both, that occurs within the freely interbreeding group. Accordingly, concepts that define species strictly in terms of the genetics of reproductive isolating mechanisms need revision." (Carson 1999: 509)

Starting from this conceptual basis, he identified the escape from the co-adapted gene complex as the initial genetic change and, thus, a critical step in the formation of new species. He presented the Founder-Flush model (Carson 1975, see Introduction) as one possible way. The predictions of Mayr's and Carson's models differ in one crucial aspect. Mayr assumed that arbitrary genetic sampling by the founder is followed by a further loss of genetic diversity, from which the population only starts to recover slowly after it is firmly established. In contrast, Carson proposed that a founder event is immediately followed by a "founder flush" leading to a instant rise in variability (and a break-up of co-adapted gene complexes). If the pattern shown in 4.1.1 is tested against these predictions, Mayr's hypothesis must be rejected and *O. polyphemus s.l.* emerges as a striking example of the founder flush model.

4.4.3 The process – moving peaks in dynamic landscapes

The verbal model by Carson demonstrates, how co-adapted gene complexes can be broken up in the flush phase, leading to new combinations. How such a new stable condition can be realised and how it may be interpreted with respect to concepts of fitness maximisation and adaptive change can best be understood by translating the model into Sewall Wright's visual concept of adaptive landscapes. The question asked by this approach is, how a population can move from one adaptive peak to the next (Fig. 27, top panel), or more precisely, how and why do the founders leave an adaptive peak and cross the adaptive valley.

The following scenario emerges from adopting a population-focus perspective as proposed by Carson: From the viewpoint of the whole population, the position of the centre of variation in the adaptive landscape (the position of the peak) is irrelevant, but from the viewpoint of each animal, the individual distance from this centre represents the value of personal fitness.

The structure of the fitness landscape depends on the interactions of the individuals of a population with the environment and among each other. In analogy to the ecological niche, a fitness landscape cannot be occupied, but is actually formed by the population. In addition it should not be forgot that the adaptive landscape is merely a heterogeneous dynamic multidimensional fitness-space with "gravitating" areas which functions as attractors.

In sexually reproducing species under sexual selection, the structure of the fitness-space can only be estimated from a population perspective or is defined by population structure, respectively. There is no 'objectively' recognizable fitness-space that is independent from the population nor does a fitness-space for a species or an individual exist. Thus, the fitness-space can change even in a stable environment if the population structure changes (bottleneck, founder flush). Every fitness-space is dynamic and in continuous flux through extrinsic and intrinsic (population) factors, which has prompted the introduction of the term „adaptive seascape" (Merrell 1994).

A founder event would accordingly incorporate the establishment of a new fitness space (Fig. 27, stage 1). The relaxation of sexual selection during the flush phase allows the existence of a fitness plateau instead of a fitness peak for the characters involved in sexual selection (Fig. 27, stage 2). The "formation of a plateau" in this picture is the local relaxation in attractors establishing a section in the space, which can be freely occupied by the population during the flush phase. After the return of sexual selection and the breakdown of effective population size, a peak is formed again, and with some probability, it will occupy a different place from the one in the source population (Fig. 27, stage 3). This can be regarded as a peak move rather than as a peak shift. The movements of the population on the plateau are almost entirely random, and this generates an undirected peak movement in series of founder events. Consequently, there is no observable cline or trend in the changes of the *O. polyphemus s.l.* populations. Similarities between populations can also be due to the random peak movements, i.e. have originated convergently or in parallel. This also explains, why geographically and genetically rather distant populations were recovered in the same clade in earlier cluster analyses (Wessel 1997).

The model used here may well be termed a Darwinian-Wrightian-Mayrian-Carsonian Peak-Move-Model. From this perspective, one can now also pose the question whether the "adaptive landscape" is a descriptive or rather a predictive model? If predictive, at what level, population or individual? If descriptive, for the current situation only or retrospective?

The structure of the landscape is retrospectively descriptive for a population. It is the result of the actual inclusive fitness of the single individuals, each representing a concrete genotype. Only those coordinates (gene combinations) can be described exactly that have been actually realized, and for non-realized coordinates must be extrapolated. The resulting landscape is in turn predictive for single individuals by setting the probability or a probability space for the potential inclusive fitness. The adaptive landscape does not allow predictions about changes on the population level as changes in population structure are effecting in turn the structure of the landscape.

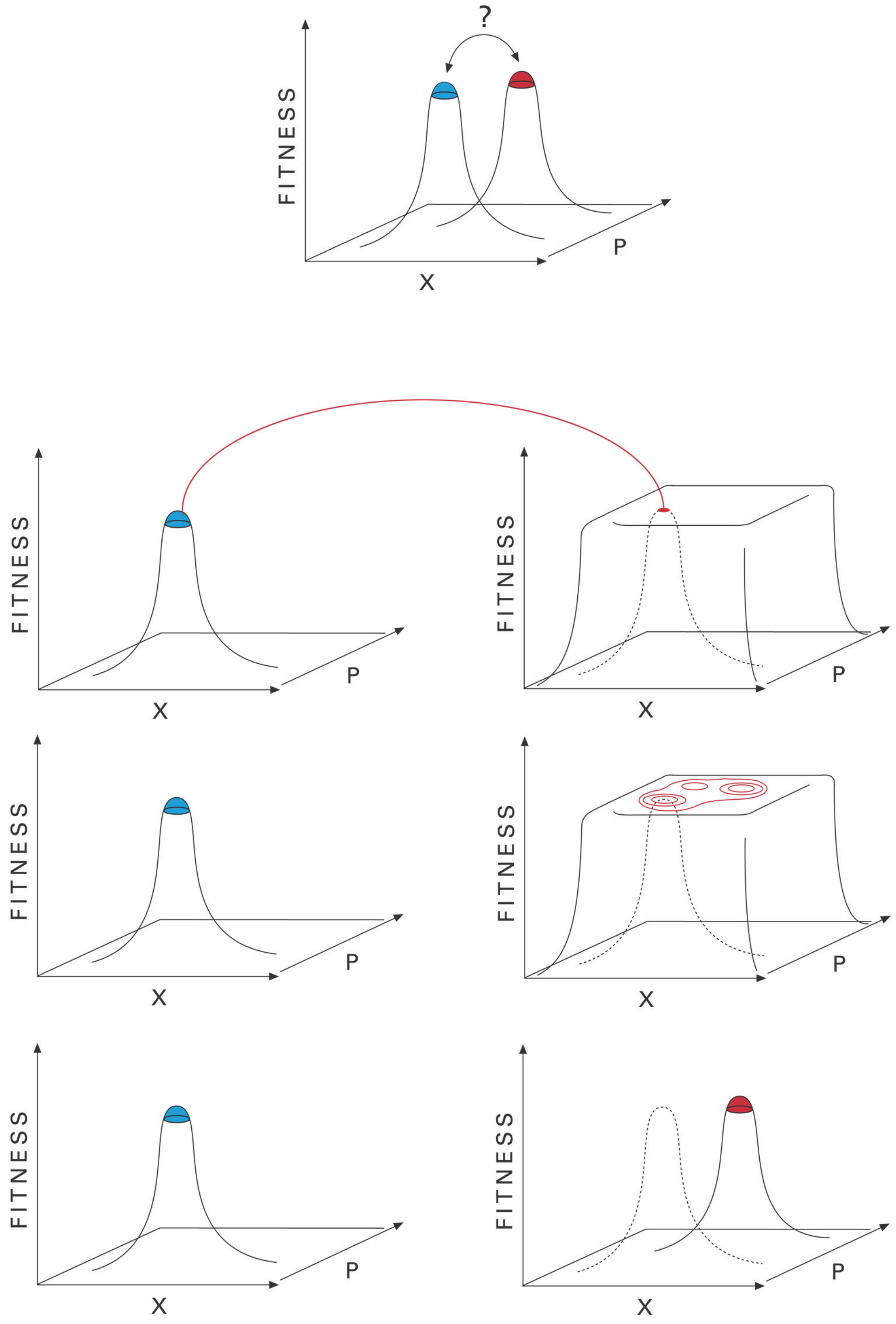


Figure 27. Schematic representation of the “peak move” by “founder flush”, for explanation see text.

4.4.4 The process – speciation and adaptation

Can the peak move model also explain speciation? Principally, the model is certainly best suited to explain changes in characters subject to sexual selection, even though many other correlated characters may be effected as well. Using an experimental approach, Powell (1978) could show that it works at least for pre-mating isolation. This may speed up speciation processes involving reinforcement upon secondary contact, and if populations are separated for a longer period of time, the changes induced by drift will likely also cause reproductive isolation as a by-product.

Most interesting in this context is whether the peak move can (or must) generate non-adaptive change, which would consequently render non-adaptive radiations possible or even probable. By way of introduction it should be noted that the terms adaptive or adaptation are frequently used in a rather unidimensional sense, as if every trait of an organism is independently subjected to selection and, thus, exposed to a continuous optimization process that can only distinguish between adaptive or non-adaptive changes. Early on, it was pointed out by Weismann that species "nicht lediglich Anpassungscomplexe [sind], sondern zugleich auch blosse Variationscomplexe, deren einzelne Bestandtheile nicht alle Anpassungen sind, nicht alle also die Grenze von Gut und Schlecht erreichen”[11] (1902, II: 346-47) and elsewhere he states that "[...] eine Art sich auf diese oder jene Weise den gegebenen Lebensverhältnissen anpassen kann und es keineswegs blos je eine bestangepasste Form für jede Art geben muss [...]"[12](1872: 21). Incidentally, this looks like an anticipation of the critique of the adaptationist program as forcefully expressed by Gould and Lewontin (1979) much later.

An adaptive radiation can be unambiguously defined by its result: several species that have realized a variety of ecological niches in the process of their differentiation. Following Gittenberger (1991), a non-adaptive radiation then may be interpreted as allopatric differentiation, that does not comprise the formation of different ecological niches. Admittedly, this would effectively bar the descendant species of the radiation to coexist in sympatry despite their mutual reproductive isolation.

In contrast, Sudhaus argues that “non-adaptation cannot be demonstrated, since it is principally impossible to show that a structure has no function” and then

---

[11] "are not merely adaptation complexes, but at the same time also mere variation complexes, the single parts of which are not all adaptations, so they do not all approach the limits of good and bad.”

[12] "[...] a species can adapt to the existing conditions in several ways and there is not necessarily only a single optimal way of adaptation for each species [...]"

proceeds to link “functionlessness and non-adaptation” (2004: 128). Sudhaus is right in his assertion of the relationship between form and function being so complex that it is difficult to obtain even unambiguous evidence for the function of a certain structure, let alone its non-functionality. However, there seems to be confusion, about “non-adaptive” referring not to a structure, but a process in this case. A non-adaptive radiation is the diversification of a species without diversification of its niche. In this context, the non-adaptive transformation of a structure does not imply a loss of function, but rather that different modifications of this structure will have a (roughly) equal fitness value in a given adaptive landscape.

From this perspective, the peak move model explicitly postulates a non-adaptive change of traits influenced by sexual selection. Returning to the actual case study these may be the mating calls of the cave planthoppers. During the founder flush phase, a wide range of signals will be of a roughly identical adaptational value, within certain limits, which also determine the limits of the adaptive plateau. While the functionality of the different signals that differ between populations will not be different within each population, its adaptional value will be very different in other populations. In this sense, the radiation of *Oliarus polyphemus s.l.* may be interpreted as non-adaptive.

4.4.5 The process – tempo of evolution

Finally, an exciting question is how fast the processes of this non-adaptive radiation via founder effect will act. So far, the maximum age of the colonized lavaflows has been used for calibration. Alternatively, these data may be compared to dates obtained through the use of a molecular clock calibrated independently in other systems. For insects the most reliable substitution rate estimates have been obtained for COI, where rates range from a sequence divergence of 1.2% per mya in cave beetles (Caccone & Sbordoni 2001) to 2.2-2.8% per mya in cicadas (Buckley et al. 2001). For comparison, Farrell (2001) found a rate of 1.5% per mya for beetles as well and Brower (1994) 2.3% per mya for Lepidoptera.

If these rates are applied to *O. polyphemus s.l.*, divergence time estimates for the separation of populations exceed those derived from geographic distribution data up to a hundred-fold, even though relative distances support the geography-based scenario. Divergence time estimates based on genetic distance for the Kaumana Cave and Lanikai Cave populations range from 1.5 to 3.5 mya and, thus, exceed the entire existence span of Hawai’i Island by a factor of three to seven. The distance between dominant haplotype D and Kaumana population corresponds to a divergence time of 0.5 to 1.17 mya – still considerably exceeding the age of the island. Even the population in Surprise Cave would have diverged 8,300 to 36,000 years ago.

Given that these scenarios are highly unlikely or even impossible, another hypothesis must be sought to explain the high divergence time estimates. If the dispersal of *O. polyphemus s.l.* indeed involved a series of thousands or tens of thousands of founder events with the consequences described above, this might actually explain the amplified accumulation of mutations in a neutral marker. While this hypothesis will of course need to be tested using additional molecular data, it is certainly smoothly congruent with the scenario outlined above.

Metastudies of applications of the molecular clock have also revealed a 10 to 20 fold difference in divergence time estimates based on the same genetic region in different clades of the same taxon but using a different calibration depth, or even 100-fold deviations in comparisons of phylogenetic and pedigree based studies in primates including man (see e.g. Ho et al. 2005, Sigurđardóttir et al. 2000, for review see Pulquério & Nichols 2007). Attempts at explanation largely focus on differences in population size in these cases (see e.g. the Nearly Neutral Theory of Evolution by Ohta 1992, 2003).

Other factors might also cause an acceleration of (genetic) differentiation. As discussed above, the probability of individuals emigrating and becoming potential founders is correlated with population size. If so, it might be expected that the emigration pressure will increase rapidly during the founder flush phase immediately after a founder event, resulting e.g. in a fast colonization of large areas with newly formed habitats. All founder individuals would then stem from the phase of highest variability of the parent population and consequently, have a higher probability of carrying new or rare allele and gene combinations. Within a short time, this process could then amplify the already acting effects of arbitrary genetic sampling and peak move.

How fast is speciation within the *O. polyphemus s.l.* clade actually in comparison to other well studied radiations? Mendelson and Shaw proposed a simple estimator for rates of diversification (2005, suppl. inf.: 3)[13] and calculated a rate of speciation of 4.17 Sp/Mya for the Laupala cricket species of Hawai'i Island (based on a number of 6 species and and assumed age of 430,000 years for Hawai'i Island). So far, this is the highest speciation rate documented for inverte-

---

[13] For rates of diversification $r = \frac{\ln N - \ln N_0}{t}$, where N is the number of extant species, N_0 is the number of founding lineages, and t is divergence time. For young lineages a pure birth model with no extiction is assumed (see Yule 1925). Thus for young, monophyletic clades the speciation rate is $r = \frac{\ln N}{t}$.

brates, more than an order of magnitude higher than the one usually assumed for arthropods and only surpassed by that of African cichlids (see Coyne & Orr 2004).

Assuming that the *O. polyphemus s.l.* clade comprises five species and an age of the clade corresponding to the age of island, which is the most conservative estimate possible, a comparable rate of speciation is obtained (3.74 Sp/mya). If the age of the Hualalai systems (130,000 years, largest expansion of surface, see Moore & Clague 1992) is employed as a somewhat more realistic estimate of the maximum age a rate of the clade, a rate of 12.4 Sp/mya emerges. Assuming in addition that dispersal and cave colonization proceeded from the Hualalai system, and using on the three species of the Mauna Loa/Kilauea clade and a maximum age of 10,000 years, a speciation rate of nearly 110 Sp/mya becomes plausible. Even this estimate is rather conservative in light of the hypothesis developed above. To conclude, *Oliarus polyphemus s.l.* clearly is the model system with the fastest ever documented rates of differentiation and diversification, which exceed commonly assumed rates by several orders of magnitude.

4.5 Perspectives of a model (system)

> One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: "Why do these animals behave as they do?" [...] We must hope that the descriptive phase is not going to come to a premature ending. [...] Contempt for simple observation is a lethal trait in any science, and certainly in a science as young as ours.
>
> Niko Tinbergen (1963: 411-412)

It was the aim of this study to establish a new model system for the investigation of current questions about the mechanisms of genetic change at the level of the organism and concepts of evolution by sexual selection and founder effects. The preliminary hypothesis of differentiation and diversification of cave planthoppers of the *O. polyphemus s.l.* complex by the Founder Flush model of Carson and its re-interpretation as a peak move model as presented here has established the empirical basis and theoretical framework for tackling advanced aspects of the system. Ernst Mayr e.g. suggested with respect to this model system:

> "Bei den Höhlen-Arten die oberirdische Vorfahren haben, muss klar zwischen den beiden Artbildungsformen unterschieden werden. Die Kladisten kennen nur Artbildung durch 'splitting' einer Stammlinie. Wie es jetzt immer klarer wird, ist Artbildung durch Knospung (budding) viel häufiger. Hier ändert sich die Elternart (Stammlinie) überhaupt nicht, aber sie sendet eine Kolonie aus (eine founder population) die relativ schnell zu einer neuen Art wird. Wie das Abreissen der Verbindung zwischen Elternpopulation und der neuen werdenden Art stattfindet, hat glaube ich noch niemand sorgfältig rekonstruiert."[14] (Mayr, pers. comm., letter of February 10th 1998)

The next steps towards a better exploitation of the potential of this model system seem obvious. First, it will be important to obtain a thorough understanding of the phylogenetic frame of its amazing evolutionary processes. A phylogeny of the entire Hawai'ian *Oliarus* (*Nesoliarus*) clade based on morphological, biogeographic and molecular evidence is in progress (Hoch, unpublished data). Secondly, detailed data on the morphology and behaviour of the cave planthoppers will be insdispensable. Currently, the modification of head morphology including

---

[14] "[...] One must distinguish clearly between the two modes of speciation in cave species with epigean ancestors. Cladists only know speciation by 'splitting' of a lineage. It is increasingly becoming evident that speciation by budding is much more frequent. In this case, the stem species does not change at all, but it produces a colony (a founder population) which comparatively fast evolves into a new species. How exactly the link between the parent population and the incipient species is severed has not been properly studied yet, I believe."

sense organs as well as non-reductive morphological adaptations is being investigated by ultrastructural methods such as μCT and 3D-reconstruction (Hoch, Kühbacher & Wessel, unpublished data). Observations of behaviour in the animals' natural habitat as well as playback and crossbreeding experiments are planned, the construction of an artificial cave in the laboratory is already in process.

Genetic work will proceed along two lines: population genetic studies using fast-evolving markers (microsatellites) are already in preparation, and a cooperation project looking into the genomics of cave adaptation is planned (Project Speleogenomics: Culver, Friedrich, Hoch & Wessel).

From a theoretical perspective, it will be necessary to improve the concepts proposed here based on and linked to empirical data. With respect to the suggested founder effect models, the next step will be to proceed from the testing of qualitative predictions to making quantitative predictions (see Taborsky 2008). The models presented verbally or visually so far must, thus, be amended through formalisation and ultimately mathematical modelling. A formalization is not without its specific risks, though. As expressed by Hull:

> "As always, making an area of science mathematical carries with it dangers and costs. The danger is that the medium becomes the message as more and more of the publications deal with mathematical problems. Empirical issues become noteworthy by their absence. [...] Making an area mathematical also has its costs. It becomes so complicated and arcane that few scientists working in this area can understand it." (Hull 2002: 120, in respect to Fisher's introduction of fitness (Fisher 1930))

It will prove a major challenge to improve upon the precision of the concepts without abandoning the accessibility and vividness of the verbal models and without an oversimplification of the complexity inherent to organismic systems.

The concluding statement shall be left to the great philosopher of science, Sir Karl Popper:

> "Niemals setzt sich die Wissenschaft das Phantom zum Ziel, endgültige Antworten zu geben oder auch nur wahrscheinlich zu machen; sondern ihr Weg wird bestimmt durch ihre unendliche, aber keineswegs unlösbare Aufgabe, immer wieder neue, vertiefte und verallgemeinerte Fragen aufzufinden und die immer nur vorläufigen Antworten immer von neuem und immer strenger zu prüfen."[15] (1934[16])

---

[15] "Science never pursues the illusory aim of making its answers final, or even probable. Its advance is, rather, towards the infinite yet attainable aim of ever discovering new, deeper, and more general problems, and of subjecting its ever tentative answers to ever renewed and ever more rigorous tests." (Popper 1959: 281)

[16] Cited after Popper 1989: 225.

5 Acknowledgements

I sincerely thank Hannelore Hoch for providing the topic, her supervision and our fruitful and cordial teamwork during the last years. Our joint fieldwork, together with Manfred Asche, was exciting and profitable in every sense, and both were always very generous in sharing their knowledge and experience.

This study would not have been possible without the immense help of Frank Howarth and Fred Stone, *mahalo* for the good companionship in the field and the liberal provision of material and information.

Apart from the author no one is likely to be more familiar with this thesis than Thomas von Rintelen. I thank him for numerous rounds of discussion, practical as well as theoretical support, and his help with translation. Björn Stelbrink provided invaluable help by obtaining literature and assisting in the preparation of figures, particularly during the "critical phases" of this work. Kristina von Rintelen and Björn also painstakingly proof-read this manuscript and, together with Thomas, they were always ready to raise my motivation and provide moral support for finally writing down what has been occupying my mind for the last couple of years.

I am also grateful to all other members and "associates" of the Biosystematics research group within the last decade, who helped to create and maintain a pleasant working environment: Dirk Berger, Petra Erbe, Viktor Hartung, Petra Hirschberger, Elke Hochberg, Barbara Hosfeld, Sebastian Kalbfleisch, Julia Kasper, Franziska Knopf, and Sophia Seidel.

Many colleagues in the Museum für Naturkunde have made work here enjoyable over the years. I particularly wish to thank some of them: Martina Rißberger has always endeavoured to make any task involving the museum's library a worthwhile experience; Nils Hoff has been readily available to aid in solving problems involving graphics, and I have been able to learn many things from him; Jason Dunlop has exhibited a large amount of patience during the correction and translation of numerous texts.

I thank Wolfgang Höhne and the entire Protein Structure research group of the Charité, Berlin for the cordial reception during my *Zivildienst* and manifold support during the following years. I especially wish to distinguish Grit Zahn for her constant readiness to yield practical advise, and Abdel Maghnouij for his help with my first steps in molecular genetics.

Günter Tembrock has significantly influenced my way of thinking through his work and personality, I owe him a great deal of my biological knowledge. The late Ernst Mayr has encouraged my work through several suggestions and ideas and particularly his enthusiasm for the model system.

I am deeply grateful to my parents for always supporting me unconditionally.

This study was supported by the Research Training Group (Graduiertenkolleg) ”Evolutionary Transformations and Mass Extinctions” (DFG-GRK 503 - Evolutionäre Transformationen und Faunenschnitte) in co-operation with the Research Training Group “Model Studies of Structures, Properties and Recognition of Biological Macromolecules” (DFG-GRK 80 - Modellstudien zu Struktur, Eigenschaften und Erkennung biologischer Makromoleküle).

6 References

Allred, K. & Allred, C. (1997). Development and morphology of Kazumura Cave, Hawaii. *J. Cave Karst Stud.* **59**(2): 67–80.

Anderson, S. (1994). Area and endemism. *Q. Rev. Biol.* **69**: 451–471.

Anderson-Teixeira, K. J., Vitousek, P. M. & Brown, J. H. (2008). Amplified temperature dependence in ecosystems developing on the lava flows of Mauna Loa, Hawai'i. *P. Natl. Acad. Sci. USA* **105**(1): 228–233.

Aristotle (384–322 B.C.) – see Balme (1992).

Asche, M. (1987). Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera, Auchenorrhyncha). In: Vidano, C. & Arzone, A. (eds). *6th Auchenorrhyncha Meeting, Turin, Italy, September 7–11, 1987, Proceedings.* Consiglio nazionale delle Ricerche, Italy, special project IPRA: 47–53.

Asche, M. (1997). A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pac. Sci.* **51**(4): 366–376.

Avise, J. C. (1994). *Molecular markers, natural history and evolution*. Chapman & Hall, New York: 511 pp.

Avise, J. C. (2000). Cladists in wonderland. *Evolution* **54**: 1828–1832.

Avtzis, D. N., Arthofer, W. & Stauffer, C. (2008). Sympatric occurrence of diverged mtDNA lineages of *Pityogenes chalcographus* (Coleoptera, Scolytinae) in Europe. *Biol. J. Linn. Soc.* **94**: 331–340.

Babbage, C. (1838). *The ninth Bridgewater treatise. A fragment.* 2nd Ed. John Murray, London: 270 pp.

Balme, D. M. (1992). Aristotle's *De Partibus Animalium I and De Generatione Animalium I* (with passages from Book II. 1–3). Edited and translated with notes by D. M. Balme. With a report on recent work and an additional bibliography by A. Gothelf. Oxford University Press, Oxford: 190 pp.

Barnard, J. L. (1977). The cavernicolous fauna of Hawaiian lava tubes, 9. Amphipoda (Crustacea) from brackish lava ponds on Hawaii and Maui. *Pac. Insects* **17**: 267–299.

Barr, T. C. (1966). Evolution of cave biology in the United States, 1822–1965. *B. Natl. Speleol. Soc.* **28**: 15–21.

Barr, T. C. (1967a). Observations on the ecology of caves. *Am. Nat.* **101**: 475–491.

Barr, T. C. (1967b). Ecological studies in the Mammoth Cave System of Kentucky. I. The biota. *Int. J. Speleol.* **3**: 147–203, pl. 37–64.

Barr, T. C. (1968). Cave ecology and the evolution of troglobites. *Evol. Biol.* **2**: 35–102.

Barr, T. C. & Holsinger, J. R. (1985). Speciation in cave faunas. *Annu. Rev. Ecol. Syst.* **16**: 313–337.

Barr, T. C., Hyman, L. H., Hobbs, H. H., Jr., Goodnight, C. J. & M. L., Christiansen, K., Park, O., Chamberlin, J. C., Malcolm, D. R., Causey, N. B. & Nicholas, Brother G. (1960). Speciation and raciation in cavernicoles. *Am. Midl. Nat.* **64**: 1–160.

Barr, T. C. & Kuehne, R. A. (1971). Ecological studies in the Mammoth Cave System of Kentucky. I. The ecosystem. *Ann. Speleol.* **26**: 47–96.

Barrett, P. H., Gautrey, P. J., Herbert, S., Kohn, D. & Smith, S. (1987). *Charles Darwin's notebooks, 1836–1844. Geology, transmutation of species, metaphysical enquiries.* Cornell University Press, Ithaca, New York: 747 pp.

Barton, N. H. (ed.) (2001). Special issue on speciation. *Trends Ecol. Evol.* **16**: 325–413.

Barton, N. H. & Charlesworth, B. (1984). Genetic revolutions, founder effects and speciation. *Annu. Rev. Ecol. Syst*. **15**: 133–164.

Bell, P. D. (1980). Transmission of vibrations along plant stems: implications for insect communication. *J. New York Entomol. S*. **88**: 210–216.

Bellinger, P. F. & Christiansen, K. A. (1974). The cavernicolous fauna of Hawaiian lava tubes, 5. Collembola. *Pac. Insects* **16**: 31–40.

Benedix, J. H. & Howard, D. J. (1991). Calling song displacement in a zone of overlap and hybridization. *Evolution* **45**: 1751–1759.

den Bieman, C. F. M. (1986). Acoustic differentiation and variation in planthoppers of the genus *Ribautodelphax* (Homoptera, Delphacidae). *Neth. J. Zool.* **36**: 461–480.

Billings, W. D. (1938). The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr*. **8**: 437–500.

Blaxter, M., Mann, J., Chapman, T., Thomas, F., Whitton, C., Floyd, R. & Abebe, E. (2005). Defining operational taxonomic units using DNA barcode data. *Phil. Trans. R. Soc. Lond. B* **360**: 1935–1943.

Boake, C. R. B. & Poulsen, T. (1997). Correlates versus predictors of courtship success: courtship song in *Drosophila silvestris* and *D. heteroneura*. *Anim. Behav.* **54**: 699–704.

Booji, C. J. H. (1982). Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae), interspecific and geographic variation in acoustic behaviour. *Z. Tierpsychol.* **58**: 31–52.

Bortz, J., Lienert, G. A. & Boehnke, K. (1990). *Verteilungsfreie Methoden in der Biostatistik.* Springer, Berlin: 939 pp.

Bourgoin, T. (1997). Habitat and ant-attendance in Hemiptera: a phylogenetic test with emphasis on trophobiosis in Fulgoromorpha. *Mem. Mus. Natl. Hist. Nat. (Fr.)* **173**: 109–124.

Bourgoin, T. & Campbell, B. C. (2002). Inferring a phylogeny for Hemiptera: falling into the ‘autapomorphic trap’. In: Holzinger, W. & Gusenleitner, F. (eds). *Zikaden. Leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha).* Oberösterreichisches Landesmuseum, Linz: 67–82.

Bousfield, E. L. & Howarth, F. G. (1976). The cavernicolous fauna of Hawaiian lava tubes, 8. Terrestrial Amphipoda (Talitridae), including a new genus and species with notes on its biology. *Pac. Insects* **17**: 144–154.

Brambilla, M., Janni, O., Guidali, F. & Sorace, A. 2008. Song perception among incipient species as a mechanism for reproductive isolation. *J. Evol. Biol.* **21**(3): 651–657.

Brauer, F. (1868). Bericht über die Leistungen in der Naturgeschichte der Insekten während der Jahre 1867–68. *Arch. Naturgeschichte* **34**(2): 344–347.

Bretagnolle, V. (1995). Systematics of the soft–plumaged petrel *Pterodroma mollis* (Procellariidae): new insight from the study of vocalizations. *Ibis* **137**: 207–218.

Bridle, J. R. & Butlin, R. K. (2002). Mating signal variation and bimodality in a mosaic hybrid zone in *Chorthippus* grasshopper species. *Evolution* **56**: 1184–1198.

Brindle, A. (1980). The cavernicolous fauna of Hawaiian lava tubes, 12. A new species of blind troglobitic earwig (Dermaptera: Carcinophoridae), with a revision of the related surface-living earwigs of the Hawaiian Islands. *Pac. Insects* **21**: 261–274.

Brower, A. V. Z. (1994). Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *P. Natl. Acad. Sci. USA* **91**: 6491–6495.

Buckley, T. R., Simon, C. & Chambers, G. K. (2001). Phylogeography of the New Zealand cicada *Maoricicada campbelli* based on mitochondrial DNA sequences: ancient clades associated with cenozoic environmental change. *Evolution* **55**: 1395–1407.

Burchfield, R. W. (ed.) (1972). *A supplement to the Oxford English Dictionary, being a corrected re-issue with an introduction, supplement, and bibliography of a new English dictionary on historical principles; founded mainly on the materials collected by the Philological Society. Suppl. Vol. 1: A–G.* Oxford UP, Oxford: 1331 pp.

Busnel, R. G. (ed.) (1963). *Acoustic behaviour of animals.* Elsevier, Amsterdam: 933 pp.

Busnel, R. G., Pasquinelly, F. & Dumortier, B. (1955). La tremulation du corps et la transmission aux supports des vibrations en résultant comme moyen d'information à courte portée des Ephippigères mâles et femelles. *B. Soc. Zool. Fr.* **80**: 18–22.

Butlin, R. K. (1989). Reinforcement of premating isolation. In: Otte, D. & Endler, J. A. (eds). *Speciation and its consequences.* Sinauer, Sunderland, MA: 158–179.

Butlin, R. (1995). Reinforcement: an idea evolving. *Trends Ecol. Evol.* **10**: 432–434.

Butlin, R. K. & Ritchie, M. G. (1991). Variation in female mate preferences across a grasshopper hybrid zone. *J. Evol. Biol.* **4**: 227–240.

Caccone, A. & Sbordoni, V. (2001). Molecular biogeography of cave life: a study using mitochondrial DNA from bathysciine beetles. *Evolution* **55**: 122–130.

Carson, H. L. (1968). The population flush and its genetic consequences. In: Lewontin, R. C. (ed). *Population Biology and Evolution*. Syracuse UP, Syracuse, NY: 123–137.

Carson, H. L. (1975). The genetics of speciation at the diploid level. *Am. Nat.* **109**: 83–92.

Carson, H. L. (1996). Pacific Basin biotas and evolutionary theory. In: Keast, A. & Miller, S. E. (eds). *The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and process.* SPB Academic Publishing bv, Amsterdam: 7–17.

Carson, H. L. (1999). Sexual selection in populations: The facts require a change in the genetic definition of the species. In: Singh, R. S. & Krimbas, C. B. (eds). *Evolutionary Genetics: From Molecules to Morphology.* Vol 1. Cambridge UP, Cambridge, MA: 495–512.

Carson, H. L. (2003). Mate choice theory and the mode of selection in sexual populations. *P. Natl. Acad. Sci. USA* **100**: 6584–6587.

Carson, H. L. & Clague, D. A. (1995). Geology and biogeography of the Hawaiian Islands. In: Wagner, W. L. & Funk, V. A. (eds). *Hawaiian biogeography: evolution on a hot spot archipelago*. Smithsonian Institute Press, Washington, D.C.: 14–29.

Carson, H. L. & Kaneshiro, K. Y. (1976). *Drosophila* of Hawaii: systematics and ecological genetics. *Annu. Rev. Ecol. Syst.* **7**: 311–345.

Carson, H. L., Lockwood, J. P. & Craddock, E. M. (1990). Extinction and recolonization of local populations on a growing shield volcano. *P. Natl. Acad. Sci. USA* **87**: 7055–7057.

Carson, H. L. & Templeton, A. R. (1984). Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.* **15**: 97–131.

Casas, J., Magal, C. & Sueur, J. (2007). Dispersive and non-dispersive waves through plants: implications for arthropod vibratory communication. *Proc. R. Soc. B* **274**: 1087–1092.

Casserius, J. (1600). *De vocis auditusque organis historia anatomica singulari fide methode ac industria concinnata tractatibus duobus explicata ac varii iconibus aere excusis.* Baldinus, Ferrariae (Ferrara): 191, 126 pp.

China, W. E. & Fennah, R. G. (1952). A remarkable new genus and species of Fulgoroidea (Homoptera) representing a new family. *Ann. Mag. Nat. Hist.* **12**(5): 189–199.

Christiansen, K. A. & Bellinger, P. F. (1992). *Insects of Hawaii*. Vol 15. Collembola. HUP, Honolulu: 445 pp.

Church, S. A. & Taylor, D. R. (2002). The evolution of reproductive isolation in spatially structured populations. *Evolution* **56**: 1859–1862.

Clague, D. A. (1996). The growth and subsidence of the Hawaiian-Emperor volcanic chain. In: Keast, A. & Miller, S. E. (eds). *The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and process.* SPB Academic Publishing bv, Amsterdam: 35–50.

Clague, D. A. & Dalrymple, G. B. (1975). Cretaceous K-Ar ages of volcanic rocks from the Musicians seamounts and the Hawaiian ridge. *Geophys. Res. Lett.* **2**: 305–308.

Clague, D. A. & Dalrymple, G. B. (1987). The Hawaiian-Emperor volcanic chain. In: Decker, R. W., Wright, T. L. & Stauffer, P. H. (eds). *Volcanism in Hawaii.* U.S. Geological Survey Professional Paper 1350, U.S. Government Printing Office, Washington, D.C.: 1–54.

Clague, D. A. & Jarrard, R. D. (1973). Tertiary Pacific plate motion deduced from the Hawaiian-Emperor chain. *B. Geol. Soc. Am.* **84**: 1135–1154.

Claridge, M. F. (1983). Acoustic signals and species problems in the Auchenorrhyncha. *Proc. 1st Int. Workshop on Leafhoppers and Planthoppers of Economic Importance*: 111–120.

Claridge, M. F. (1985). Acoustic signals in the Homoptera: Behavior, taxonomy, and evolution. *Annu. Rev. Entomol.* **30**: 297–317.

Claridge, M. F. (1990). Acoustic recognition signals: barriers to hybridisation in Homoptera Auchenorrhyncha. *Can. J. Zool.* **68**: 1741–1746.

Claridge, M. F. (1993). Speciation in insect herbivores – the role of acoustic signals in leafhoppers and planthoppers. In: Lees, D. R. & Edwards, D. (eds). *Evolutionary patterns and processes.* (Linnean Society Symposium Series 14) Linnean Society, London: 285–297.

Claridge, M. F., den Hollander, J. & Morgan, J. C. (1985a). Variation in courtship signals and hybridization between geographically definable populations of the rice brown planthopper, *Nilaparvata lugens* (Stål). *Biol. J. Linn. Soc.* **24**: 35–49.

Claridge, M. F., den Hollander, J. & Morgan, J. C. (1985b). The status of weed associated populations of the brown planthopper, *Nilaparvata lugens* (Stål) – host race or biological species? *Zool. J. Linn. Soc.* **84**: 77–90.

Claridge, M. F., den Hollander, J. & Morgan, J. C. (1988). Variation in hostplant relations and courtship signals of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stål), from Australia and Asia: a test of the recognition species concept. *Biol. J. Linn. Soc.* **35**: 79–93.

Claridge, M. F. & Nixon, G. A. (1986). *Oncopsis flavicollis* (L): associated with tree birches (*Betula*): a complex of biological species or a host plant utilization polymorphism?. *Biol. J. Linn. Soc.* **27**: 381–397.

Claridge, M. F. & Reynolds, W. J. (1973). Male courtship songs and sibling species in the *Oncopsis flavicollis* species group (Hemiptera: Cicadellidae). *J. Entomol. Ser. B. Taxon. Syst.* **42**: 29–39.

Clement, M., Posada, D. & Crandall, K. A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**(10): 1657–1659.

Cocroft, R. B. & McNett, G. D. (2006). Vibratory communication in treehoppers (Hemiptera: Membracidae). In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 305–318.

Cocroft, R. B., Shugart, H. J., Konrad, K. T. & Tibbs, K. (2006). Variation in plant substrates and its consequences for insect vibrational communication. *Ethology* **112**(8): 779–789.

Cokl, A. & Virant-Doberlet, M. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annu. Rev. Entomol.* **48**: 29–50.

Cokl, A., Virant-Doberlet, M. & Zorovic, M. (2006). Sense organs involved in the vibratory communication of bugs. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 71–80.

Cooper, W. S. (1923). The recent ecological history of Glacier Bay, Alaska: Permanent quadrats at Glacier Bay, an initial report upon a long-period study. *Ecology* **4**: 355–365.

Cooper, W. S. (1931). A third expedition to Glacier Bay, Alaska. *Ecology* **12**: 61–95.

Cooper, W. S. (1939). A fourth expedition to Glacier Bay, Alaska. *Ecology* **20**: 130–159.

Cowles, H. C. (1899). The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot. Gaz.* **27**: 95–117, 167–202, 281–308, 361–391.

Cox, G. W. (1999). *Alien species in North America and Hawaii. Impacts on natural ecosystems.* Island press, Washington, D.C.: 387 pp.

Coyne, J. A. & Orr, H. A. (1989). Patterns of speciation in *Drosophila*. *Evolution* **43**: 362–381.

Coyne, J. A. & Orr, H. A. (2004). *Speciation*. Sinauer Ass., Sunderland, MA: 545 pp.

Crocker, R. L. & Mayor, J. (1955). Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecology* **43**: 427–448.

Culver, D. C. (1970a). Analysis of simple cave communities. I. Caves as islands. *Evolution* **24**: 463–474.

Culver, D. C. (1970b). Analysis of simple cave communities: niche separation and species packing. *Ecology* **51**(6): 949–958.

Culver, D. C. (1982). *Cave Life. Evolution and Ecology.* Harvard University Press, Cambridge, MA: 190 pp.

Culver, D. C. & White, W. (2004). *Encyclopedia of caves.* Elsevier Academic Press, Amsterdam: 680 pp.

Cunningham, C. W., Zhu, H., & Hillis, D. M. (1998). Best-fit maximum likelihood models for phylogenetic inference: empirical tests with known phylogenies. *Evolution* **52:** 978–987.

Dachnowski, A. P. (1912). *Peat deposits of Ohio: their origin, formation and uses.* (Geological Survey of Ohio Bulletin, 16) Geological Survey of Ohio, Columbus: 424 pp.

Dachnowski, A. P. (1926). *Factors and problems in the selection of peatlands for different uses.* (U.S. Department of Agriculture Bulletin, 1419) Gov. Pr. Off., Washington: 24 pp.

Dalrymple, G. B., Lanphere, M. A. & Jackson, E. D. (1974). Contributions to the petrography and geochronology of volcanic rocks from the leeward Hawaiian Islands. *B. Geol. Soc. Am*. **85**: 727–738.

Darwin, C. R. (1859): *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London: 502 pp.

Darwin, C. R. (1871): *The descent of man and selection in relation to sex*. 2 vols. John Murray, London. 423, 475 pp.

Decker, R. W., Wright, T. L. & Stauffer, P. H. (eds) (1987). *Volcanism in Hawaii*. 2 vols. U.S. Geological Survey Professional Paper, 1350: 1667 pp.

Deharveng, L. & Bedos, A. (2000). The cave fauna of southeast Asia. Origin, evolution and ecology. In: Wilkens, H., Culver, D. C. & Humphreys, W. F. (eds). *Subterranean ecosystems. (Ecosystems of the world 30)*. Elsevier, Amsterdam: 603–632.

DeLorme (ed.) (1999). *Hawaii Atlas: Topo maps of the entire state. (1:84,000; WGS84)* 1st ed. DeLorme Mapping Company, Yarmouth/Maine: 64 pp.

DeQueiroz, A. & Wimberger, P. H. (1993). The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. *Evolution* **47**: 46–60.

Detrick, R. S. & Crough, S. T. (1978). Island subsidence, hot spots, and lithospheric thinning. *J. Geophys. Res.* **83**: 1236–1244.

Dobzhansky, T. (1940). *Genetics and the origin of species*. 2nd ed. Columbia UP, New York: X+364 pp.

Dodd, D. M. B. & Powell, J. R. (1985). Founder-flush speciation: an update of experimental results with *Drosophila*. *Evolution* **39**(6): 1388–1392.

Dragoni, M., Piombo, A. & Tallarico, A. (1995). A model for the formation of lava tubes by roofing over a channel. *J. Geophys. Res.* **100**: 8435–8447.

Drosopoulos, S. (1985): Acoustic communication and mating behaviour in the *Muellerianella* complex (Homoptera–Delphacidae). *Behaviour* **94**: 183–201.

Drosopoulos, S. & Claridge, M. F. (eds) (2006). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 532 pp.+DVD-ROM

Eberhard, M. J. B. & Picker, M. D. (2008). Vibrational communication in two sympatric species of Mantophasmatodea (Heelwalkers). *J Insect Behav.* **21**: 240–257.

Eggers, F. (1937). Zur hypothetischen Homologie verschiedensegmentiger Tympanalorgane. *Zool. Anz.* **118**: 289–298.

Eldredge, L. G. & Miller, S. E. (1995). How many species are there in Hawaii? *Bishop Mus. Occas. Pap.* **41**: 3–18.

Eldredge, L. G. & Miller, S. E. (1997). Numbers of Hawaiian species: (Suppl. 2), including a review of freshwater invertebrates. *Bishop Mus. Occas. Pap*. **48**: 3–22.

Emeljanov, A. F. (1990). An attempt of construction of phylogenetic tree of the planthoppers (Homoptera, Cicadina). *Revue d´Entomologie de l´URSS* **LXIX**(2): 353–356.

Farrell, B. D. (2001). Evolutionary assembly of the milkweed fauna: cytochrome oxidase I and the age of *Tetraopes* beetles. *Mol. Phylogenet. Evol.* **18**: 467–478.

Felici, G. (1724). Lettera intorno al canto delle cicale, scritta l'anno 1717, al Sig. Pascasio Gianetti, Lettore ordinario di medicina, nell' universita di Pisa. *Giorn. De' Litterati d'Italia* **XXXVI**: 56–77.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783–791.

Fennah, R. G. (1973a). The cavernicolous Fauna of Hawaiian Lava Tubes, 4. Two new blind *Oliarus* (Fulgoroidea: Cixiidae). *Pac. Insects* **15**: 181–184.

Fennah, R. G. (1973b). Three new cavernicolous species of Fulgoroidea (Homoptera) from Mexico and Western Australia. *P. Biol. Soc. Wash.* **86**(38): 439–446.

Fennah, R. G. (1975). New cavernicolous cixiid from New Zealand (Homoptera, Fulgoroidea). *New Zeal. J. Zool.* **2**(3): 377–380.

Fennah, R. G. (1980a). A cavernicolous new species of *Notuchus* from New Caledonia (Homoptera: Fulgoroidea: Delphacidae). *Rev. Suisse Zool.* **87**(3): 757–759.

Fennah, R. G. (1980b). New and little-known neotropical Kinnaridae (Homoptera, Fulgoroidea). *P. Biol. Soc. Wash.* **93**(3):674–696.

Fisher, B. L. & Smith, M. A. (2008). A revision of Malagasy species of *Anochetus* Mayr and *Odontomachus* Latreille (Hymenoptera: Formicidae). *PloS One* **3**(5): e1787.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection.* Clarendon Press, Oxford: 272 pp.

Fitch, W. M. (1971). Toward defining the course of evolution: minimum change for a specific tree topology. *Syst. Zool.* **20:** 406–416.

Fleischer, R. C., McIntosh, C. E. & Tarr, C. L. (1998). Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar-based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Mol. Ecol.* **7**: 533–545.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotech.* **3:** 294–299.

Funkhouser, J. G., Barnes, I. L. & Naughton, G. G. (1968). The determination of a series of ages of Hawaiian volcanoes by the potassium-argon method. *Pac. Sci.* **22**: 369–372.

Furrer, A. M. & Kirchner, W. H. (1990). Vibrational communication in honeybee queens. *7th Int. Meet. Insect Sound & Vibration, Piran* (Abstracts): 17.

Futuyma, D. J. (1998). *Evolutionary biology.* 3rd ed. Sinauer Ass., Sunderland, MA: 763 pp.

Futuyma, D. J. (2006). Ernst Mayr, genetics and speciation. *Trends Ecol. Evol.* **21**(1): 7–8.

Gagné, W. C. & Howarth, F. G. (1975a). The cavernicolous fauna of Hawaiian lava tubes, 6. Mesoveliidae or Water treaders (Heteroptera). *Pac. Insects* **16**: 399–413.

Gagné, W. C. & Howarth, F. G. (1975b). The cavernicolous fauna of Hawaiian lava tubes, 7. Emesinae or Thread-legged bugs (Heteroptera: Reduviidae). *Pac. Insects* **16**: 415–426.

Gaudichaud-Beaupré, C. (1830). Botanique. In: de Freycinet, L. C. de Saulces (1824–1844). *Voyage autour du monde, entrepris par ordre du roi, ... exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820 ; publié sous les auspices ... le Comte Corbière ... pour la pertie historique et les sciences naturelles, et de ... le Comte Chabrol de Crouzol ... pour la partie Nautique. Part 12.* Pillet-ainé, Paris: 465–522.

Gause, G. F. (1934). *The struggle for existence.* Williams & Wilkins, Baltimore: 163 pp.

Gerhardt, H. C. (1994). Reproductive character displacement of female mate choice in the grey treefrog, *Hyla chrysoscelis*. *Anim. Behav.* **47**: 959–969.

Gerhardt, H. C. & Huber, F. (2002). *Acoustic Communication in Insects and Anurans*. University of Chicago Press, Chicago, London: 531 pp.

Gertsch, W. J. (1973). The cavernicolous fauna of Hawaiian lava tubes, 3. Araneae (Spiders). *Pac. Insects* **15**: 163–180.

Ghiselin, M. T. (1988). The individuality thesis, essences, and laws of nature. *Biol. Phil.* **3**: 467–474.

Giffard, W. M. (1925). A review of the Hawaiian Cixiidae, with descriptions of species (Homoptera). *P. Hawaii. Entomol. Soc.* **6**: 1–121.

Gittenberger, E. (1991). What about non-adaptive radiation? *Biol. J. Linn. Soc.* **43**: 263–272.

Gittenberger, E. (2004). Radiation and adaptation, evolutionary biology and semantics. *Org. Divers. Evol.* **4**: 135–136.

Gnaspini, P. & Trajano, E. (2000). Guano communities in tropical caves. In: Wilkens, H., Culver, D. C. & Humphreys, W. F. (2000). *Subterranean ecosystems. (Ecosystems of the world 30).* Elsevier, Amsterdam: 251–268.

Gogala, M. (1985). Vibrational songs of land bugs and their production. In: Kalmring, K. & Elsner, N. (eds). *Acoustic and vibrational communication in insects.* (Proc. XVII. Int. Cong. Entomol.) P. Parey, Berlin: 143–150.

Gogala, M. (2006). Vibratory signals produced by Heteroptera – Pentatomorpha and Cimicomorpha. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 275–296.

Gould, S. J. (1984). Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire, and Curacao: a way of studying nonadaptation. *Syst. Zool.* **33**: 217–237.

Gould, S. J. (2002). *The Structure of Evolutionary Theory.* Belknap Press, Harvard University Press, Cambridge, London: 1433 pp.

Gould, S. J. & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* **205**: 581–598.

Greeley, R. (1971). Observations of actively forming lava tubes and associated structures, Hawaii. *Mod. Geol*. **2**: 207–223.

Greeley, R. (1972). Additional observations of actively forming lava tubes and associated structures, Hawaii. *Mod. Geol*. **3**: 157–160.

Gressitt, J. L. (1971). Relative faunal disharmony of insects of pacific islands. In: Asahina, S. et al. (eds). *Entomological essays to commemorate the retirement of Professor K. Yasumatsu*. Hokuryukan Publ. Co. Ltd., Tokyo: 15–24.

Gurney, A. B. & Rentz, D. C. (1978). The cavernicolous fauna of Hawaiian lava tubes, 10. Crickets (Orthoptera, Gryllidae). *Pac. Insects* **18**: 85–103.

Haeckel, E. (1906). *Prinzipien der Generellen Morphologie der Organismen*. Georg Reimer, Berlin: 447 pp.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Sym. Ser.* **41**: 95–98.

Hardin, G. (1960). The competitive exclusion principle. *Science* **131**: 1292–1297.

Hardy, D. E. (1965). *Insects of Hawaii. A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on their Origin, Distribution, Hosts, Parasites, etc. Vol. 12. Diptera: Cyclorrhapha II, Series Schizophora, Section Acalypterae I, Family Drosophilidae.* University of Hawaii Press, Honolulu: 814 pp.

Hardy, D. E. & Kaneshiro, K. Y. (1981). Drosophilidae of Pacific Oceania. In: Ashburner, M., Carson, H. L. & Thompson, J. N. (eds). *The genetics and biology of* Drosophila*.* Academic Press, New York: 309–348.

Haskell, P. T. (1961). *Insect sounds.* Witherby, London: 189 pp.

Hebert, P. D. N., Cywinska, A., Ball, S. L. & deWaard, J. R. (2003a). Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. B* **270**: 313–321.

Hebert, P. D. N., Ratnasingham, S. & deWaard, J. R. (2003b). Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proc. R. Soc. Lond. B* **270**: S96–S99.

Heinroth, O. (1911). Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. In: Schalow, H. (Hrsg.). *Verhandlungen des V. Internationalen Ornithologen-Kongresses in Berlin 30. Mai bis 4. Juni 1910.* Deutsche Ornithologische Gesellschaft, Berlin: 589–702.

Hennig, W. (1950). *Grundzüge einer Theorie der phylogenetischen Systematik.* Deutscher Zentralverlag, Berlin: 370 pp.

Hennig, W. (1981). *Insect phylogeny.* Wiley, Chichester: 514 pp.

Henry, C. S. (1979). Acoustical communication during courtship and mating in the green lacewing *Chrysopa carnea* (Neuroptera: Chrysopidae). *Ann. Entomol. Soc. Am.* **72**: 68–79.

Henry, C. S. (1982). Reproductive and calling behavior in two close related, sympatric lacewing species, *Chrysopa oculata* and *C. chi* (Neuroptera: Chrysopidae). *P. Entomol. Soc. Wash.* **84**: 191–203.

Henry, C. S. (1994): Singing and cryptic speciation in insects. *Trends Ecol. Evol.* **9**: 388–392.

Henry, C. S. (2006). Acoustic communication in neuropterid insects. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 153–166.

Hey, J., Waples, R. S., Arnold, M. L., Butlin, R. K. & Harrison, R. G. (2003). Understanding and confronting species uncertainty in biology and conservation. *Trends Ecol. Evol.* **18**: 597–603.

Hirschberger, P. (2001). Stridulation in *Aphodius* dung beetles: Behavioral context and intraspecific variability of song pattern in *Aphodius ater* (Scarabaeidae). *J. Insect Behav.* **14**: 69–88.

Ho, S. Y. W., Phillips, M. J., Cooper, A. & Drummond, A. J. (2005). Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Mol. Biol. Evol.* **22**(7): 1561–1568.

Hoch, H. (1988). A new cavernicolous planthopper species (Homoptera: Fulgoroidea: Cixiidae) from Mexico. *Mitt. Schweiz. Entomol. Ges.* **61**: 295–302.

Hoch, H. (1990). Cavernicolous Meenoplidae (Homoptera, Fulgoroidea) from Australia. *Occas. Pap. Bishop Mus.* **30**: 188–203.

Hoch, H. (1991) Cave-dwelling Cixiidae (Homoptera, Fulgoroidea) from the Azores. *Bocagiana* **149**: 1–9.

Hoch, H. (1993). A new troglobitic planthopper species (Hemiptera: Fulgoroidea: Meenoplidae) from Western Australia. *Rec. Western Aust. Mus.* **16**(3): 393–398.

Hoch, H. (1994). Homoptera (Auchenorrhyncha, Fulgoroidea). In: Juberthie, C. & Decu, V. (eds). *Encyclopaedia Biospeologica.* Tome I. Société de Biospéologie, Moulis–Bucarest: 313–325.

Hoch, H. (1996). A new cavernicolous planthopper of the family Meenoplidae from New Caledonia (Hemiptera: Fulgoroidea). *Rec. Western Aust. Mus.* **17**: 451–454

Hoch, H. (1999). The Hawaiian cave planthoppers (Homoptera: Fulgoroidea: Cixiidae) – a model for rapid subterranean speciation? *Int. J. Speleol.* **26**(1–2): 21–31.

Hoch, H. (2002). Hidden from the light of day: planthoppers in subterranean habitats (Hemiptera: Auchenorrhyncha: Fulgoromorpha). In: Holzinger, W. & Gusenleitner, F. (eds). *Zikaden. Leafhoppers, planthoppers and cicadas (Insecta: Hemiptera: Auchenorrhyncha).* Oberösterreichisches Landesmuseum, Linz (Denisia 4): 139–146.

Hoch, H. & Asche, M. (1988). A new troglobitic meenoplid from a lava tube in Western Samoa (Homoptera, Fulgoroidea, Meenoplidae). *J. Nat. Hist.* **22**: 1489–1494.

Hoch, H. & Asche, M. (1993). Evolution and speciation of cave-dwelling Fulgoroidea in the Canary Islands (Homoptera: Cixiidae & Meenoplidae). *Zool. J. Linn. Soc.* **109**: 53–101.

Hoch, H., Asche, M., Burwell, C., Monteith, G. M. & Wessel, A. (2006a). Morphological alteration in response to endogean habitat and ant association in two new planthopper species from New Caledonia (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Delphacidae). *J. Nat. Hist.* **40**(32–34): 1867–1886.

Hoch, H., Bonfils, J., Reynaud, B. & Attié, M. (2003). First record of troglobitic Hemiptera from La Réunion (Fulgoromorpha: Cixiidae). *Ann. Soc. Entomol. Fr. (n.s.)* **39**(3): 265–270.

Hoch, H., Deckert, J. & Wessel, A. (2006b). Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). *Biol. Lett.* **2**(2): 222–224.

Hoch, H. & Howarth, F. G. (1989a). Reductive evolutionary trends in two new cavernicolous species of a new Australian cixiid genus (Homoptera, Fulgoroidea). *Syst. Entomol.* **14**: 179–196.

Hoch, H. & Howarth, F. G. (1989b). Six new cavernicolous cixiid planthoppers in the genus *Solonaima* from Australia (Homoptera, Fulgoroidea). *Syst. Entomol.* **14**: 377–402.

Hoch, H. & Howarth, F. G. (1993). Evolutionary dynamics of behavioral divergence among populations of the Hawaiian cave-dwelling planthopper *Oliarus polyphemus* (Homoptera: Fulgoroidea: Cixiidae). *Pac. Sci.* **47**: 303–318.

Hoch, H. & Howarth, F. G. (1999). Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zool. J. Linn. Soc.* **127**: 453–475.

Hoch, H. & Izquierdo, I. (1996). A cavernicolous planthopper in the Galápagos Islands (Homoptera, Auchenorrhyncha, Cixiidae). *J. Nat. Hist.* **30**: 1495–1502.

Hoch, H., Oromi, P. & Arechavaleta, M. (1999). *Nisia subfogo* sp. n., a new cave-dwelling planthopper from the Cape Verde Islands (Hemiptera: Fulgoromorpha: Meenoplidae). *Rev. Acad. Canaria Cienc.* **11**(3–4): 189–199.

Hoch, H. & Wessel, A. (2006). Communication by substrate-borne vibrations in cave planthoppers. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 187–197.

Holcomb, R. T. (1987). Eruptive history and long-term behavior of Kilauea Volcano. In: Decker, R. W., Wright, T. L. & Stauffer, P. H. (eds). *Volcanism in Hawaii*. 2 vols. U.S. Geological Survey Professional Paper, 1350: 261–350.

Hoskin, C. J., Higgie, M., McDonald, K. R. & Moritz, C. (2005). Reinforcement drives rapid allopatric speciation. *Nature* **437**: 1353–1356.

Howard, D. J. (1993) Reinforcement: Origin, dynamics, and fate of an evolutionary hypothesis. In: Harrison, R. G. (ed.). *Hybrid zones and the evolutionary process*. Oxford University, Press New York: 46–69 pp.

Howarth, F. G. (1972). Cavernicoles in lava tubes on the Island of Hawaii. *Science* **175**: 325–326.

Howarth, F. G. (1973). The cavernicolous fauna of Hawaiian lava tubes, 1. Introduction. *Pac. Insects* **15**: 139–151.

Howarth, F. G. (1979). An inexpensive constant temperature chamber for field and laboartory use. *Environ. Entomol.* **8**: 236–237.

Howarth, F. G. (1981). Non-relictual troglobites in the tropical Hawaiian caves. *Proc. 8th Int. Cong. Speleol.*: 539–541.

Howarth, F. G. (1982a). Adaptive radiation among Hawaiian insects. *The Nature Conservancy News* **32**: 24–26.

Howarth, F. G. (1982b). Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian cave insects. *Entomol. Gen.* **8**(1): 17–26.

Howarth, F. G. (1983). Ecology of cave arthropods. *Annu. Rev. Entomol.* **28**: 365–389.

Howarth, F. G. (1986). The tropical cave environment and the evolution of troglobites. *9th Cong. Int. Speleol., Barcelone 1986*, Vol. 2: 153–155.

Howarth, F. G. (1987). The evolution of non-relictual tropical troglobites. *Int. J. Speleol.* **16**: 1–16.

Howarth, F. G. (1990). Hawaiian terrestrial arthropods: An overview. *Bishop Mus. Occas. Pap.* **30**: 4–26.

Howarth, F. G. & Hoch, H. (2005). Adaptive shifts. In: Culver, D. C. & White, W. B. (eds): *Encyclopedia of caves*. Elsevier Academic Press, Amsterdam: 17–24.

Howarth, F. G., Hoch, H. & Asche, M. (1990). Duets in darkness: species-specific substrate-borne vibrations produced by cave-adapted cixiid planthoppers in Hawaii (Homoptera: Fulgoroidea). *Mém. Biospéol.* **XVI**: 77–80.

Howarth, F. G., James, S. A., McDowell, W., Preston, D. J. & Imada, C. T. (2007). Identification of roots in lava tube caves using molecular techniques: implications for conservation of cave arthropod faunas. *J. Insect Conserv.* **11**: 251–261.

Howarth, F. G. & Mull, W. P. (1992). *Hawaiian insects and their kin.* University of Hawaii Press, Honolulu: 160 pp.

Hrncir, M., Barth, F. G. & Tautz, J. (2006). Vibratory and airborne-sound signals in bee communication (Hymenoptera). In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 421–436.

Huelsenbeck, J. P., Ronquist, F., Nielsen, R. & Bollback, J. P. (2001). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294**: 2310–2314.

Hull, D. L. (1976). Are species really individuals? *Syst. Zool.* **25**: 174–191.

Hull, D. L. (2002). Recent philosophy of biology: a review. *Acta Biotheor.* **50**: 117–128.

Hutchinson, G. E. (1958). Concluding Remarks. *Cold Spring Harb. Sym.* **22**: 415–427.

Ichikawa, T. (1976). Mutual communication by substrate vibration in the mating behaviour of planthoppers (Homoptera: Delphacidae). *Appl. Entomol. Zool.* **11**(1): 8–23.

Ivanov, V. D. & Rupprecht, R. (1992). Substrate vibration for communication in adult *Agapetus fuscipes* (Trichoptera: Glossosomatidae). *Proc. VII. Int. Symp. Trichoptera, Umeå, Sweden*: 273–278.

Jasinska, E. J. & Knott, B. (2000). Root-driven faunas in cave waters. In: Wilkens, H., Culver, D. C. & Humphreys, W. F. (eds). *Subterranean ecosystems. (Ecosystems of the world 30).* Elsevier, Amsterdam: 287–307.

Jeffery, W. R. 2008. Emerging model systems in evo-devo: cavefish and microevolution of development. *Evol. Dev.* **10**(3): 265–272.

Johnson, E. A. (1979). Succession an unfinished revolution. *Ecology* **60**: 238–240.

Johnson, E. A. & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecol. Lett.* **11**: 1–13.

Kanmiya, K. (2006a). Mating behaviour and vibratory signals in whiteflies (Hemiptera: Aleyrodidae). In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series). CRC–Taylor & Francis, Boca Raton, London, New York: 365–380.

Kanmiya, K. (2006b). Communcation by vibratory signals in Diptera. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series). CRC–Taylor & Francis, Boca Raton, London, New York: 381–396.

Kaneshiro, K. Y. (1983). Sexual selection, and direction of evolution in the biosystematics of Hawaiian Drosophilidae. *Annu. Rev. Entomol.* **28**: 161–178.

Kaneshiro, K. Y. (1993). Habitat-related variation and evolution by sexual selection. In: Kim, K. C. & McPheron, B. A. (eds). *Evolution of insect pests.* John Wiley & Sons, New York: 89–101.

Kaneshiro, K. Y. (2006). Dynamics of sexual selection in the Hawaiian Drosophilidae: A paradigm for evolutionary change. *Proc. Hawaiian Entomol. Soc.* **38**: 1–19.

Kaneshiro, K. Y., Gillespie, R. G. & Carson, H. L. (1995). Chromosomes and male genitalia of Hawaiian *Drosophila*: Tools for interpreting phylogeny and geography. In: Wagner, W. L. & Funk, V. A. (eds). *Hawaiian Biogeography: evolution on a hot spot archipelago*. Smithsonian Institute Press, Washington, D.C.: 57–71.

Kauahikaua, J., Cashman, K. V., Mattox, T. N., Heliker, C. C., Hon, K. A., Mangan, M. T. & Thornber, C. R. (1998). Observations on basaltic lava streams in tubes from Kilaues volcano, island of Hawai'i. *J. Geophys. Res.* **103**: 27303–27323.

Kimura, M. (1981). Estimation of evolutionary distances between homologous nucleotide sequences. *P. Natl. Acad. Sci. U.S.A.* **78**: 454-458.

Kirby, W. & Spence, W. (1817). *An Introduction to Entomology, or Elements of the Natural History of Insects*. Vol. II. Longman et al., London: 530 pp.

Kirkaldy, G. W. (1909). A conspectus of the Fulgoridae of the Hawaiian Hemiptera. *Proc. Hawaiian Entomol. Soc.* **2**(2): 75–80.

Kumar, S., Tamura, K., & Nei, M. (2004). MEGA 3: Integrated software for molecular evolutionary genetics analysis and sequence alignment. *Brief. Bioinform.* **5**: 150–163.

Landois, H. (1867). Die Ton- und Stimmapparate der Insecten in anatomisch-physiologischer und akustischer Beziehung. *Z. Wiss. Zool.* **17**: 104–184.

Landois, H. (1872). Ueber ein dem sogenannten Tonapparat der Cikaden analoges Organ bei den hieseigen Gryllen. *Z. Wiss. Zool.* **22**: 348–354.

Landois, H. (1874). *Thierstimmen.* Herder'sche Verlagsbuchhandlung, Freiburg i. Br.: 229 pp.

Lavoie, K. H., Helf, K. L. & Poulson, T. L. 2007. The biology and ecology of North American cave crickets. *J. Cave Karst Stud.* **69**(1): 114–134.

Lazzari, C. R., Manrique, G. & Schilman, P. E. (2006). Vibratory communication in Triatominae (Heteroptera). In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 297–305.

Lepori, C. (1869). Nuove ricerche anatomiche e fisiologiche sopra l'organo sonoro delle cigale. *Boll. Soc. Entomol. Ital.* **1**: 221–235, pl V.

Liebherr, J. K. & Samuelson, G. A. (1992). The first endemic troglobitic carabid beetles in Hawaiian lave tubes (Coleoptera, Carabidae). *Pan-Pac. Entomol.* **68**: 157–168.

Littlejohn, M. J. & Watson, C. F. (1985). Hybrid zones and homogamy in Australian frogs. *Annu. Rev. Ecol. Syst.* **16**: 85–112.

Lockwood, J. P. & Lipman, P. W. (1987). Holocene eruptive history of Mauna Loa Volcano. In: Decker, R. W., Wright, T. L. & Stauffer, P. H. (eds). *Volcanism in Hawaii*, Vol. 1. U.S. Geol. Surv. Prof. Pap. 1350: 509–535.

Löther, R. (1972). *Die Beherrschung der Mannigfaltigkeit. Philosophische Grundlagen der Taxonomie*. Fischer, Jena: 285 pp.

MacArthur, R. H. (1968). The theory of the niche. In: Lewontin, R. C. (ed.). *Population Biology and Evolution.* Syracuse University Press, Syracuse, New York: 159–176.

MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, New Jersey: 203 pp.

Maddison, D. R. (1991). The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* **40**: 315–328.

Marascuilo, L. A. & McSweeney, M. (1977). *Nonparametric and distribution-free methods for the social sciences.* Brooks/Cole, Monterey (CA): 556 pp.

Marascuilo, L. A. & Serlin, R. C. (1988). *Statistical methods for the social and behavioral sciences.* Freeman, New York: 804 pp

Marshall, D. C. & Cooley, J. R. (2000). Reproductive character displacement and speciation in periodical cicadas, with description of new species, 13-year *Magicicada neotredecem*. *Evolution* **54**: 1313–1325.

Martin, G. P. R. & Uschmann, G. (1968). *Friedrich Rolle, 1827–1887. Ein Vorkämpfer neuen biologischen Denkens in Deutschland.* Barth, Leipzig: 151 pp.

Matz, M. V. & Nielsen, R. (2005). A likelihood ratio test for species membership based on DNA sequence data. *Phil. Trans. R. Soc. Lond B* **360**: 1969–1974.

Mayer, P. (1877). Der Tonapparat der Zikaden. *Z. Wiss. Zool. (Leipzig)* **XXVIII**: 79–92.

Mayr, E. (1940). Speciation phenomena in birds. *Am. Nat.* **74**: 249–278.

Mayr, E. (1942). *Systematics and the Origin of Species*. Columbia UP, New York: 334 pp.

Mayr, E. (1954). Change of genetic environment and evolution. In: Huxley, J., Hardy, A. C. & Ford, E. B. (eds). *Evolution as a process*. Allen & Unwin, London: 157–180.

Mayr, E. (1959). Where are we? *Cold Spring Harb. Sym.* **24**: 1–14.

Mayr, E. (1963). *Animal species and evolution.* Harvard University Press, Cambridge, MA: 797 pp.

Mayr, E. (1974). Behavior programs and evolutionary strategies*. Am. Sci*. **62**: 650–659.

Mayr, E. (1982). *The growth of biological thought: Diversity, evolution, and inheritance.* Belknap Press, Harvard UP, Cambridge, MA: 974 pp.

Mayr, E. (1984). The Triumph of the Evolutionary Synthesis. *Times Literary Suppl.* 2, Februar 1984: 1261–1262.

Mayr, E. (1988). *Toward a new philosophy of biology. Observations of an Evolutionist.* Harvard University Press, Cambridge, London: 564 pp.

Mayr, E. & Ashlock, P. D. (1991). *Principles of Systematic Zoology*. 2nd ed., McGraw-Hill, New York: 475 pp.

Mayr, E. & Bock, W. J. (2002). Classifications and other ordering systems. *J. Zool. Syst. Evol. Res.* **40**: 169–194.

Mayr, E., Linsley, E. G. & Usinger, R. L. (1953). *Methods and Principles of Systematic Zoology*. McGraw-Hill, New York, Toronto, London. 328 pp.

McCracken, K. G. & Sheldon, F. H. (1997). Avian vocalizations and phylogenetic signal. *P. Natl. Acad. Sci. USA* **94**: 3833–3836.

McDougal, I. (1979). Age of shield-building volcanism of Kauai and linear migration of volcanism on the Hawaiian Island chain. *Earth Planet Sci. Lett.* **46**: 31–42.

McDowell, W. M. (2002). *An Ecological Study of* Metrosideros polymorpha *Gaud. (Myrtaceae) Roots in Lava Tubes.* M.S. thesis, University of Hawai'i at Manoa, Botanical Sciences (Botany-Ecology, Evolution and Conservation Biology): 91 pp., 2 maps.

Meissner, K. (1976). *Homologieforschung in der Ethologie: Voraussetzungen, Methoden und Ergebnisse.* Fischer, Jena: 184 pp.

Meffert, L. M. & Bryant, E. H. (1991). Mating propensity and courtship behavior in serially bottlenecked lines of the housefly. *Evolution* **45**(2): 293–306.

Mendelson, T. C. & Shaw, K. L. 2005. Sexual behaviour: Rapid speciation in an arthropod. *Nature* **433**: 375–376.

Mendelson, T. C. & Shaw, K. L. 2006. Close-range acoustic signaling and mate choice in Hawaiian crickets (Gryllidae: *Laupala*). *Behav. Ecol. Sociobiol.* **59**(6): 770–776.

Merrell, D. J. (1994). *The adaptive seascape. The mechanism of evolution.* University of Minnesota Press, Minneapolis, London: 259 pp.

Meyer, J. B. (1855). *Aristoteles Thierkunde: Ein Beitrag zur Geschichte der Zoologie, Physiologie und alten Philosophie*. Reimer, Berlin: 520 pp.

Michelsen, A., Fink, F., Gogala, M. & Traue, D. (1982). Plants as transmission channels for insect vibrational songs. *Behav. Ecol. Sociobiol.* **11**: 269–281.

Michelsen, A., Kirchner, W. H., Andersen, B. B. & Lindauer, M. (1986). The tooting and quacking vibration signals of honeybee queens: a quantitative analysis. *J. Comp. Physiol.* **158**: 605–611.

Miller, S. E. & Eldredge, L. G. (1996). Numbers of Hawaiian species: (Suppl. 1). *Bishop Mus. Occas. Pap.* **45**: 8–17.

Mitomi, M., Ichikawa, T. & Okamoto, H. (1984). Morphology of the sound-producing organ in adult rice brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Appl. Entomol. Zool.* **19**: 407–417.

Mook, J. H. & Bruggemann, C. G. (1968). Acoustical communication by *Lipara lucens* (Diptera, Chloropidae). *Entomol. Exp. Appl.* **11**: 397–402.

Moore, T. E. (1993). Acoustic signals and speciation in cicadas (Insecta: Homoptera: Cicadidae). In: Lees, D. R. & Edwards, D. (eds). *Evolutionary patterns and processes.* (Linnean Society Symposium Series, 14) Linnean Society, London: 269–284.

Moore, J. G. & Clague, D. A. (1992). Volcano growth and evolution of the island of Hawaii. *Bull. Geol. Soc. Amer.* **104**: 1471–1484.

Morgan, W. J. (1972). Deep mantle convection plumes and plate motions. *B. Am. Assoc. Pet. Geol.* **56**: 203–213.

Morris, G. K. (1980). Calling display and mating behavior of *Copiphora rhinoceros* Pictet (Orthoptera: Tettigoniidae). *Anim. Behav.* **28**: 42–51.

Moya, A., Galiana, A. & Ayala, F. J. (1995). Founder-effect speciation theory: failure of experimental corroboration. *P. Natl. Acad. Sci. USA* **92**: 3983–3986.

Muchmore, W. B. (1979). The cavernicolous fauna of Hawaiian lava tubes, 11. Troglobitic Pseudoscorpion (Pseudoscorpionida: Chthoniidae). *Pac. Insects* **20**: 187–190.

Muchmore, W. B. (1983). The cavernicolous fauna of Hawaiian lava tubes, 14. A second troglobitic *Tyrannochthonius* (Pseudoscorpionida: Chthoniidae). *Int. J. Entomol*. **25**: 84–86.

Muchmore, W. B. (1989). A third cavernicolous *Tyrannochthonius* from Hawaii (Pseudoscorpionida: Chthoniidae). *Pan-Pac. Entomol*. **65**: 440–442.

Nei, M., Maruyama, T. & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. *Evolution* **29**: 1–10.

Niemiller, M. L., Fitzpatrick, B. M. & Miller, B. T. (2008). Recent divergence with gene flow in Tennessee cave salamanders (Plethodontidae: *Gyrinophilus*) inferred from gene genealogies. *Molecular Ecology* **17**(9): 2258–2275.

Nishida, G. M. (ed) (2002). *Hawaiian terrestrial arthropod checklist.* Fourth edition. Bishop Museum Techical Report, 22: iv, 310 pp.
[Searchable hawaiian arthropod checklist database:
http://www2.bishopmuseum.org/HBS/checklist/query.asp?grp=Arthropod]

Noor, M. A. F. (1999). Reinforcement and other consequences of sympatry. *Heredity* **83**: 503–508.

Nosil, P. (2008). Perspective: Speciation with gene flow could be common. *Molecular Ecology* **17**(9): 2103–2106.

Nylander, J. A. A. (2004). MrModeltest v2.2. Evolutionary Biology Center, Uppsala University, Uppsala: computer program distributed by the author.

Ohta, T. (1992). The nearly neutral theory of molecular evolution. *Annu. Rev. Ecol. Syst.* **23**: 263–268.

Ohta, T. (2003). Origin of the neutral and nearly neutral theories of evolution. *J. Biosci.* **28**: 371–377.

Oosting, H. J. (1942). An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.* **28**: 1–126.

Ortiz-Barrientos, D., Counterman, B. A., Noor, M. A. F. (2004). The genetics of speciation by reinforcement. *PLoS Biol.* **2**(12): e416,
doi: 10.1371/journal.pbio.0020416.

Ossiannilsson, F. (1949). Insect drummers. A study on the morphology and function of the sound-producing organ of Swedish Homoptera Auchenorrhyncha with notes on their sound-production. *Opusc. Entomol. Suppl.* **10**: 1–145.

Otte, D. (1989). Speciation in Hawaiian crickets. In: Otte, D. & Endler, J. A. (eds). *Speciation and its consequences.* Sinauer, Sunderland, MA: 482–526.

Palumbi, S. R. (1996). Nucleic acids II: The polymerase chain reaction. In: Hillis, D. M., Moritz, C. & Mable, B. K. (eds). *Molecular systematics*. Sinauer, Sunderland, MA: 205–247.

Paterson, H. E. H. (1985). The recognition concept of species. In: Vrba, E. S. (ed). *Species and speciation.* (Transvaal Museum Monograph, 4) Transvaal Museum, Pretoria: 21–29.

Patterson, B. & Gittings, B. (1996). *AGI GIS Dictionary.* Association for Geographic Information & Department of Geography at the University of Edinburgh: http://www.geo.ed.ac.uk/agidict/

Pearman, J. V. (1928). On sound production in the Psocoptera and on a presumed stridulatory organ. *Entomol. Month. Mag.* **14**: 179–186.

Pérez-Barros, P., D'Amato, M. E., Guzmán, N. V. & Lovrich, G. A. (2008). Taxonomic status of two South American sympatric squat lobsters, *Munida gregaria* and *Munida subrugosa* (Crustacea: Decapoda: Galatheidae), challenged by DNA sequence information. *Biol. J. Linn. Soc.* **94**: 421–434.

Peterson, D. W., Holcomb, R. T., Tilling, R. I. & Christiansen, R. L. (1994). Development of lava tubes in the light of observations at Mauna Ulu, Kilauea volcano, Hawaii. *B. Volcanol.* **56**: 343–360.

Peterson, D. W. & Swanson, D. A. (1974). Observed formation of lava tubes during 1970–71 at Kilauea volcano, Hawaii. *Stud. Speleol.* **2**: 209–222.

Pickett, S. T. A., Parker, V. T. & Fiedler, P. L. (1992). The new paradigm in ecology: implications for conservation biology. In: Fiedler, P. L. & Jain, S. K. (eds). *Conservation biology: the theory and practice of nature conservation, preservation and management.* Chapman & Hall, New York: 65–88.

Pontedera, J. (1718). De Cicada in epistola ad Sherardum. Appended to: Pontedera, J. (1718). *Compendium tabularum botanicarum, in quo plantae CCLXXII. Ab eo in Italia nuper detectae recensentur. Accessit ejusdem epistola ad G. Sherardum.* Manfrè, Patavii (Padua): XVIII, 168 pp.

Popper, K. R. (1959). The logic of scientific discovery. (Translated by the author, with assistance by J. & L. Freed) Hutchinson, London: 480 pp.

Popper, K. R. (1989). *Logik der Forschung.* 9th Ed. J.C.B. Mohr, Tübingen: 477 pp.

Popple, L. W., Walter, G. H. & Raghu, S. 2008. The structure of calling songs in the cicada *Pauropsalta annulata* Goding and Froggatt (Hemiptera: Cicadidae): evidence of diverging populations? *Evol. Ecol.* **22**: 203–215.

Posada, D. & Crandall, K. A. (2001). Selecting the best-fit model of nucleotide substitution. *Syst. Biol.* **50**: 580–501.

Powell, J. R. (1978). The founder-flush speciation theory: an experimental approach. *Evolution* **32**(3): 465–474.

Poulson, T. L. & Lavoie, K. H. (2000). The trophic basis of subsurface ecosystems. In: Wilkens, H., Culver, D. C. & Humphreys, W. F. (eds). *Subterranean ecosystems. (Ecosystems of the world 30)* Elsevier, Amsterdam: 231–249.

Poulson, T. L. & White, W. B. (1969). The cave environment: limestone caves provide unique natural laboratories in which biological and geological processes are being studied. *Science* **165**: 971–981.

Price, J. P. & Clague, D. A. (2002). How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *P. Roy. Soc. Lond. B Bio.* **269** : 2429–2435.

Price, J. P. & Elliott-Fisk, D. (2004). Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. *Pac. Sci.* **58**: 27–45.

Price, J. J. & Lanyon, S. M. (2002). Reconstructing the evolution of complex bird song in the Oropendolas. *Evolution* **56**: 1514–1529.

Provine, W. B. (1986). *Sewall Wright and evolutionary biology*. (Science and its conceptual foundations) Univ. Chicago Press, Chicago: 545 pp.

Pulquério, M. J. F. & Nichols, R. A. (2007). Dates from the molecular clock: how wrong can we be? *Trends Ecol. Evol.* **22**(4): 180–184.

Racovitza, E. G. (1907). Essai sure les problèmes biospéologiques. *Arch. Zool. Exp. Gen.* **4**(6): 371–488.

de Réaumur, R. A. F. (1741). *Mémoires pour servir à l'histoire des insectes. Tom. V. Partie I. Quatrième mémoire. Sur les cigales.* Paris, Amsterdam: 145–206.

Remane, R. (1968). Ergänzungen und kritische Anmerkungen zu der Heteropteren- und Cicadinen-Fauna der Makaronesischen Inseln. *Bocagiana* **16**: 1–15.

Remane, R. & Hoch, H. (1988). Cave-dwelling Fulgoroidea (Homoptera Auchenorrhyncha) from the Canary Islands. *J. Nat. Hist.* **22**: 403–412.

de Remes Lenicov, A. M. (1992). Fulgoroideos sudamericanos. I. Un nuevo género y especie de Cixiidae cavernícola de la Patagonia (Insecta: Homoptera). *Neotropica* **38**(100): 155–160.

Riedl, R. (1966). *Biologie der Meereshöhlen. Topographie, Faunistik und Ökologie eines unterseeischen Lebensraumes*. P. Parey, Hamburg, Berlin: 636 pp.

Ringo, J. M. (1977). Why 300 species of Hawaiian *Drosophila*? The sexual selection hypothesis. *Evolution* **31**(3): 694–696.

Ritchie, M. G. 2007. Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* **38**: 79–102.

Rivera, M. A. J., Howarth, F. G., Taiti, S. & Roderick, G. K. (2002). Evolution in Hawaiian cave-adapted isopods (Oniscidea: Philosciidae): vicariant speciation or adaptive shift? *Mol. Phylogenet. Evol.* **25**: 1–9.

Roderick, G. K. & Gillespie, R. G. (1998). Speciation and phylogeography of Hawaiian terrestrial arthropods. *Mol. Ecol.* **7**: 519–531.

Rodríguez, F., Oliver, J. F., Marín, A., & Medina, J. R. (1990). The general stochastic model of sequence substitution. *J. Theor. Biol.* **142**: 485-501.

Rodriguez, R. L., Sullivan, L. E. & Cocroft, R. B. (2004). Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Evolution* **58**: 571–578.

Ronquist, F. & Huelsenbeck, J. P. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Roth, L. M. & Hartmann, H. B. (1967). Sound production and its evolutionary significance in the Blattaria. *Ann. Entomol. Soc. Am.* **60**: 740–752.

Rotondo, G. M., Springer, V. G., Scott, G. A. J. & Schlanger, S. O. (1981). Plate movement and island integration – a possible mechanism in the formation of endemic biotas, with special reference to the Hawai'i islands. *Syst. Zool.* **30**: 12–21.

Rovner, J. S. & Barth, F. G. (1981). Vibratory communication through living plants by a tropical wandering spider. *Scien*ce **214**: 464–466.

Rozas, J., Sánchez-DelBarrio, J. C., Messegyer, X. & Rozas, R. 2003. DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19**: 2496–2497.

Rundle, H. D., Mooers, A. Ø. & Whitlock, M. C. (1998). Single founder-flush events and the evolution of reproductive isolation. *Evolution* **52**(6): 1850–1855.

Rupprecht, R. (1968). Das Trommeln von Plecopteren. *Z. Vergl. Physiol.* **59**: 38–71

Saitou, N. & Nei, M. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* **4**: 406–425.

Sbordoni, V. (1982). Advances in speciation of cave animals. In: Barigozzi, C. (ed.). *Mechanisms of speciation.* Liss, New York: 219–240.

Schmidt, C. (2007). Revision of the Neotropical Scleropactidae (Crustacea: Oniscidea). *Zool. J. Linn. Soc.* **151**(Suppl. 1): 1–339.

Schluter, D. (2000). *The ecology of adaptive radiation.* Oxford University Press, Oxford: 288 pp.

Schultz, G. A. (1973). The cavernicolous fauna of Hawaiian lava tubes, 2. Two new genera and species of blind isopod crustaceans (Oniscoidea: Philosciidae). *Pac. Insects* **15:** 153–162.

Seddon, N. & Tobias, J.A. (2007). Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biol. J. Linn. Soc.* **90**: 173–188.

Servedio, M. R. & Noor, M. A. F. (2003). The role of reinforcement in speciation: theory and data. *Annu. Rev. Ecol. Syst.* **34**: 339–364.

Shingleton, K. E. (2001). *Population structure and evolutionary history of a cave-adapted planthopper in the Hawaiian Islands*. PhD thesis, Washington Univ., St. Louis, MO: 201 pp.

Siegel, S. & Castellan, N. J., jr. (1988). *Nonparametric statistics for the behavioral sciences.* 2nd ed. McGraw-Hill, New York: 399 pp.

Sigurđardóttir, S., Helgason, A., Gulcher, J. R., Stefansson, K. & Donnelly, P. (2000). The mutation rate in the human mtDNA control region. *Am. J. Hum. Genet.* **66**: 1599–1609.

Simoes, P., Santos, J., Fragata, I., Mueller, L. D., Rose, M. R. & Matos, M. (2008). How repeatable is adaptive evolution? The role of geographical origin and founder effects in laboratory adaptation. *Evolution* **62**(8): 1817–1829.

Simon, C. M., Gagne, W. C., Howarth, F. G. & Radovsky, F. J. (1984). Hawai'i: a natural entomological laboratory. *B. Entomol. Soc. Am.* **30**: 9–17.

Sket, B. (1986). Why all cave animals do not look alike – a discussion on adaptive value of reduction processes. *B. Natl. Speleol. Soc.* **47**: 78–85.

Slobodchikoff, C. N. & Spangler, H. G. (1979). Two types of sound production in *Eupsophulus castaneus* (Coleoptera: Tenebrionidae). *Coleopts. Bull.* **33**: 239–243.

Sober, E. (1984). *The nature of selection. Evolutionary theory in philosophical focus.* MIT Press, Cambridge: 383 pp.

Sokal, R. R. & Rohlf, F. G. (1995). *Biometry: the principles and practice of statistics in biological research.* 3rd Ed. Freeman, New York: 887 pp.

Steinberger, B. & O'Connell, R. J. (1998). Advection of plumes in mantle flow: implications for hotspot motion, mantle viscosity and plume distribution. *Geophys. J. Int.* **132**: 412–434.

Stewart, K. W. (1997). Vibrational communication in insects: epitome in the language of stoneflies? *Am. Entomol.* **43**: 81–91.

Stewart, K. W. (2001). Vibrational communication (drumming) and mate-searching behavior of stoneflies (Plecoptera); evolutionary considerations. In: Dominguez, E. (ed). *Trends in Research in Ephemeroptera and Plecoptera*. (Proc. IX Int Conf. Ephemeroptera & XIII Int. Symp. Plecoptera, 1998, Tafí de Valle) Kluwer, New York: 217–225.

Stewart, K. W. & Sandberg, J. B. (2006). Vibratory communication and mate searching behaviour in stone flies. In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 179–186.

Stewart, K. W., Szczytko, S. W. & Maketon, M. (1988). Drumming as a behavioral line of evidence for delineating species in the genera *Isoperla*, *Pteronarcys* and *Taeniopteryx* (Plecoptera). *Ann. Entomol. Soc. Am.* **81**: 689–699.

Stone, F. D. (2004). Blattodea in the genus *Nocticola* from Australian cave & surface habitats. In: LaSalle, J., Patten, M. & Zalucki, M. (eds). *Entomology – Strength in Diversity*. (XXII International Congress of Entomology, Brisbane 2004) Austr. Entomol. Soc., Brisbane: S14W66 (abstract on CD-ROM).

Stone, F. D. & Howarth, F. G. (2005). Hawaiian cave biology: status of conservation and management. In: Warner, M. (ed). *2005 National Cave and Karst Management Symposium.* NCKMS, Albany: 21–26.

Stone, F. D., Howarth, F. G., Hoch, H. & Asche, M. (2005). Root communities in lava tubes. In: Culver, D.C. & White, W.B. (eds). *Encyclopedia of caves*. Elsevier Academic Press, Amsterdam: 477–484.

Strickberger, M. W. (2000). *Evolution.* 3rd ed. Jones & Bartlett, Sudbury, MA: 722 pp.

Strübing, H. (1958). Lautäußerung – der entscheidende Faktor für das Zusammenfinden der Geschlechter bei Kleinzikaden (Homoptera – Auchenorrhyncha). *Zool. Beitr. N.F.* **4**: 15–21.

Strübing, H. (1977a). Lauterzeugung oder Substratvibration als Kommunikationsmittel bei Kleinzikaden? (diskutiert am Beispiel von *Dictyophora europaea* – Homoptera-Cicadina: Fulgoroidea). *Zool. Beitr.* **23**: 323–332.

Strübing, H. (1977b). Neue Ergebnisse zur Kommunikation bei Kleinzikaden. *Verh. Deut. Zool. Ges.* **1977**: 336.

Strübing, H. (1983). Die Bedeutung des Kommunikationssignals für die Diagnose von *Euscelis*-Arten (Homoptera Cicadina). *Zool. Jahrb. Allg. Zool. Physiol.* **87**: 343–351.

Strübing, H. (2006). Vibratory communication and mating behaviour in the European lantern fly, *Dictyophara europea* (Dictyopharidae, Hemiptera). In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 351–356.

Strübing, H. & Drosopoulos, S. (2006). Photoperiodism, morphology and acoustic behaviour in the leafhopper genus, *Euscelis*. In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 255–262.

Strübing, H. & Hasse, A. (1975). Ein Beitrag zur Neuen Systematik – demonstriert am Beispiel zweier *Javesella*-Arten (Homoptera-Cicadina: Delphacidae). *Zool. Beitr. N.F.* **21**: 517–543.

Strübing, H. & Rollenhagen, T. (1988). Ein neues Aufnehmersystem für Vibrationssignale und seine Anwendung auf Beispiele aus der Familie Delphacidae (Homoptera-Cicadina). *Zool. Jahrb. Allg. Zool. Physiol*. **92**: 245–268.

Swofford, D. L. (2003). PAUP* (version 4.0). Phylogenetic analysis using parsimony (*and other methods). Sinauer, Sunderland, MA: computer program.

Sudhaus, W. (2004). Radiation within the framework of evolutionary ecology. *Org. Divers. Evol.* **4**: 127–134.

Sudhaus, W. & Rehfeld, K. (1992). *Einführung in die Phylogenetik und Systematik.* Gustav Fischer Verlag, Stuttgart: 241 pp.

Sueur, J. & Aubin, T. (2004). Acoustic signals in cicada courtship behaviour (order Hemiptera, genus *Tibicina*). *J. Zool.* **262**: 217–224.

Synave, H. (1953). Une cixiide troglobie découvert dans les galéries souterraines de Namoroka (Hemiptera – Homoptera). *Nat. Malgache* **5**(2): 175–179.

Taborsky, M. (2008). The use of theory in behavioural research. *Ethology* **114**: 1–6.

Taiti, S. & Howarth, F. G. (1996). Terrestrial isopods from the Hawaiian islands (Crustacea: Oniscidea). *Bishop Mus. Occ. Pap.* **45**: 59–71.

Taiti, S. & Howarth, F. G. (1997). Terrestrial isopods (Crustacea, Oniscidea) from Hawaiian caves. *Mem. Biospeol*. **XXIV**: 97–118.

Tamura, K. & Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* **10**: 512-526.

Tarduno, J. A., Duncan, R. A., Scholl, D. W., Cottrell, R. D., Steinberger, B., Thordarson, T., Kerr, B. C., Neal, C. R., Frey, F. A., Torii, M. & Carvallo, C. (2003). The Emperor Seamounts: southward motion of the Hawaiian hotspot plume in earth’s mantle. *Science* **301**: 1064–1069.

Tembrock, G. (1959). *Tierstimmen. Eine Einführung in die Bioakustik*. Ziemsen, Wittenberg: 285 pp.

Tembrock, G. (1960). Homologie-Forschung an Caniden-Lauten. *Zool. Anz.,* Suppl. **23**: 320–326.

Tembrock, G. (1971). *Biokommunikation. Informationsübertragung im biologischen Bereich.* Rowohlt, Reinbek: 281 pp.

Tembrock, G. (1982/83). *Spezielle Verhaltensbiologie.* 2 Vols. Fischer, Stuttgart: 1040 pp.

Tembrock, G. (1989). Homologisieren in der Ethologie. *Zool. Beitr. N. F.* **32**(3): 425–436.

Tembrock, G. (1996). *Akustische Kommunikation bei Säugetieren.* Wiss. Buchgesellschaft, Darmstadt: 181 pp.

Tembrock, G. (2005). *Tierstimmenforschung. Eine Einführung in die Bioakustik.* 4th Ed. Westarp Wiss. Verl. Ges., Hohenwarsleben: 240 pp.

Templeton, A. R. (1980). The theory of speciation via the founder principle. *Genetics* **91**: 1011–38.

Templeton, A. R. (2006). *Population genetics and microevolutionary theory.* Wiley-Liss, Hoboken: 705 pp.

Templeton, A. R., Crandall, K. A. & Sing, C. F. (1992). A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* **132**: 619–633.

Thomassen, H. A. & Povel, G. D. E. (2006). Comparative and phylogenetic analysis of the echo clicks and social vocalizations of swiftlets (Aves: Apodidae). *Biol. J. Linn. Soc.* **88**: 631–643.

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., & Higgins, D. G. (1997). The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Res.* **25**: 4876–4882.

Tinbergen, N. (1963). On aims and methods of ethology. *Z. Tierpsychologie* **20**: 410–433.

Tishechkin, D. Yu. (2006). Vibratory communication in Psylloidea (Hemiptera). In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series) CRC–Taylor & Francis, Boca Raton, London, New York: 357–364.

Toews, D. P. L. & Irwin, D. E. 2008. Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. *Molecular Ecology*: doi: 10.1111/j.1365-294X.2008.03769.x

Traue, D. (1978). Zur Biophysik der Schallabstrahlung bei Kleinzikaden am Beispiel von *Euscelis incisus* Kb. (Homoptera-Cicadina: Jassidae). *Zool. Beitr. N.F.* **24**: 155–164.

Vandel, A. (1964). *Biospéologie. La biologie des animaux cavernicoles.* Gauthier Villars, Paris: 619 pp.

Vandergast, A. G., Gillespie, R. G. & Roderick, G. K. (2004). Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth and the potential for accelerated evolution. *Mol. Ecol.* **13**: 1729–1743.

de Vrijer, P. W. F. (1984). Variability in calling signals of the planthopper *Javesella pellucida* (F.) (Homoptera: Delphacidae) in relation to temperature, and consequences for species recognition during distant communication. *Neth. J. Zool.* **34**: 388–406.

de Vrijer, P. W. F. (1986). Species distinctiveness and variability of acoustic calling signals in the planthopper genus *Javesella* (Homoptera: Delphacidae). *Neth. J. Zool.* **36**: 162–175.

Wagner, M. (1868). *Die Darwin'sche Theorie und das Migrationsgesetz der Organismen*. Duncker & Humblot, Leipzig: VIII, 62 pp.

Wagner, M. (1870). *Ueber den Einfluss der geographischen Isolirung und Coloniebildung auf die morphologischen Veränderungen der Organismen: ein Beitrag zur Streitfrage des Darwinismus*. Akademische Buchdruckerei Straub, München: 22 pp.

Wagner, M. (1889). *Die Entstehung der Arten durch räumliche Sonderung: Gesammelte Aufsätze*. Schwabe, Basel: 667 pp.

Wagner, W. L. & Funk, V. A. (1995). *Hawaiian biogeography: Evolution on a hot spot archipelago*. Smithsonian Institution Press, Washington: 467 pp.

Weismann, A. (1872). *Ueber den Einfluss der Isolirung auf die Artbildung*. Wilhelm Engelmann, Leipzig: 108 pp.

Weismann, A. (1886). Ueber den Rückschritt in der Natur. *Ber. Naturforsch. Ges. Freiburg i. Br.* **2**: 1–30.

Weismann, A. (1902). *Vorträge über Descendenztheorie*. 2 vols. Gustav Fischer, Jena: 456, 462 pp.

Wessel, A. (1997). *Morphologische und ethologische Differenzierung bei Populationen der Höhlenzikade* Oliarus polyphemus *Fennah aus Hawaii*. Diploma Thesis, Humboldt-Universität zu Berlin: 199 pp.

Wessel, A. (2006). Stridulation in the Coleoptera — an overview. In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect Sounds and Communication. Physiology, Behaviour, Ecology and Evolution.* (Contemporary Topics in Entomology series). CRC–Taylor & Francis, Boca Raton, London, New York: 397–403.

Wessel, A., Erbe, P. & Hoch, H. (2004). Pattern and process in subterranean speciation: comparative analysis of Australian and Hawaiian cave planthopper radiations (Hemiptera: Fulgoromorpha: Cixiidae). In: LaSalle, J., Patten, M. & Zalucki, M. (eds). *Entomology – Strength in Diversity*. (XXII International Congress of Entomology, Brisbane 2004) Austr. Entomol. Soc., Brisbane: S14W68 (abstract on CD-ROM).

Wessel, A., Erbe, P., Hoch, H. (2007). Pattern and process: Evolution of troglomorphy in cave planthoppers of Australia and Hawai'i — preliminary observations. *Acta carsologica* **36**(1): 199–206.

Wessel, A. & Hoch, H. (1999). Remane's statistic species criterion applied to Hawaiian cave planthoppers. *Reichenbachia* **33**: 27–35.

Wilkens, H. (1986). The tempo of regressive evolution: Studies of the eye reduction in stygobiont fishes and decapod crustaceans of the Gulf Coast and west Atlantic region. *Stygol.* **2**: 130–143.

Wilkens, H., Culver, D. C. & Humphreys, W. F. (2000). *Subterranean ecosystems. (Ecosystems of the world 30)* Elsevier, Amsterdam: 791 pp.

Wilson, J. T. (1963a). A possible origin of the Hawaiian islands. *Can. J. Phys.* **41**: 863–870.

Wilson, J. T. (1963b). Evidence from islands on the spreading of the ocean floors. *Nature* **197**: 536–538.

de Winter, A. J. & Rollenhagen, T. (1990). The importance of male and female acoustic behaviour for sexual isolation in *Ribautodelphax* planthoppers (Homoptera, Delphacidae). *Biol. J. Linn. Soc.* **40**: 191–206.

Wolfe, E. W. & Morris, J. (1996). *Geological map of the Island of Hawaii. (1:100,000; Universal Transverse Mercator Projection) MAP I-2524-A.* (Miscellaneous investigations series) U.S. Department of the Interior, U.S. Geological Survey, Hawaii County, Hawaii: 3 sheets.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics* **16**: 97–159.

Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth Annual Congress of Genetics* **1**: 356–366. [Reprinted in Provine1986: 161–177.]

Wright, S. (1937). The distribution of gene frequencies in populations. *P. Natl. Acad. Sci. USA* **23**: 307–320.

Wright, S. (1988). Surfaces of selective value revisited. *Am. Nat.* **131**(1): 115–123.

Xia, X. & Xie, Z. (2001). DAMBE: Data analysis in molecular biology and evolution. *J. Hered.* **92**: 371–373.

Yule, G. U. (1925). A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S. *Philosophical Transactions of the Royal Society of London, Series B* **213**: 21–87.

Zacharda, M. (1982). The cavernicolous fauna of Hawaiian lava tubes, 13. A new subgenus and two new species of Rhagidiidae (Acari: Eupodoidea). *Pac. Insects* **24**: 275–280.

Zachariassen, D. E. (1977). Communication by sound between desert tenebrionids. *Norw. J. Entomol.* **24**: 35–36.

Zanotti, F. M. (1731). De Cicadis majoribus. *De Bononiensi scientiarum et artium instituto atque academia commentarii. (R. Accad. Sci. Inst. Bologna)* **1**: 79–82.

Zhang, A. B., Sikes, D. S., Muster, C. & Li, S. Q. (2008). Inferring species membership using DNA sequences with back-propagation neural networks. *Syst. Biol.* **57**: 202–215.

Ziegler, A. C. (2002). *Hawaiian natural history, ecology, and evolution.* University of Hawai'i Press, Honolulu: 477 pp.

Zimmerman, E. C. (1948a). *Insects of Hawaii. A manual of the insects of the Hawaiian islands, including an enumeration of the species and notes on their origin, distribution, hosts, parasites, etc. Vol 1, Introduction.* University of Hawaii Press, Honolulu: 206 pp.

Zimmerman, E. C. (1948b). *Insects of Hawaii. A manual of the insects of the Hawaiian islands, including an enumeration of the species and notes on their origin, distribution, hosts, parasites, etc. Vol 4, Homoptera: Auchenorhyncha.* University of Hawaii Press, Honolulu: 268 pp.

Zimmerman, E. C. (1958). Three hundred species of *Drosophila* in Hawaii? A challenge to geneticists and evolutionists. *Evolution* **12**: 557–558.

Appendix

Checklist of Hawai’ian cave animals

Abbreviations:

acc.	accidental (in caves)
com.	common
cosmop.	cosmopolitan
dz	dark zone
end.	endemic
fac.	facultative (cave species/resident)
immat.	immature
intr.	introduced
jap.	japanese
oblg.	obligate (cave species/resident)
obs.	observation
(-)p	pond
polyn.	polynesian
(-)r	room (cave chamber)
tb.	troglobite
tp.	troglophile
tm.	troglomorphic
tropicop.	tropicopolitan
tx.	trogloxene
tz	twilight(-transition) zone
visit.	(cave) visitor

For cited literature see References.

Eumetazoa	
Plathelminthes	
"Turbellaria"	
Seriata	
Tricladida	
Terricola	
Gen. sp. ? (land planarian) [own obs.]	Hawaii: Kazumura Cave
Annelida	
Clitellata	
"Oligochaeta" [Howarth 1973]	Hawaii
Arthropoda	
Chelicerata	
Arachnida	
Araneae	
Araneomorphae	
Dysderidae	
Dysdera crocata [Gertsch 1973]	Kauai (intr., cosmop.)
Oonopidae	
***Oonops* sp.** [Gertsch 1973]	Hawaii (immat., presumed tb.)
Scytodidae	
Scytodes longipes [Gertsch 1973, Howarth et al. 2007]	Hawaii; Oahu; Kauai; Maui(E) (intr., tx.)
Ochyroceratidae	
Theotima makua Gertsch, 1973	Oahu: Makua Cave: twz; Kauai: Koloa: Knudsen Cave #1; Koloa Cave #1
Pholcidae	
Smeringopus elongatus [Gertsch 1973]	Oahu; Kauai (intr.)
Nesticidae	
Nesticus pallidus [Gertsch 1973]	Kauai (intr., tp.)
Nesticus mogera [Gertsch 1973, Howarth et al. 2007]	Hawaii; Kauai; Maui (intr. jap., tx.)

Linyphiidae	
Erigoninae	
Erigone stygius Gertsch, 1973	Hawaii: Kipuka Puaulu: Bird Park Cave #1: final r.
Linyphiinae	
Meioneta gagnei Gertsch, 1973 [Howarth et al. 2007]	Maui: Keoneoio: Kalua O Lapa Cave: dz
Meioneta sp. [Gertsch 1973]	Kauai (tp.)
Theridiidae	
Achaearanea tepidariorum [Gertsch 1973]	Hawaii; Kauai (intr., cosmop.)
Argyrodes argyrodes [Gertsch 1973]	Kauai (intr.)
Argiopidae	
Cyclosa albisternis ? [Gertsch 1973]	Kauai (intr.)
Lycosidae	
Lycosa howarthi Gertsch, 1973	Hawaii: Volcano: Hongo Store Cave; Kazumura Cave: dz; Bird Park Cave #1: final r.
Adelocosa Gertsch, 1973	
Adelocosa anops Gertsch, 1973	Kauai: Koloa Cave #2: dz
Heteropodidae	
Heteropoda venatoria [Howarth et al. 2007]	Hawaii: North Kona (intr., acc.)
Agelenidae	
Tegenaria domestica [Gertsch 1973]	Hawaii (intr., cosmop.)
Clubionidae	
Corinna cetrata [Gertsch 1973]	Oahu; Kauai (intr., polyn.)
Gen. sp. ? [Gertsch 1973]	Oahu (immat.)
Gnaphosidae	
Gen. sp. ? [Gertsch 1973]	Oahu (immat.)
Salticidae	
Bavia aericeps [Gertsch 1973]	Hawaii (intr.)
Palpigrada	
Koeneniidae	
Koenenia ? *hanseni*? [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac.?)
Pseudoscorpiones	
Pseudoscorpionida	
Chthoniidae	
Tyrannochthonius howarthi Muchmore, 1979	Hawaii: Ainahou Petroglyph Cave: dz
Tyrannochthonius pupukeanus Muchmore, 1983	Oahu: Pupukea Lava Cave
Tyrannochthonius stonei Muchmore, 1989	Maui: Ulupalukua: KaluAuAu Dripping Cave: tz/dz
Acari	
Eupodoidea	
Rhagidiidae	
Foveacheles (Trofocheles) Zacharda, 1982	
Foveacheles (Trofocheles) goffi Zacharda, 1982	Hawaii: Kau Forest Res.: Manu Cave: dz Molokai: Kawela: Wheelchair Cave
Foveacheles (Trofocheles) tenorioae Zacharda, 1982	Hawaii: Kipuka Puaulu Cave #3; Kau Forest Res.: Manu Cave; Kaumana Cave
Foveacheles sp. [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., oblg.)
Crustacea	
Malacostraca	
Peracarida	
Amphipoda	
Talitridae	
Spelaeorchestia Bousfield & Howarth, 1976	
Spelaeorchestia koloana Bousfield & Howarth, 1976	Kauai: Koloa: Koloa Cave #1, 2, 3; Limestone Quarry Cave
Talitroides alluaudi [Bousfield & Howarth 1976]	Kauai; Oahu (intr., tropicop.)
Talitroides topitotum [Bousfield & Howarth 1976]	Kauai; Hawaii (intr., cosmop.)
Corophiidae	
Grandidierella palama Barnard, 1977 [aqua.]	Maui: Waianapanapa Cave
Grandidierella koa Barnard, 1977 [aqua.]	Hawaii: open lavap.
Eusiridae	
Paramoera rua Barnard, 1977 [aqua.]	Maui: Hana: Waianapanapa Cave: dzp
Paramoera paakai Barnard, 1977 [aqua.]	Hawaii: Tokyo-land lava pond: open lavap
Paramoera lokowai Barnard, 1977 [aqua.]	Hawaii: Honaunau well #1
Gammaridae	
Hadzia (Liagoceradocus) lonomaka Barnard, 1977 [aqua.]	Maui: Capa Kinau: Nukuele #1: open lavap
Maera sp. C [Barnard 1977] [aqua.]	Maui: brackish p.
Nuuanu amikai [Barnard 1977] [aqua.]	Oahu: open sea; Maui: lava p.
Rotomelita Barnard, 1977	
Rotomelita ana Barnard, 1977 [aqua.]	Maui: Waianapanapa Cave: dzp
Rotomelita lokoa Barnard, 1977 [aqua.]	Hawaii: Makalawena N-3: open lavap
Hyalidae	
Parhyale hawaiensis [Barnard 1977] [aqua.]	Maui; Hawaii: open p.s

Isopoda	
Oniscoidea	
Trichonisciidae	
Haplophthalmus danicus [Taiti & Howarth 1996]	Maui: Ulupalakua: Ulupalakua c., Po'okanaka c.
Stylonisdiidae	
(*Trichoniscus pusillus* [Schultz 1973])	
Styloniscus mauritiensis [Taiti & Howarth 1997]	Hawaii: Kaumana Cave, Hamakua For. Cave Kauai: Waikanaloa Cave
Philosciidae	
Hawaiioscia Schultz, 1973	
Hawaiioscia rotundata Taiti & Howarth, 1997	Kauai: Koloa: Koloa Cave #2
Hawaiioscia microphthalma Taiti & Howarth, 1997	Oahu: Pupukea: Pupukea Cave
Hawaiioscia **sp. nov.** [Taiti & Howarth 1997]	Oahu: cave 17
Hawaiioscia parvituberculata Schultz, 1973	Maui: La Perouse Bay: Keoneoio Kalua O Lapa Cave: dz
Hawaiioscia paeninsulae Taiti & Howarth, 1997	Molokai: Kalaupapa: Fisherman's Shack Cave #1
Haplophiloscia Schultz, 1973 [*Papuaphiloscia*]	
Haplophiloscia laevis Schultz, 1973	Hawaii: Kaumana Cave: dz (intr., tp., sev. isl.)
Littorophiloscia **sp. nov.** [Taiti & Howarth 1997, Howarth et al. 2007]	Hawaii: Hualalai: Barnabys Cave, Upper Ohia cave; Mauna Loa: 10265 T40D c., Keahou Border c., Lanikai
(*Philoscia sp. #1* [Schultz 1973]	Maui; Oahu; Kauai)
(*Philoscia sp. #2* [Schultz 1973]	Kauai; Maui; Hawaii)
Tropicana minuta [Taiti & Howarth 1997]	Kauai; Maui
Burmoniscus meeusei [Taiti & Howarth 1997, Howarth et al. 2007]	Kauai; Oahu; Molokai; Hawaii; Maui(E)
Squamiferiidae (Platyarthridae? [Taiti & Howarth 1997])	
Trichorhina tomentosa [Schultz 1973, Taiti & Howarth 1997, Howarth et al. 2007]	Oahu; Kauai; Maui; Hawaii: North Kona (intr., fac.)
Trichorhina heterophthalma [Taiti & Howarth 1997]	Kauai: Koloa: Limestone Quarry C.
Porcellionidae	
Metoponorthus pruinosus [Schultz 1973, Taiti & Howarth 1997]	Oahu; Kauai; Maui; Hawaii
Porcellio laevis [Schultz 1973, Taiti & Howarth 1997]	Oahu; Kauai; Hawaii
Porcellio scaber [Schultz 1973, Taiti & Howarth 1997]	Kauai; Maui; Hawaii
Porcellio dilatatus dilatatus [Taiti & Howarth 1997]	Kauai; Hawaii
Porcellio dilatatus [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl.: tw (intr., fac.)
Porcellionides pruinosus [Howarth et al. 2007]	Hawaii: North Kona (intr., fac,)
Scleropactidae	
Aulaconiscus Taiti & Howarth, 1997 [Schmidt 2007]	
Aulaconiscus caecus Taiti & Howarth, 1997	Kauai; Oahu; Maui
Armadilliidae	
Cubaris murina [Taiti & Howarth 1997]	Hawaii
Reductoniscus costulatus [Schultz 1973]	Oahu
Chilopoda	
Pleurostigmophora	
Lithobiomorpha	
Lithobiidae	
Lithobius sp. nov. [Howarth & Mull 1992]	Maui (East)
Progoneata	
Symphyla	
Scolopendrellidae ? [Howarth et al. 2007]	
Gen. sp. [Howarth et al 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac.)
Scutigerellidae	
Hanseniella unguiculata ? [Howarth et al. 2007]	Hawaii: North Kona (intr., fac.)
Diplopoda	
Helminthomorpha	
Nematophora	
Spirostreptida	
Cambalidae	
Nannolene **sp. nov.** [Howarth & Mull 1992]	Hawaii
Nannolene **sp.** [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., obl.)
Dimerogonus **sp. nov. ?** [Howarth 1973]	Hawaii: Kazumura Cave
Polydesmida	
Paradoxosomatidae	
Oxidus gracilis [Howarth 1973, Howarth et al. 2007]	Hawaii: Kazumura Cave; North Kona (intr., tp.) Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac.)
Haplodesmidae	
Prosopodesmus jacobsoni [Howarth et al. 2007]	Hawaii: North Kona (intr., fac.)

Hexapoda	
Zygentoma	
Nicoletiidae	
Nicoletia sp. [Howarth 1973]	Hawaii: Kazumura Cave (intr., tp.)
Nicoletia phytophila [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl.; Hawaii: North Kona (intr., fac.)
Collembola	
Poduromorpha	
Neanuridae	
Frieseinae	
Friesea sublimis [Bellinger & Christiansen 1974]	Kauai (tx.)
Morulininae	
Protanura hawaiiensis Bellinger & Christiansen, 1974 [***Neanura h.*** Christiansen & Bellinger 1992]	Hawaii: Kazumura Cave; Bird Park Cave #1: dz
Onychiuridae	
Onychiurinae	
Onychiurus (Onychiurus) folsomi [Bellinger & Christiansen 1974]	Hawaii (tx.)
Entomobryomorpha	
Entomobryidae	
Entomobryinae	
Entomobryia sp. [Howarth et al. 2007]	Hawaii: North Kona (end.?, fac.)
Entomobrya (Entomobrya) multifasciata [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Hawaii (tx.)
Sinella (Coecobrya) caeca [Bellinger & Christiansen 1974]	Hawaii; Oahu (tp.)
Sinella (Coecobrya) lua Christiansen & Bellinger, 1992	Oahu: Pupukea Lava Tube
Sinella (Coecobrya) nupa Christiansen & Bellinger, 1992	Maui: Waikau Cave: dz [tb, tm]
Sinella (Sinella) yos(h)iia Bellinger & Christiansen, 1974 [Howarth et al. 2007]	Hawaii: Kazumura Cave; Kaumana Cave; Mauna Loa Strip Trail: Foot Lava Tube; North Kona Maui: Hana: Holoinawawai Stream Cave
Sinella kukae Christiansen & Bellinger 1992 [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., obl.)
Lepidocyrtinae	
Lepidocyrtus pallidus [Christiansen & Bellinger 1992]	?
Lepidocyrtus cf. cyaneus [Bellinger & Christiansen 1974]	Maui
Lepidocyrtus cf. ruber [Bellinger & Christiansen 1974]	Kauai (tx.)
Pseudosinella sp. [Bellinger & Christiansen 1974]	Oahu
Hawinella Bellinger & Christiansen, 1974	
Hawinella lava Bellinger & Christiansen, 1974	Oahu: Makua Cave Hawaii: Mountain View: Kazumura Cave
Isotomidae	
Isotominae	
Isotoma (Desoria) notabilis [Bellinger & Christiansen 1974]	Hawaii (tp.)
Proisotominae	
Folsomia candida [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Hawaii; Kauai; Maui; Lanai; Oahu (intr. tp.)
Proisotoma (Ballistura) centralis [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Kauai (tx.)
Anurophorinae	
Cryptopygus thermophilus [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Kauai (tx.)
Paronellidae	
Salina celebensis [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Hawaii (tx.)
Cyphoderidae	
Cyphoderus similis [Bellinger & Christiansen 1974, Christiansen & Bellinger 1992]	Oahu (tx.)
Dermaptera	
Carcinophoridae	
Euborellia annulipes [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac. or acc.)
Anisolabis howarthi Brindle, 1980	Hawaii: Pahoa Cave; Kazumura Cave;
Blattariae [Howarth 1973]	(intr. tx.)
Blattidae	
Periplaneta americana [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl.; Hawaii: North Kona (intr., fac.)

Ensifera	
Grylloida	
Gryllidae	
Thaumatogryllus cavicola Gurney & Rentz, 1978	Hawaii: Bird Park Cave #1&3; Thurston Lava Tube; Kealakekua: Upper Papaloa Cave; Stonewall Cave; Pond Cave; (Upper) Shelter Cave
***Thaumatogryllus* sp.** [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., obl.)
Caconemobius varius Gurney & Rentz, 1978	Hawaii: Kaumana Cave; Kazumura Cave; Bird Park Cave #1; Kealakekua: Pond Cave;
Caconemobius howarthi Gurney & Rentz, 1978	Maui: Hana: Offal Cave; Holoinawawai Stream Cave; Waihoi Valley Trench Cave; Lower Wananalua Cave
Homoptera	
Auchenorrhyncha	
Fulgoromorpha	
Cixiidae	
Oliarus kalaupapae Hoch & Howarth, 1999	Molokai: Kalaupapa Pk.: Fisherman's Shack Cave #1, Kalaupapa Cave #3
Oliarus priola Fennah, 1973	Maui (East): Hana: Holoinawawai Stream Cave
Oliarus gagnei Hoch & Howarth, 1999	Maui (East): Ulupalakua Cave #2
Oliarus waikau Hoch & Howarth, 1999	Maui (East): Waikamoi Rain Forest Res.: Waikau Cave
Oliarus polyphemus Fennah, 1973 [sp. compl.]	Hawaii: Bird Park Cave: dz; Kaumana Cave: dz; Kazumura Cave: dz
Oliarus lorettae Hoch & Howarth, 1999	Hawaii: Kiholo Bay: Ana Lima Kipo Lava Tube, Blue Lake Cave
Oliarus makaiki Hoch & Howarth, 1999	Hawaii: Hualalai: Yellow Jacket Cave
Oliarus sp. (near *koanoa*) [Howarth et al. 2007]	Hawaii: North Kona (end., fac.)
Sternorrhyncha	
Aphidina	
Aphididae	
Rhopalosiphoninus latysiphon [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac.)
Coccina	
Pseudococcidae	
Sp. nov. ? [see Howarth & Mull 1992]	Hawaii
Heteroptera	
Mesoveliidae	
Speovelia aaa Gagné & Howarth, 1975	Hawaii: Mountain View: Kazumura; Kurtistown Lave Tube
Reduviidae	
Ectrichodiinae	
Haematoloecha rubescens [Howarth et al. 2007]	Maui(E): Thaumatogryllus Cave Compl. (intr., com. visit.)
Emesinae	
Nesidiolestes ana Gagné & Howarth, 1975	Hawaii: Emesine Lava Tube; Kahuku Ranch: Alahaka Lava Tube
Coleoptera	
Carabidae	
Trechitae	
Bembidiini	
Tachys arcanicola [Howarth 1973]	Hawaii: Kazumura Cave (intr., tp.)
Harpalinae	
Platynini	
Platyni	
Atelothrus howarthi Samuelson & Liebherr, 1992	Maui: Haleakala: Kipahulu V.: dz
Atelothrus aaae Samuelson & Liebherr, 1992	Maui: Haleakala: Kipahulu V.: dz
Hymenoptera	
Formicidae	
Pheidole megacephala [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., visit.)
Paratrechina bourbonica [Howarth et al. 2007]	Hawaii: North Kona (intr., visit.)
Solenopsis sp. [Howarth et al. 2007]	Hawaii: North Kona (intr., visit.)
Lepidoptera	
Noctuidae	
***Schrankia* sp. nov.** [see Howarth 1973]	Hawaii: Kazumura
***Schrankia* sp. A** [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., obl.)
Schrankia sp. B [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., fac.)
***Schrankia* sp. C** [Howarth et al. 2007]	Hawaii: North Kona (end., tb.)
Tineidae	
Opogona omoscoma [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., acc.)

Diptera	
"Nematocera"	
(nematocerous larvae [Howarth 1973])	Hawaii
Tipulomorpha	
Tipulidae	
***Limonia* sp. nov. ?** [see Howarth 1973]	Hawaii: Kazumura Cave (tp.)
Limoniidae	
Dicranomyia sp. [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cvae Compl. (end., fac.)
Bibionomorpha	
Sciaridae [Howarth 1973]	Hawaii: Kazumura Cave
Phytosciara vulcanata ? [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., fac.)
Culicomorpha	
Ceratopogonidae	
Forcipomyia ? [Howarth 1973]	Hawaii: Kazumura Cave
Forcipomyia cf. pholetor Wirth & Howarth, 1982 [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (end., fac.)
Brachycera	
Eremoneura	
Phoridae [Howarth 1973]	Hawaii: Kazumura Cave
Gen. sp. [Howarth et al. 2007]	Hawaii: North Kona (intr.?, fac.)
Megaselia scalaris [Howarth et al. 2007]	Maui(E): *Thaumatogryllus* Cave Compl. (intr., fac.)
Calliphoridae [Howarth 1973]	Hawaii: Kazumura Cave
Chordata	
Craniota	
Mammalia	
Carnivora	
Canoidea	
Viverridae	
Herpestes auropunctatus [Howarth 1973]	Hawaii
Rodentia	
Muridae	
Rattus rattus [Howarth 1973]	Hawaii
Primates	
Hominidae	
Homo sapiens sapiens [own obs.]	Hawaii (intr., visit.)

Eigenständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Tabellarischer Lebenslauf

Andreas Wessel
Leipziger Straße 54, D-10117 Berlin

Geboren: 30. November 1973 in Berlin, DDR
Familienstand: ledig
Nationalität: Deutsch

Schule	
1980 – 1990	Polytechnische Oberschule “Klara Schabbel” – Berlin-Prenzlauer Berg
1988 – 1989	Mathematisch-naturwissenschaftliche Spezialschule „Heinrich Hertz“ – Berlin-Mitte
1990 – 1992	Gymnasium „Käthe Kollwitz“ – Berlin-Mitte
1992	Abitur

Universität	
1994	Vordiplom, Humboldt-Universität zu Berlin, Biologie
1998	Diplom-Biologe, Humboldt-Universität zu Berlin (Fächer: Zoologie, Genetik & Verhaltensbiologie)
1998 – 2001	Stipendiat im Graduiertenkolleg “Evolutionäre Transformationen und Faunenschnitte”, Museum für Naturkunde der Humboldt-Universität zu Berlin
2002 – 2008	Wissenschaftlicher Mitarbeiter, Museum für Naturkunde der Humboldt-Universität zu Berlin, AG Biosystematik (Prof. Hannelore Hoch)

Lehrtätigkeit	
1997 – 2006	Fachkurs „Einführung in die Evolutionsbiologie“ Hoch, v. Rintelen & Wessel
2007	Vorlesung „Einführung in die Evolutionsbiologie“ Glaubrecht, Köhler, Müller, v. Rintelen & Wessel
Seit 2001	Grundkurs „Zoologische Bestimmungsübungen“ Hoch, Mess & Wessel
Seit 2005	Fachkurs „Diversity of Life – II. A practical approach“ Brinkmann, Glaubrecht, Hoffmann, v. Rintelen, Rödel & Wessel

Forschungsreisen	Hawai’i 1999, 2000; Indonesien 2004, 2005

Sonstige Tätigkeiten	
1997 – 1998	Zivildienst an der Charité, Humboldt-Universität zu Berlin

Publikationsliste

Andreas Wessel

Wissenschaftliche Publikationen

Wessel, A., Erbe, P. & Hoch, H. (2007). Pattern and process: evolution of troglomorphy in the cave-planthoppers of Australia and Hawai'i – preliminary observations (Insecta: Hemiptera: Fulgoromorpha: Cixiidae). *Acta carsologica* **36**(1): 199-206.
reprinted in:
Kranjc, A., Gabrovsek, F., Culver, D. C. & Sasowsky, I. D. (eds) (2007). *Time in Karst.* (Karst Waters Institute Special Publication, 12) KWI, Leesburg: 199-206.

Hoch, H. & **Wessel, A. (**2006). Communication by substrate-borne vibrations in cave planthoppers (Auchenorrhyncha: Hemiptera: Fulgoromorpha: Cixiidae) In: Drosopoulos, S. & Claridge, M.F. (eds). *Insect sounds and communication. Physiology, behaviour, ecology and evolution.* (Contemporary topics in entomology) Taylor & Francis CRC Press, Boca Raton: 187-197.

Wessel, A. (2006). Stridulation in the Coleoptera – an overview. In: Drosopoulos, S. & Claridge, M. F. (eds). *Insect sounds and communication. Physiology, behaviour, ecology and evolution.* (Contemporary topics in entomology) Taylor & Francis CRC Press, Boca Raton: 397-403.

Hoch, H., Deckert, J. & **Wessel, A.** (2006). Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). *Biology Letters* **2**(2): 222-224.

Hoch, H., Asche, M., Burwell, C., Monteith, G. & **Wessel, A.** (2006). Morphological alteration in response to endogeic habitat and ant association in two new planthopper species from New Caledonia (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Delphacidae). *Journal of Natural History* **40**(32-34): 1867-1886.

Wessel, A. & H. Hoch (1999). Remane's statistic species criterion applied to Hawaiian cave planthoppers (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Cixiidae). *Reichenbachia – Zeitschrift für taxonomische Entomologie* **33**(1): 27-35.

Wissenschaftshistorische Publikationen

Stelbrink, B. & **Wessel, A.** (2008). D. E. Z. – A history in numbers. *Deutsche Entomologische Zeitschrift* **55**(1): 7-12.

Wessel, A. (2008). Günter Tembrock und die Exzellenz. In: Wessel, A. (Hrsg.). *„Ohne Bekenntnis keine Erkenntnis". Günter Tembrock zu Ehren.* (Berliner Studien zur Wissenschaftsphilosophie und Humanontogenetik, 25) Kleine Verlag, Bielefeld: 19-20.

Wessel, A. (2008). Continuation and amendment of the Catalogue raisonné of Günter Tembrock. In: Wessel, A. (Hrsg.). *„Ohne Bekenntnis keine Erkenntnis". Günter Tembrock zu Ehren.* (Berliner Studien zur Wissenschaftsphilosophie und Humanontogenetik, 25) Kleine Verlag, Bielefeld: 149-153.

Wessel, A. (2007). D. E. Z. – A History. 150 years of scientific publishing in entomology. *Deutsche Entomologische Zeitschrift* **54**(2): 156-167.

Wessel, A., Stelbrink, B. & Hoff, N. (2007). History of the Deutsche Entomologische Zeitschrift, founded in 1857 as Berliner Entomologische Zeitschrift. *Deutsche Entomologische Zeitschrift* **54**(Suppl.): 1 folded colour plate.

Wessel, A. (2004). Catalogue raisonné (1940-2003) of Günter Tembrock. *Deutsche Entomologische Zeitschrift* **2004**(Special Iss.): 49-84.

Wessel, A. (2002). Abenteuer Erkenntnis. In: Schulz, J. (Hrsg.). *Fokus Biologiegeschichte. Festschrift zum 80. Geburtstag der Biologiehistorikerin Ilse Jahn.* Akadras, Berlin: 235-238.

Herausgegebene Publikationen

Wessel, A. (Hrsg.) (2008). *„Ohne Bekenntnis keine Erkenntnis". Günter Tembrock zu Ehren.* (Berliner Studien zur Wissenschaftsphilosophie und Humanontogenetik, 25) Kleine Verlag, Bielefeld: 159 S.

Wessel, A. (Guest ed.) (2004). Special Issue in Honour of Günter Tembrock*. Deutsche Entomologische Zeitschrift – An International Journal of Systematic Entomology, Special Iss. 2004.* Wiley-VCH, Weinheim: X+84 pp.

Publizierte Abstracts

Wessel, A., Erbe, P. & Hoch, H. (2007). Comparative analysis of cave-planthopper radiations in Australia and Hawai'i – preliminary results (Hemiptera: Fulgoromorpha: Cixiidae). *Acta carsologica* **36**(1): 239-240. [Talk abstract]

Erbe, P., **Wessel, A.** & Hoch, H. (2007). Radiation scenarios for Australian cave-adapted planthoppers. *Acta carsologica* **36**(1): 213-214. [Poster abstract]

Erbe, P., **Wessel, A.** & Hoch, H. (2007). Cave-dwelling planthoppers of the genus *Solonaima* (Insecta: Hemiptera: Cixiidae) in Australia: relicts or explorers. *Acta carsologica* **36**(1): 214. [Poster abstract]

Hoch, H., Deckert, J. & **Wessel, A.** (2007). Neue Musik auf alten Instrumenten – zur intraspezifischen Kommunikation von Coleorrhyncha (Hemiptera). *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck* **Suppl. 17**(Entomologentagung 2007 – Abstracts): 81. [Poster abstract]

Wessel, A. (2007). Bioakustik der Käfer (Coleoptera) – Ein Überblick. *Berichte des naturwissenschaftlich-medizinischen Vereins in Innsbruck* **Suppl. 17**(Entomologentagung 2007 – Abstracts): 267. [Talk abstract]

Wessel, A., P. Erbe, H. Hoch (2004). Pattern and process in subterranean speciation: comparative analysis of Australian & Hawai'ian cave planthopper radiations (Hemiptera: Fulgoromorpha: Cixiidae). *Entomology – strength in diversity (XXII International Congress of Entomology), Brisbane Queensland Australia 2004*, Abstracts: S14W68 (CD-ROM). [Talk abstract]

Wessel, A., P. Erbe, H. Hoch (2004). Muster und Prozess: Vergleichende Analyse von Radiationen australischer und hawai'ischer Höhlen-Zikaden (Hemiptera: Fulgoromorpha: Cixiidae). *Organisms, Diversity & Evolution* **4** (*Electr. Suppl.* 6): 61. [Talk abstract]

Buchbesprechungen

Wessel, A. (2008). [Book review: Schmidt-Loske, K. 2007. Die Tierwelt der Maria Sibylla Merian. Arten, Beschreibungen und Illustrationen.] *Deutsche Entomologische Zeitschrift* **55**(1): 198.

Wessel, A. (2001). [Buchbesprechung zu Tembrock, G. 2000. Angst. Naturgeschichte eines psychobiologischen Phänomens.] *Zeitschrift für Humanontogenetik* **4**(1):

Wessel, A. (2000). Zurück in die Zukunft – *Fetal Programming* und Funktionelle Teratologie. [Buchbesprechung zu Nathanielsz, P. W. 1999. Life in the Womb. The Origin of Health and Desease.] *Zeitschrift für Humanontogenetik* **3**(1/2):

Wessel, A. (1999). Vollendung der Darwinschen Revolution. [Buchbesprechung zu Gould, S. J.1998. Illusion Fortschritt. Die vielfältigen Wege der Evolution.] *Zeitschrift für Humanontogenetik* **2**(1): 86-88.

Wessel, A. (1998). Jahrhundert der Biologie [Buchbesprechung zu Mayr, E. 1997. This is biology – the science of the living world.] *Zeitschrift für Humanontogenetik* **1**(1): 99-100.

Wessel, A. (1997). [Buchbesprechung zu Westheide, W. & Rieger, R. 1996. Spezielle Zoologie.] *Deutsche Entomologische Zeitschrift* **44**(1): 125.

Wessel, A. (1997). [Buchbesprechung zu Penzlin, H. 1996. Tierphysiologie.] *Mitteilungen aus dem Zoologischen Museum Berlin* **73**(1): 164.

Populärwissenschaftliche Publikationen

Wessel, A. (2008). Wer zählt die Arten, nennt die Namen … *sciencegarden – Magazin für junge Forschung* (www.sciencegarden.de) 1. April 2008: http://www.sciencegarden.de/content/2008-03/wer-z%C3%A4hlt-die-arten-nennt-die-namen

Wessel, A. & Stelbrink, B. (2007). Zweiundzwanzigtausend Insektenarten beschrieben – 150 Jahre Deutsche Entomologische Zeitschrift. *HUMBOLDT – Die Zeitung der Alma Mater Berolinensis* **52**(2): 4.

Wessel, A. (2007). „Er begeistert, weil er selbst begeistert ist!“. Günter Tembrock ist seit 70 Jahren an der Berliner Universität. An ihn wurde erstmals die Humboldt-Universitäts-Medaille verliehen. *HUMBOLDT – Die Zeitung der Alma Mater Berolinensis* **52**(2): 5.

Wessel, A. & Hoch, H. (2007). Höhlenzikaden auf Hawai’i – Liebesgesänge und die Entstehung der Arten. In: Glaubrecht, M., Kinitz, A. & Moldzyk, U. (Hrsg.) 2007. *Als das Leben laufen lernte. Evolution in Aktion.* Prestel Verlag, München: 222-225.

Wessel, A. & Hoch, H. (2007). Cave planthoppers on Hawaii - love songs and the origin of species. In: Glaubrecht, M., Kinitz, A. & Moldzyk, U. (eds) 2007. *Evolution in Action.* Prestel Verlag, München: 222-225.

Wessel, A. (2004). Doktorarbeit nach 60 Jahren publiziert – Ehrung für den Gründer der Bioakustik, Prof. Dr. em. Dr. rer. nat. Dr. h.c. Günter Tembrock. *HUMBOLDT – Die Zeitung der Alma Mater Berolinensis* **48**(8): 13.

Wessel, A. (2000). Genopoly. [Craig Venter in Berlin] *junge Welt* 12.10.2000:

Wessel, A. (2000). Die Natur der Angst. Zu Günter Tembrock: "Angst. Naturgeschichte eines psychobiologischen Phänomens." *junge Welt* 5.12.2000:

Wessel, A. (1999). Mensch und Hormone. Berliner Forscher Dörner für den „Right Livelihood Award“ nominiert. *junge Welt* 16.7.1999: 12.

Wessel, A. (1999). Die Wurzeln der Gesundheit. Günter Dörner und die „neue Wissenschaft“ von der „Programmierung im Mutterleib“. *junge Welt* 30./31.10.1999, (Wochenendbeilage): 8.

Wessel, A. (1999). Es entwickelt sich. Ernst Mayr, der größte lebende Evolutionsforscher, wurde 95. *junge Welt* 10./11.7.1999 (Wochenendbeilage): 8.