JOURNAL OF CRUSTACEAN BIOLOGY, 22(1): 15–27, 2002

# PHYLOGENETIC RELATIONSHIPS OF *GOMPHOCYTHERE* (OSTRACODA) IN LAKE TANGANYIKA, EAST AFRICA

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A B S T R A C T

We examined the distribution of 44 morphological characters for 16 extant species of an ostracode genus, *Gomphocythere,* in Africa, to test hypotheses concerning character development and speciation patterns. Using heuristic searches conducted with the phylogenetic reconstruction program PAUP (beta version, 4.0), we found 2 trees of 98 steps (CI = 0.56). The skewness of tree length distribution reveals significant phylogenetic structure in the data. Nodes are supported by 1 to 11 character-state changes, and these character changes are sometimes reversed or paralleled elsewhere, accounting for much of the homoplasy in the reconstructions. By systematically removing both hard- and soft-part characters in separate analyses, hard-part characters were found to be far more homoplasious in their distribution across the phylogenetic tree, while soft parts are minimally homoplasious, suggesting that they are far more conservative while the hard parts are more prone to ecophenotypic variation. This phylogeny provides the basis for evaluating speciation mechanisms and the role of ecological factors in the diversification of ostracodes in this lake system.

Ostracodes are small, bivalved crustaceans, found in both marine and non-marine environments. There are three major extant suborders: Myodocopida, Platycopida, and Podocopida. *Gomphocythere,* the ostracode genus we examine here, is a member of the suborder Podocopida and the family Limnocytheridae. Limnocytheridae is the family that represents the major non-marine radiation within the primarily marine superfamily Cytheroidea.

Sars (1910) described *Limnicythere* (*sic*) *obtusata* from Lake Victoria. He later redescribed this taxon and designated it as the type species of the genus *Gomphocythere* (Sars, 1924). The genus shows a wide range of carapace morphologies but typically has pronounced brood pouches in females, robust carapace reticulation, a distinctive inverse lophodont hinge structure, and the presence of alae and nodes in some species (Grekoff, 1953). Ventral ridges and lateral crests were also originally thought to be typical of *Gomphocythere* until Klie (1939) described *Gomphocythere angusta,* which has neither of these features. De Deckker (1981) cited these ventral ridges and lateral crests as the main difference between *Gomphocythere* and his newly erected Australian genus, *Gomphodella,* but the validity of the latter group is doubtful due to the problematic nature of these characters as diagnostic for generic delineation. Species within *Gomphocythere* are primarily recognized by the shape of the carapace and hemipenis morphology and occasionally by valve ornamentation. Table 1 is a composite listing of the current taxonomy of *Gomphocythere* including four new *Gomphocythere* species as well as the outgroups used in this analysis.

*Gomphocythere* Sars, *Cytheridella* Daday, and *Gomphodella* De Deckker were placed in a separate tribe Cytheridellini, subfamily Limnocytherinae, and family Limnocytheridae by Danielopol *et al.* (1990). This tribe was originally placed within the subfamily Limnocytherinae (Danielopol *et al.,* 1990) because its members have sieve pores that are not present in members of the Timiriaseviinae, another subfamily of Limnocytheridae. However, based upon several other morphological features (i.e., nature of mandibular palp, hinge structure, and position of furca on hemipenis), Martens (1995) transferred the tribe Cytheridellini to the subfamily Timiriaseviinae. The exact evolutionary relationships

Table 1 Taxonomy of species used in this analysis, including the four newly designated species endemic to Lake Tanganyika (Park and Martens, 2001).

| |
|---|
| Subclass Ostracoda Latreille, 1806 |
| Order Podocopida Müller, 1894 |
| Suborder Podocopa Sars, 1866 |
| Superfamily Cytheracea Baird, 1850 |
| Family Limnocytheridae Klie, 1938 |
| Subfamily Timiriaseviinae Martens, 1995 |
| Tribe Cytheridelli Danielopol and Martens, 1990 |
| Genus *Gomphocythere* Sars, 1924 |
| *Gomphocythere aethiopis* Rome, 1970 |
| *Gomphocythere alata* Rome, 1962 |
| *Gomphocythere angulata* Lowndes, 1932 |
| *Gomphocythere angusta* Klie, 1939 |
| *Gomphocythere capensis* Müller, 1914 |
| *Gomphocythere coheni* Park and Martens, 2001 |
| *Gomphocythere cristata* Rome, 1962 |
| *Gomphocythere curta* Rome, 1962 |
| *Gomphocythere downingi* Park and Martens, 2001 |
| *Gomphocythere expansa* Sars, 1924 |
| *Gomphocythere lenis* Rome, 1962 |
| *Gomphocythere obtusata* Rome, 1962 |
| *Gomphocythere ortali* Rome, 1962 |
| *Gomphocythere parcedilatata* Rome, 1977 |
| *Gomphocythere simplex* Rome, 1962 |
| *Gomphocythere wilsoni* Park and Martens, 2001 |
| *Gomphocythere woutersi* Park and Martens, 2001 |
| Genus *Cytheridella* Daday, 1905 |
| *Cytheridella chariessa* Rome, 1977 |
| Genus *Gomphodella* De Deckker, 1981 |
| Subfamily Limnocytherinae Klie, 1938 |
| Tribe Limnocytherini Klie, 1938 |
| Genus *Limnocythere* Brady, 1867 |
| *Limnocythere dadayi* Martens, 1990 |
| Genus *Leucocythere* Kaufmann, 1892 |

between the Cytheridellini, Limnocytherinae, and Timiriaseviinae has yet to be determined; however, one of us (Martens) regards Cytheridellini as a transitionary group between the Limnocytherinae and the Timiriaseviinae, although they share most characters with the latter subfamily.

Sixteen described living species of *Gomphocythere* can be found today in Africa and the Middle East (Israel). *Cytheridella,* the sister group to *Gomphocythere,* is found in South America, North America, and Australia, whereas *Gomphodella,* which is not included in this study, is restricted to Australia (Table 2).

The distribution of *Gomphocythere* in the East African lakes is poorly understood. Several *Gomphocythere* species appear to be endemic to single, large, inland lakes; however, there are also more widely distributed species that can be found in several localities on the African continent (Sars, 1924; Rome, 1962; Martens, 1990).

*Gomphocythere* is represented in Lake Tanganyika by nine known endemic species: *G. alata, G. cristata, G. curta, G. lenis,* and *G. simplex* (see Rome, 1962); *G. coheni, G. downingi, G. wilsoni,* and *G. woutersi* (see Park and Martens, 2001). In spite of the apparent diversity of this flock, Rome (1962) is the only previous author to specifically address the taxonomy of *Gomphocythere* species in Lake Tanganyika. His specimens were almost all females (except for *G. alata* and *G. cristata*), hence the original description of these species are almost entirely based on female characters. During the present survey, we found both males and females of most *Gomphocythere* species, and we used sexually dimorphic characters as well as additional morphological information in our analysis.

We provide the first detailed phylogenetic analysis of the evolutionary relationships within the ostracode genus *Gomphocythere*. The phylogeny constructed provides the means to document character acquisitions and

Table 2. Number of specimens used in the acquisition of character state information for all phylogenetic analyses. Hard and soft parts are designated as well as specific numbers of specimens for each sex.

| Species | Number of Specimens | | | | Location |
|---|---|---|---|---|---|
| | Hard Parts | | Soft Parts | | |
| | Male | Female | Male | Female | |
| *G. aethiopis* | 1 | 1 | 1 | 1 | Ethiopia |
| *G. alata* | 121 | 91 | 1 | 5 | Lake Tanganyika |
| *G. angulata* | 1 | 1 | 1 | 1 | Lake Awasse, Lake Turkana, Lake Albert |
| *G. angusta* | 1 | 1 | 1 | 0 | Lake Victoria |
| *G. capensis* | 8 | 4 | 7 | 4 | Molopo Oog, RSA |
| *G. coheni* | 16 | 23 | 1 | 3 | Lake Tanganyika |
| *G. cristata* | 14 | 17 | 5 | 7 | Lake Tanganyika |
| *G. curta* | 28 | 23 | 1 | 6 | Lake Tanganyika |
| *G. downingi* | 87 | 52 | 3 | 5 | Lake Tanganyika |
| *G. lenis* | 5 | 4 | 1 | 1 | Lake Tanganyika |
| *G. obtusata* | 2 | 1 | 1 | 1 | Lake Victoria, Republic of South Africa |
| *G. ortali* | 6 | 5 | 6 | 5 | Israel |
| *G parcedilatata* | 1 | 1 | 1 | 1 | Lake Kivu |
| *G simplex* | 3 | 2 | 0 | 1 | Lake Tanganyika |
| *G. wilsoni* | 42 | 69 | 2 | 1 | Lake Tanganyika |
| *G. woutersi* | 2 | 2 | 1 | 1 | Lake Tanganyika |
| *C. chariessa* | 1 | 1 | 1 | 1 | Africa |
| *Leucocythere* sp. | 1 | 1 | 1 | 1 | Africa, Asia, Europe |
| *L. dadayi* | 1 | 1 | 1 | 1 | Lake Rukwa |

their evolution in a historical context. This analysis also provides the phylogenetic framework required for future hypothesis testing of *Gomphocythere* speciation mechanisms in the Lake Tanganyikan system. It is critical to understand evolutionary relationships before erecting taxonomic divisions or testing speciation hypotheses; otherwise, there is a substantial risk of creating artificial categories and patterns that do not reflect evolutionary history.

## Materials and Methods

### Collections

We analyzed 16 *Gomphocythere* species from Lake Tanganyika and elsewhere in Africa, including South Africa, the Ethiopian rift lakes, Lake Albert, Lake Kivu, and Lake Turkana. We used all known *Gomphocythere* available to us from current collections at the Royal Belgian Institute of Natural Sciences, the University of Arizona, and the literature. The species from Lake Tanganyika were cited above; those from outside of Lake Tanganyika include: *Gomphocythere aethiopis, G. angulata, G. angusta, G. capensis, G. obtusata, G. ortali,* and *G. parcedilatata*.

Specimens used in our analysis from Lake Tanganyika were taken from over 350 samples collected on many separate expeditions, including the Belgian Hydrobiological expedition of 1946–47, and the expeditions of Cohen, 1986, 1989; Martens, 1990; Cohen *et al.,* 1992; and Martens, 1992. Specimens from the 1990, 1991, and the two 1992 expeditions were sorted and stored in alcohol until dissections were made. Material from species from other parts of Africa was found in the Royal Belgian Institute of Natural Sciences ostracode collections, and descriptions in the literature were also used.

### Dissections and Illustrations

Dissections of all specimens were made using a Leica Wild M-10 binocular dissecting microscope and a Leica Wild polarizing light microscope. Soft parts were dissected in glycerin and sealed on a glass slide. Valves were stored dry. All specimens are curated in the Royal Belgian Institute of Natural Sciences, except for material from the Cohen *et al.,* 1992 expedition, which is curated at the University of Arizona Laboratory of Paleontology.

*Camera lucida* drawings were made, and photographs were taken of all soft-part material as well as of valves and carapaces whenever sufficient material was available. Additional qualitative character analysis was accomplished by comparing Scanning Electron Microscopy photographs at a variety of magnifications that were taken of all *Gomphocythere* and outgroup species in this analysis.

### Outgroup Selection

An outgroup is defined as any group used in a phylogenetic analysis that is not included in the taxon under study. It is used to provide a broader phylogenetic context and thus aid in determining the root of the ingroup or the ancestral states (Farris, 1972, 1982; Watrous and Wheeler, 1981; Maddison *et al.,* 1984; Maddison and Maddison, 1992). Outgroup comparison preferably requires an *a priori* identification of the closest relatives to the ingroup (Wiley *et al.,* 1991). By including several sister groups (that are thus assumed to be taxonomically closely related), it is possible to perform an outgroup analysis to determine character polarity (Maddison *et al.,* 1984). *Cytheridella* is most closely related to *Gomphocythere*. Species of *Cytheridella* were included as outgroups in our analysis, but *Gomphodella* was excluded because of lack of available material or adequate descriptions in the literature. In addition to *Cytheridella,* a species of *Limnocythere* and *Leucocythere* were also included. These latter two genera are closely related to *Gomphocythere,* belonging to the same family (Limnocytheridae) but not the same subfamily.

## Characters and Character States

Characters are defined based upon homologous structures and are coded as a numeric or alphabetic symbol that represents a particular character state (Wagner, 1989; Pogue and Mickevich, 1990). We defined and coded 44 morphological characters as unordered for all 19 taxa in our analysis. Similar numbers of hard-part characters (1–21) as well as soft-part characters (22–44) were identified for the composite analysis, using male and female data sets separately (Appendix 1). The complete matrix showing the presence and absence of characters and multistate values is provided in Appendix 2. Multistate characters (11) were coded as ordered, if they had successively additive states. A brief introduction to the characters and character states is given below (numbers between brackets refer to the list in Appendix 2).

*Valves.*—Hinges (21) play an important role in ostracode taxonomy because they are fundamental morphological elements controlling most other valve features (Moore, 1961; Van Morkhoven, 1962; Hartmann and Puri, 1974). *Gomphocythere* has an inverse lophodont hinge (Martens, 1990) that is considered a subtype of the merodont type: the LV has anterior and posterior cardinal teeth that fit into corresponding sockets of the RV; the RV has a median cardinal bar fitting into the cardinal groove in the LV (Fig. 1). The outgroups in this analysis (e.g., *Limnocythere dadayi, Leucocythere* sp., and *Cytheridella chariessa*) have different hinge types (e.g., lophodont, adont, and amphidont), but if cardinal teeth occur, they are on the RV (Colin and Danielopol, 1978). The reversal of a hinge structure is not uncommon in ostracodes, and the value of this character has been disputed (Martin, 1940; Van Morkhoven, 1962). However, the hinge structure in *Gomphocythere* sp. does not exhibit hinge reversal.

The central (or adductor) muscle scars (9) are the attachment locations of the closing muscles that run transversally from valve to valve. All Cytheroidea, the superfamily to which *Gomphocythere* belongs, have four scars arranged in a vertical row. Only inclination of this row (vertical or posteriorly tilted) is used here (Fig. 1).

*Brood Pouch and Alar Prolongations.*—*Gomphocythere* often have ventral swellings in the females, alar prolongations, and hollow tubercles. Unlike brood pouches found in Paleozoic ostracodes, brood chambers in post-Paleozoic ostracodes are not as conspicuous from the surrounding valve surface. The pouches cause the carapace to exhibit an inverted, heart-shaped form in transverse vertical section. Presence or absence of a brood pouch was coded as a character in this analysis because it is morphologically prominent. A brood pouch (4) is present in all *Gomphocythere,* whereas in the outgroup it is absent. Alar prolongations (16) appear as wing-shaped lateral extensions, causing a distinct arrow-shape in dorsal view and a triangular outline in transverse vertical section. Alar prolongations always point backwards and can be modified into different forms (Fig. 1).

*Sieve Pore Canals.*—Sieve pores (8) are sensory organs similar to the mechanoreceptors of insects. They serve to connect the inside of the shell with the outside environment. Their presence or absence are features commonly used by taxonomists. Sieve pores are larger than open pores. Larger sized pores are usually sieve pores rather than open pores and are either rounded or subrounded (Fig. 1). At present, the absence of open pores and the presence of sieve pores is a characteristic feature of the tribe Cytheridellini, into which *Gomphocythere* has been placed by Danielopol *et al.* (1990). The morphology of pore systems and their position on the carapace is thought to have a close relationship with the habitat and the behavior of ostracodes (Tsukagoshi, 1990). The sieve pores were coded as normal/radial. All *Gomphocythere* have penetrative sieve pores. Unfortunately, little previous work has been undertaken to determine the utility of sieve pores as species-defining morphological features in ostracodes (Rosenfeld and Vesper, 1977).

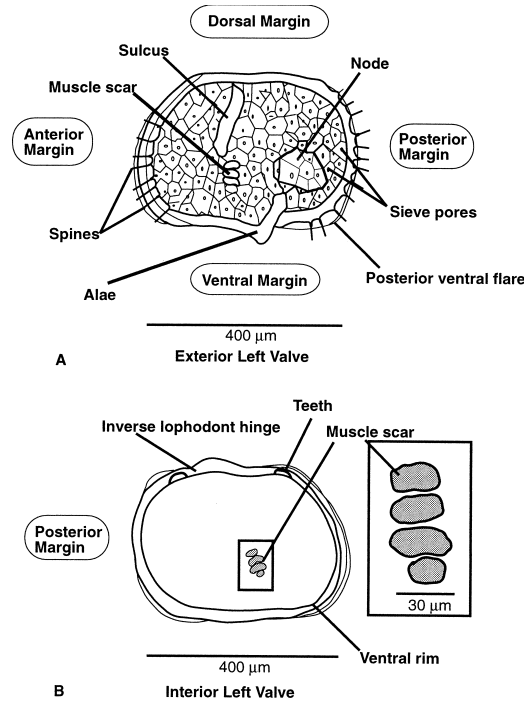


Fig. 1. Schematic drawings of hard-part morphologies of *Gomphocythere* ostracodes. Anterior, posterior, dorsal, and ventral margins are labeled. Diagram A represents the outer carapace morphologies, while diagram B represents the inner carapace morphologies. Scale is indicated.

*Surface Ornamentation.*—The surfaces of the lateral outer margins of the ostracode valves are either smooth or ornamented with pits, punctuations, spines, striae, ridges, or costae, and reticulation (Fig. 1). These features are important for strengthening and armoring the carapace. Ornamentation on *Gomphocythere* valves typically does not differ between male and female of the same species, but is not necessarily a morphologically stable feature and may show clinal variation in dispersed populations (Carbonnel and Jacobzone, 1977; Okada, 1982). While using ornamentation as a character, a distinction should be made between primary and secondary features. Primary ornamentation in this analysis includes the major morphological features that often encompass structural elements. Secondary ornamentation characteristics include the more superficial details such as small nodes and ridges (Fig. 1).

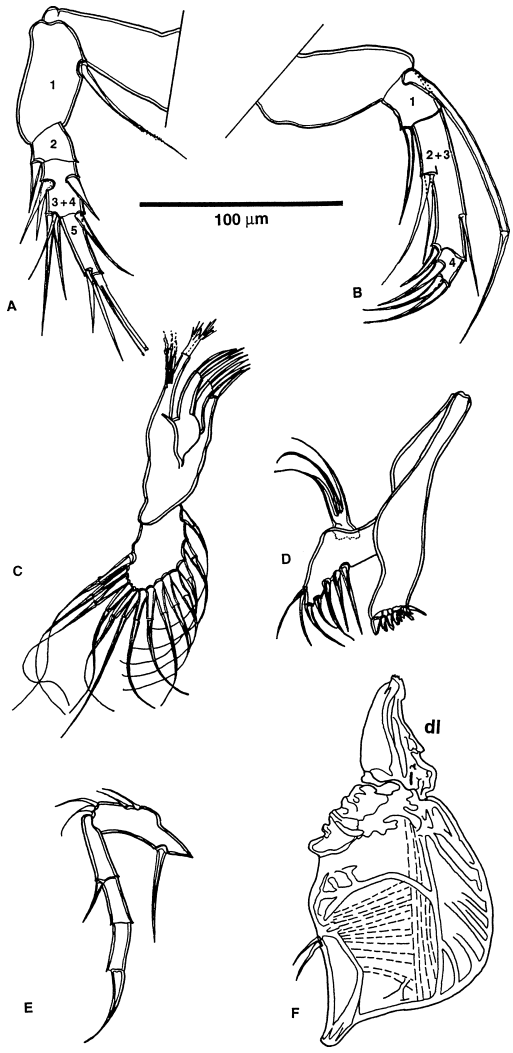


Fig. 2. Drawings of soft-part morphologies of *Gomphocythere downingi*. A, A1; B, A2; C, Mx1; D, Md; E, P3; F, hemipenis of male; dl indicates the distal lobe on the hemipenis. Scale is indicated.

*Nodes, Alae, and Longitudinal Ridges.*—A node (10–13) is a bulbous protrusion found on the anterior or posterior regions of the valve surface. Nodes are considered modified flanges, keel-like thickenings of the outer calcareous lamella (Moore, 1961; Van Morkhoven, 1962; Hartmann and Puri, 1974). Flanges play an important role in closure of the valves and provide support for the selvage. Alae (15) or alar prolongations (16) are conspicuous, wing-shaped lateral extensions found on the valve surface resulting from the duplicature of the outer lamella. These structures do not affect the inner lamella and serve to support the animal in soft substrates. Alae always point posteriorly and can help in orienting isolated valves. Longitudinal, ornamental medial ridges (17) or extensions are similar to alae but traverse the entire lateral valve width. Nodes, alae, and longitudinal ridges are similar to surface ornamentation in their variability, but their presence or absence on ostracode carapaces is intraspecifically stable (Fig. 1). In *Gomphocythere,* these characters are important as synapomorphies for the various subclades within the group.

Other valve characters used here include carapace shape (5, 6), ornamentation such as reticulation (7), and tubercles (1). The latter type of ornamentation on *Gomphocythere* valves typically does not differ between male and female of the same species but is not necessarily a morphologically stable feature and may show clinal variation in dispersed populations (Carbonnel and Jacobzone, 1977; Okada, 1982).

*Appendages.*—As podocopids, the species considered here all have four pairs of cephalic limbs: first and second antenna (A1 and A2), mandibula (Md) and maxillulae (Mx); three pairs of thoracic appendages (T1–T3) (Fig. 2); and a pair of furcae. The soft-part characters used here are defined by the chaetotaxy of these appendages, such as the number of claws and setae on a segment; number of segments, especially of the antennae (26–40); as well as the shape of the limb (44) and structures on the hemipenis (23–25). The hemipenes are an important diagnostic feature in all ostracode species where males are known. These copulatory appendages are usually so large that they take up most of the posterior part of the valve, causing the valves to be longer in the male than in the female. This, along with the brood pouch in the female, contributes to the strong sexual dimorphism in this group. In all extant Limnocytherinae, the distal lobe (dl) of the hemipenis forms an integral part of the peniferum and does not hinge (Fig. 2F). In Timiriaseviinae (including the Cytheridellini) there is a movable distal lobe that is connected to the remainder of the peniferum with a hinge (Martens, 1995).

## Cladistic Analysis

*Tree-building.*—The computer program PAUP (Phylogenetic Analysis Using Parsimony, version 4.0; Swofford, 1998) was used to compute the most parsimonious tree from a character set of the 44 characters listed in Appendix 1. In our initial analyses, we counted any change from one state to another state as one step. In subsequent analyses, 22 characters were redefined as ordered based upon their successive, additive states. Additional analyses were then performed using the dataset with the redefined characters.

Exact methods that guarantee optimal reconstructions cannot be used for 19 taxa because the data matrix is too large for the algorithm and computer capabilities. Therefore, the data matrix (Appendix 2) was analyzed using the heuristic searching option that builds an initial tree or set of trees by stepwise addition of taxa and continuously searches for shorter and shorter trees by rearranging that tree (Swofford, 1998). We used the tree bisection and reconstruction (TBR) search option on trees reconstructed with the random addition sequence. To increase the likelihood of finding all islands of equally parsimonious trees (*sensu* Maddison, 1991), we included 100 random replications in each analysis. An island of equally parsimonious trees is a set of trees in which each tree is connected to every other tree in an island through a series of trees, each member of the series differing from the next by a single, minor rearrangement of branches.

All characters in our initial analysis were both unpo-

larized and undirected following Swofford and Maddison (1987), and Hauser and Presch (1991), making the initial trees produced by PAUP unrooted. Because PAUP includes the outgroup taxa in the parsimony analysis, the assumption of monophyly of the ingroup is tested in the analysis. The trees were then rooted using outgroup analysis (Maddison, 1991).

ACCTRAN (transformation that accelerates changes towards the root) and DELTRAN (transformation that delays changes away from the root) options were used to analyze the most-parsimonious reconstructions by optimizing for reversals and parallelisms, respectively (*sensu* Swofford and Maddison, 1987). The computer program MacClade (version 3.0, Maddison and Maddison, 1992) was used to aid in the exploration of equally parsimonious character distributions within the minimal-length topology discovered by PAUP. Trees were then compared with respect to their phylogenetic structure and compared with trees produced with characters that were randomized over the taxa (*sensu* Archie, 1989).

In addition, systematic removal of all hard-part characters and then all soft-part characters in separate phylogenetic analyses was carried out in order to test whether or not the selection of characters influences phylogeny reconstruction. Whether or not the same tree topologies result from these two different data sets is important for paleobiologists who must rely on only hard parts for their phylogenetic reconstructions, and are significant in the measurement of bias in the assessment of evolutionary relationships.

*Signal and Noise in the Data*.—We measured the phylogenetic structure in the character distribution data by measuring the skewness (g1) of the distribution of tree lengths of all possible trees (Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). We estimated g1 using PAUP's random trees option, which generated 105 trees according to the equiprobable tree distribution for our characters. The critical value of g1 for 20 taxa and 70 binary characters (for the probability $P = 0.01$, g1 = –0.20) provided by Hillis and Huelsenbeck (1992), offers a conservative test for the significance of phylogenetic structure. This test evaluates the structure of the data as a whole as compared to random noise. If all the variation among taxa is essentially random with respect to phylogenetic history, then there would be no basis to expect the most-parsimonious tree to be a good estimate of phylogeny. Therefore, phylogenetic signal can be determined by comparing the number of most parsimonious trees generated by the data to a randomized dataset. Measurements of phylogenetic signal were calculated and compared with those calculated by Hillis and Huelsenbeck (1992), who also subsequently tested those calculations using phylogenetic simulations, demonstrating the close relationship between these measures and the effectiveness of parsimony to correctly estimate phylogeny. No tests were done to evaluate the support for individual nodes.

## RESULTS

### Results of Phylogenetic Analysis

The computer program PAUP found two, minimal-length cladograms with a consistency index of 0.56 and a length of 98 steps. The same two trees were found in 100 replications of the search. Figure 3 shows the two most parsimonious trees using non-dimorphic characters (44) in the analysis. Skewness estimates of these trees is approximately –0.65 of the distribution of treelengths and demonstrates a strong phylogenetic signal (Fig. 4).

The unordered analysis identified two most parsimonious trees (98 steps, CI = 0.56, RI = 0.36) belonging to a single island (Fig. 3). We employed our preferred ordering for multistate characters, where only those characters with incremental addition of states (i.e., state 1-1 seta; state 2-2 setae; state 3-3 setae) were used. The trees generated from this analysis are similar to those from the unordered analysis, with the principal difference being the greater ambiguity in relationships discussed below.

The level of homoplasy revealed by these analyses (CI = 0.56) is close to that expected for 19 taxa with unordered, binary characters. The formula given by Sanderson and Donoghue (1996) predicts CI = 0.60 for unordered, binary characters, and using the parameters from their multiple regression yields CI = 0.40.

### Hard-Part Character Distributions

Results of hard-part distributions on the phylogeny indicate that the hinge is an important synapomorphy for the *Gomphocythere* subclade (Subclade B on Fig. 3). *Gomphocythere* has a characteristic inverse lophodont structure, whereas the outgroup members have either a lophodont or adont hinge structure. There was no intraspecific variation in this character, and it is extremely stable within each individual terminal taxa grouping.

In *Gomphocythere,* three muscle-scar states were coded based on the three distinct patterns. Little to no variability was observed between patterns from individuals of the same species. The distribution of the type and size of muscle scars support earlier suggestions that these characteristics are important diagnostic features for delineating species (Moore, 1961).

Surface ornamentation was coded as smooth or reticulately robust and as seen distributed over the tree, shows a high amount of homoplasy. Reticulation shows little correlation with other shell morphologies such as presence or absence of nodes (10, 11, 12, 13), alae (15), or valve shape (5, 6).

Members of subclade A have prominent

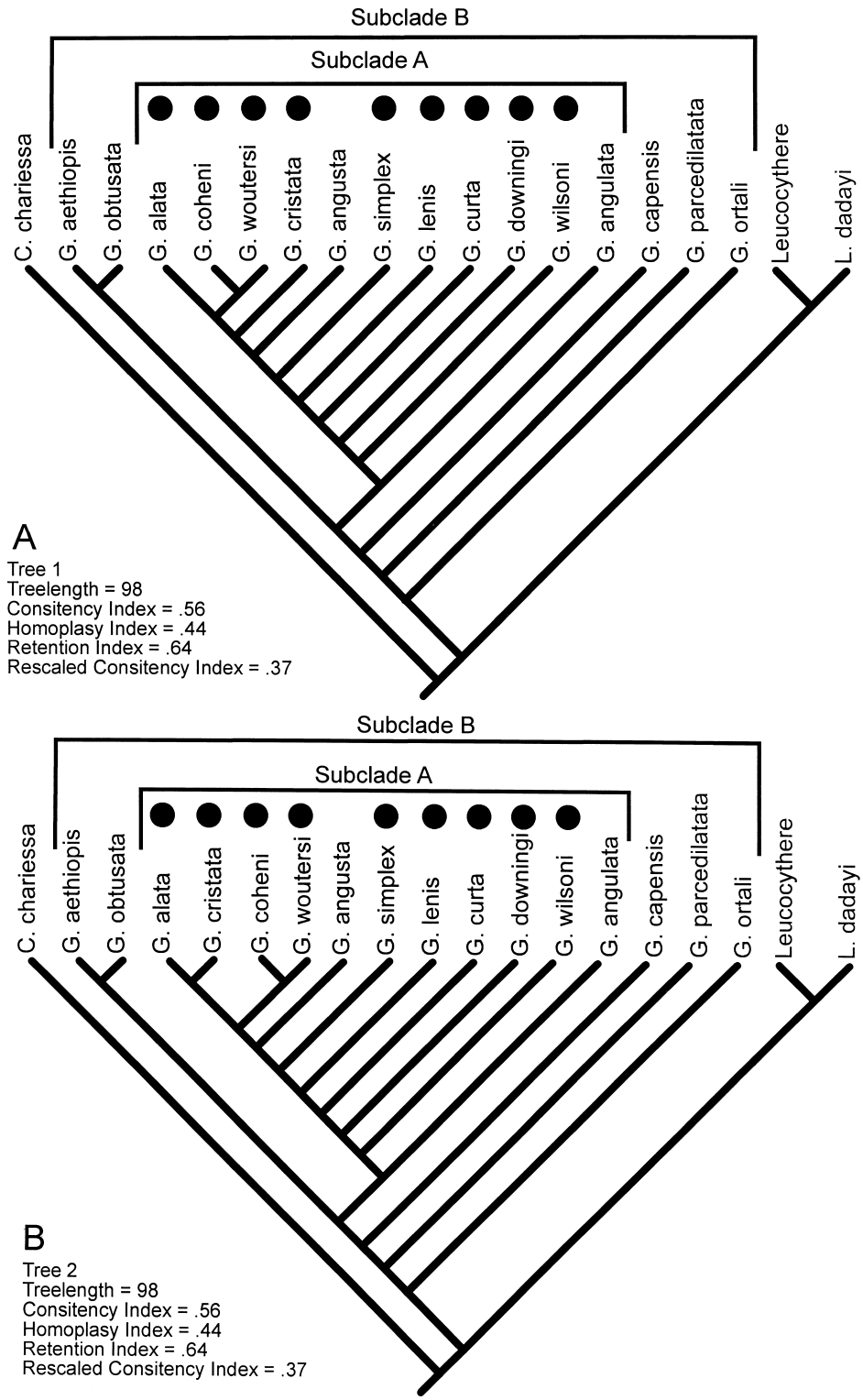


Fig. 3. Two most parsimonious trees of 98 steps, generated using only non-dimorphic characters (44 characters) in the analysis. CI = 0.56, HI = 0.44, RI = 0.64, RC = 0.37. Subclades indicated as A and B. Endemic species to Lake Tanganyika are indicated by filled circles over the taxa.

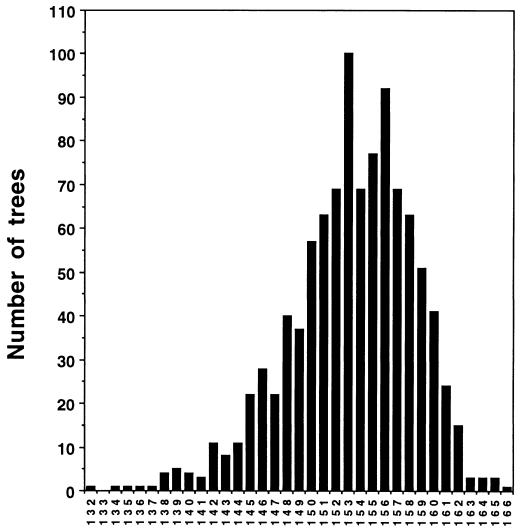


Fig. 4. Treelength distribution of most parsimonious reconstruction using unordered characters. The heavily skewed distribution indicates significant phylogenetic signal in the data. A normal distribution would indicate that the same tree topology could be obtained using random character assignments.

nodes (10–13), and four species (*G. alata, G. cristata, G. wilsoni,* and *G. downingi*) also have significant alae or alar prolongations (15, 16). The node features on these two species are stable between sexes and along ecological gradients (e.g., substrate and depth).

### Soft-Part Character Distributions

Results of the soft-part character distributions indicate that soft parts are very important in this phylogenetic reconstruction. The number of segments and the number of claws present in the A1 appendage in *Gomphocythere* is highly homoplastic (26–34). The A1 in *Gomphocythere* is quite robust, particularly in *G. coheni* and *G. alata,* unlike the A1 of more distantly related limnocytherid groups.

The mandibles were coded either as normal or bent knee (41), and the corresponding mandibular palp setae were coded as either straight or bifurcated (42). All *Gomphocythere* are united by their possession of the bent-knee mandible and by a bifurcation in the mandibular palp setae, in contrast to two of the outgroups. A reduced maxillular palp (Mx) (43) also supports the *Gomphocythere-Cytheridella* clade relative to the Limnocytherinae. The thoracic appendages (44) show similar patterns to the cephalic appendages but were far more conservative. In fact, they were uninformative and therefore largely omitted from the analysis.

Ornament morphology (1–21) can sometimes be correlated with water turbulence and possibly with sieve-pore development (8) and is considered to be strongly ecophenotypic (Liebau, 1977). In fact, the carapace surface structure is highly sensitive to adaptive evolutionary change (Benson, 1981) and is an important morphology to examine with respect to "long term" environmental change. These hard-part characters are far more plastic and ecophenotypic than the soft-part morphologies.

There is little variation in hemipenes characteristics among *Gomphocythere* (23–25). In all species, the furca (24) are on the lower lobe, away from the copulatory organ, whereas in the outgroups *Limnocythere* and *Cytheridella,* the furcae are located near the copulatory organ (24). A movable distal lobe on the hemipenes (23) unites all *Gomphocythere* with *Cytheridella* and is distinct from the fixed lobe of the *Limnocythere* and *Leucocythere*.

By sequentially removing all of the hard-part characters (1–22) and then the soft-part characters (23–44), the hard-part characters were found to be far more homoplasious in their distribution across the phylogenetic tree, while the soft parts are minimally homoplasious. Specifically, the hard part dataset yielded greater than 11,000 trees of 44 steps with a consistency index of 0.59 and a homoplasy index of 0.41, while the soft-part dataset yielded 34 most parsimonious trees of 50 steps with a consistency index of 0.58 and a homoplasy index of 0.42. The hard-part dataset is far less resolved than the soft-part dataset, given the number of trees, even though they are of shorter treelength.

## Discussion

### Definition and Analysis of Phylogenetic Structure

The distribution (e.g., skewness) of tree lengths of all tree topologies (or a random sample of them) provides a sensitive measure of phylogenetic signal. Data matrices that have a strong phylogenetic signal produce treelength distributions that are strongly skewed. Simulated phylogenies have shown that data sets that are significantly structured

Table 3. List of apomorphous characters for each terminal taxon determined by ACCTRAN optimization for each most parsimonious reconstruction

| | | ACCTRAN Apormorphy | |
|---|---|---|---|
| Node Number | Terminal Taxa | Tree 1 | Tree 2 |
| 20 | *G coheni* | 11, 12 | 11, 12 |
| 21 | *G. alata* | 20, 36 | 20, 36 |
| 21 | *G. obtusata* | 47 | 47 |
| 22 | *G. cristata* | 17, 39 | 5, 17, 39, 40 |
| 23 | *G. woutersi* | 5, 13, 41, 47, 48, 52 | 5, 13, 41, 47, 48, 53 |
| 24 | *G. simplex* | 31, 32, 34 | 31, 32, 34 |
| 25 | *G. angusta* | 20, 33 | 20, 34 |
| 26 | *G. curta* | 18, 32 | 18, 32 |
| 27 | *G. downingi* | 25 | 25 |
| 28 | *G. lenis* | 11, 29, 40, 48, 52 | 11, 29, 40, 48, 53 |
| 28 | *G. wilsoni* | 18, 20, 30 | 18, 20, 30 |
| 29 | *G. angulata* | 1, 3, 31, 39 | 1, 3, 31, 39 |
| 30 | *L. dadayi* | 10, 11, 12, 13, 14, 18 27, 28, 32, 34 | 10, 11, 12, 13, 14, 18 27, 28, 32, 34 |
| 30 | *Leucocythere* | 21, 22, 38 | 21, 22, 38 |
| 31 | *Cytheridella chariessa* | 6, 7, 31, 36, 37, 40 | 6, 7, 31, 36, 37, 40 |
| 32 | *G. ortali* | 25, 33 | 25, 33 |
| 33 | *G. parcedilatata* | 17 | 17 |
| 34 | *G. capensis* | 9 | 9 |
| 36 | *G. aethiopis* | 3, 20, 35, 36, 37 | 3, 20, 35, 36, 37 |

typically have one or two shortest trees and a skewed distribution. A data set that is more or less random will have a normal distribution of treelengths (Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). The strongly skewed treelength distribution for the unordered analysis of *Gomphocythere* is shown in Fig. 4. The skewness and permutation tests each find significant phylogenetic structure in both the unordered and ordered *Gomphocythere* data matrices. For unordered *Gomphocythere* character runs, g1 = –0.65, where 0 indicates a normal distribution (i.e., no skewness) and both –1 and 1 indicate the highest skewness.

### Phylogeny of *Gomphocythere*

Comparisons of the results of the different analyses reveal consistent support for relationships among the major subclades or "islands" of the extant *Gomphocythere*. For example, the position of subclade A is extremely well-supported in every analysis. Another area of stability within the tree is the relationship between the species *Gomphocythere downingi* and *G. wilsoni,* which is supported in every analysis.

Areas of instability and uncertainty include species that are both endemic to Lake Tanganyika and that are found in other lakes. These species are not positioned at the base of the tree, whereas the other, more stable subclades are more highly derived.

### Homoplasy and Speciation Patterns within the Phylogenetic Reconstruction

It is possible that the high level of homoplasy within this phylogeny is generated from parallelisms close to an adaptive radiation that may also be a result of the multiple colonizations of the lake. One line of evidence supporting this is that the more widely distributed species, defined as those occurring in other lakes besides Lake Tanganyika, are distributed throughout the phylogeny instead of as a sister group to a single, monophyletic clade of *Gomphocythere* endemic to Lake Tanganyika. This pattern of speciation is mirrored by the Thiarid gastropods (Michel *et al.,* 1992) and Haplochromine cichlid fish that occur in Lake Tanganyika (Sturmbauer and Meyer, 1992; Meyer, 1993; Meyer *et al.,* 1994).

## Conclusions

This study represents the first phylogenetic analysis of any ostracode group in a rift lake system. The analyses undertaken here support the monophyly of *Gomphocythere* by nine synapomorphies. The preferred phylogeny has a consistency index of 0.56, reflecting the large amount of homoplasy in the reconstruction. However, the phylogenetic structure of this analysis indicates that there is a reliable signal in the data, despite the high

amount of homoplasy. Furthermore, after removing the homoplasic characters in the analysis, the tree topology remains, indicating that despite many parallelisms, the basic topology of the tree is supported as species clusters or subclades.

The low number of autapomorphies defining species and the high amount of parallel character acquisition is consistent with the models of species flock originations in lakes via allopatric speciation or multiple invasions. In a comparison of phylogenies produced by using hard- *versus* soft-part characters, we found that removing soft-part characters decreased the resolution of the analysis. This is also true of data sets consisting only of hard parts. This is not surprising, because loss of data generally reduced resolution in any type of analysis. It is significant, however, that more resolution was lost with the omission of the soft parts and not the hard parts, suggesting that the preservational bias present in the fossil record will have an effect on the analysis of biological diversification. In particular, the absence of soft-part characters will significantly reduce the resolution of any analysis and will impede determining the processes behind the diversification patterns.

The phylogeny also provides a basis for evaluating speciation mechanisms and, in the future, the role of ecological factors in the diversification of ostracodes in this lake system.

## ACKNOWLEDGEMENTS

The authors acknowledge the following people for their help in this study. Park wishes to thank Karel Wouters and Thierry Backeljau (Royal Belgian Institute of Natural Sciences), Wayne and David Maddison (University of Arizona), Louis Kornicker and two anonymous reviewers for their help with this manuscript. She also thanks her co-authors for all that they have done to help her over the years. This work was supported by grants to Park from Sigma Xi, Chevron, the Paleontological Society, the Geological Society of America, the University of Arizona's Research and Training Grant, and the Sulzer Fund.

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RECEIVED: 10 June 2000.
ACCEPTED: 20 June 2001.

Appendix 1. Characters used in cladistic analysis.

1. Tubercle: 0-absent; 1-present
2. Ventroposterior flare: 0-absent; 1-present
3. Surface reticulation: 0-absent; 1-reduced; 2-robust
4. Brood pouch on female: 0-absent; 1-present
5. Valve shape (dorsal view: anterior-posterior): 0-oval; 1-square/rectangular
6. Dorsal view of valve shape: 0-convex; 1-heart; 2-triangular
7. Reticulation density of carapace: 0-absent; 1-<11 (per 5 $\mu m^2$); 2-12–17 (per 5 $\mu m^2$)
8. Sieve pore: 0-normal; 1-radial
9. Central muscle scar: 0-straight; 1-posterior
10. Node position: 0-absent; 1-anteroventral; 2-posteroventral; 3-mediodorsal
11. Node number: 0-absent; 1-1; 2-3
12. Maximum dorsal node size: 0-absent; 1-<0.1 mm; 2->0.1 mm
13. Maximum ventral node size: 0-absent; 1-<0.1 mm; 2->0.1 mm
14. Sulcus: 0-absent; 1-present
15. Alae: 0-absent; 1-present
16. Ventrolateral expansion; alar prolongation: 0-absent; 1-present
17. Ornamental medial ridge: 0-absent; 1-present
18. Hinge angle: 0-parallel; 1-acute
19. Shell thickness: 0-thin; 1-thick
20. Marginal pore canals: 0-<5/0.1 mm; 1->5/0.1 mm
21. Hingement: 0-lophodont; 1-inverse lophodont; 2-merodont
22. Total number of furca setae (female): 0-2 setae each; 1-2 setae and 3 lobes; 2-more than 2 setae
23. Distal lobe on hemipenis: 0-fixed; 1-movable
24. Position of furca (male): 0-above copulatory; 1-below copulatory
25. Distal lobe apex: 0-ridged; 1-smooth
26. A1 number of podomeres on endopodite: 0-4; 1-5; 2-6
27. A1 character of 3rd and 4th podomeres: 0-separated; 1-fused
28. A1 2nd endopodite podomere dorsal apical setae: 0-absent; 1-present
29. A1 number of claws on last podomere of endopodite: 0-2 + 2; 1-2 + 1
30. A1 number of mediodorsal setae on 3rd and 4th podomere: 0-1; 1-2; 2-3
31. A1 number of medioventral spines on 3rd and 4th podomere: 0-1; 1-0
32. A1 number of dorsal apical setae on 3rd and 4th podomeres: 0-1; 1-2; 2-3
33. A1 position of ventral setae on 1st endopodite: 0-absent; 1-apically inserted; 2-medially inserted
34. A1 number of ventral apical setae on 3rd and 4th podomeres: 0-0; 1-1; 2-2
35. A2 number of podomeres on endopodite: 0-3; 1-4
36. A2 1st endopodite podomere apical-ventral setae: 0-absent; 1-present
37. A2 1st endopodite podomere shape: 0-rectangular; 1-square
38. A2 number of ventral apical setae on second and third podomere of endopodite: 0-2; 1-1
39. A2 number of mediodorsal setae on 2nd and 3rd podomeres: 0-1; 1-2
40. A2 number of medioventral setae on 2nd and 3rd podomeres: 0-3; 1-2; 2-1
41. Mandibular palp: 0-bent knee; 1-normal
42. Mandibular palp setae: 0-bifurcated; 1-straight
43. Mx palp: 0-reduced; 1-normal
44. P3 size and shape of terminal claw: 0-very elongated; 1-slightly elongated and curved; 2-short and slightly curved

Appendix 2. Data Matrix for *Gomphocythere* Species and Outgroups.

| | CHARACTERS/CHARACTER STATES | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TAXA** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** | **11** | **12** | **13** | **14** | **15** | **16** | **17** | **18** | **19** | **20** | **21** | **22** |
| *G. aethiopis* | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| *G. alata* | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *G. angulata* | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *G. angusta* | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. capensis* | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. coheni* | ? | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *G. cristata* | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 |
| *G. curta* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *G. downingi* | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. lenis* | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. obtusata* | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. ortali* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| *G. parcedilatata* | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *G. simplex* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *G. wilsoni* | 1 | ? | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |
| *G. woutersi* | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| *C. chariessa* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 |
| *Leucocythere* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 2 |
| *L. dadayi* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| **TAXA** | **23** | **24** | **25** | **26** | **27** | **28** | **29** | **30** | **31** | **32** | **33** | **34** | **35** | **36** | **37** | **38** | **39** | **40** | **41** | **42** | **43** | **44** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. aethiopis* | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | 2 | ? | 1 | 0 | 0 | ? | ? | ? | 1 | 1 | 1 | 0 |
| *G. alata* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | ? | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 2 |
| *G. angulata* | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | ? | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| *G. angusta* | 1 | 1 | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 1 | 1 | ? |
| *G. capensis* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *G. coheni* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 0 |
| *G. cristata* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 2 |
| *G. curta* | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 2 |
| *G. downingi* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *G. lenis* | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *G. obtusata* | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| *G. ortali* | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *G. parcedilatata* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *G. simplex* | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 2 |
| *G. wilsoni* | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
| *G. woutersi* | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 0 |
| *C. chariessa* | 1 | ? | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| *Leucocythere* | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *L. dadayi* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |