MORPHOLOGICAL PHYLOGENY OF ALPHEID SHRIMPS: PARALLEL PREADAPTATION AND THE ORIGIN OF A KEY MORPHOLOGICAL INNOVATION, THE SNAPPING CLAW

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Abstract.—The Alpheidae—possibly the most diverse family of recent decapod crustaceans—offers attractive opportunities to study the evolution of many intriguing phenomena, including key morphological innovations like spectacular snapping claws, highly specialized body forms, facultative and obligate symbioses with many animal groups, and sophisticated behaviors like eusociality. However, studies of these remarkable adaptations remain hampered by insufficient phylogenetic information. We present the first phylogenetic hypothesis of relationships among 36 extant genera of alpheid shrimps, based on a cladistic analysis of 122 morphological characters from 56 species, and we use this hypothesis to explore evolutionary trends in morphology and species diversity. Our results strongly supported a monophyletic Alpheidae that included two hitherto difficult-to-place genera (*Yagerocaris* and *Pterocaris*). Of 35+ nodes among genera, all were supported by at least one morphological character (24 were supported by two or more) and 17 received greater than 50% jackknife support. Unfortunately, many basal nodes were only weakly supported. Six genera appeared nonmonophyletic, including the dominant genus *Alpheus* (paraphyletic due to inclusion of one clade with three minor genera). Evolutionary trends in alpheid claw form shed some revealing light on how key innovations evolve. First, several functionally significant features of the cheliped (claw bearing leg) evolved independently multiple times, including: asymmetry, folding, inverted orientation, sexual dimorphism, adhesive plaques that enhance claw cocking, and tooth-cavity systems on opposing claw fingers, a preadaptation for snapping. Many conspicuous features of alpheid claw form therefore appear prone to parallel evolution. Second, although tooth-cavity systems evolved multiple times, a functional snapping claw, which likely facilitated an explosive radiation of over 550 species, evolved only once (in *Synalpheus* + [*Alpheus* + satellite genera]). Third, adhesive plaques (claw cocking aids) also evolved multiple times, and within snapping alpheids are associated with the most diverse clade (*Alpheus* + derivative genera). This pattern of parallel preadaptation—multiple independent evolutionary origins of precursors (preadaptations) to what ultimately became a key innovation (adaptation)—suggests alpheid shrimp claws are predisposed to develop features like tooth-cavity and adhesive plaque systems for functional or developmental reasons. Such functional/developmental predisposition may facilitate the origin of key innovations. Finally, moderate orbital hoods—anterior projections of the carapace partly or completely covering the eyes—occur in many higher Alpheidae and likely evolved before snapping claws. They are unique among decapod crustaceans, and their elaboration in snapping alpheids suggests they may protect the eyes from the stress of explosive snaps. Thus one key innovation (orbital hoods) may have facilitated evolution of a second (snapping claws).

Key words.—Alpheidae, adaptive radiation, character evolution, Crustacea, Decapoda, novelty, parallel evolution.

Parallelism, Preadaptation, and Key Innovations

Examples of parallel evolution—the independent origin of functionally and structurally similar traits among closely related taxa—occur in many groups of organisms (Futuyma 1998; Levin 2001; Schluter et al. 2004). Such parallelisms, of course, pose problems for cladistic analysis because character state codings are based on similarity; homology (or homoplasy) can only be judged from tree topology after the analysis. However, parallel evolution can provide strong evidence for adaptation: the independent origin of functionally and structurally similar traits in separate but related clades typically reflects an adaptive response to similar conditions (Futuyma 1998). Such parallel adaptive responses may be facilitated by similar genetic (Schluter et al. 2004) or developmental (Nijhout 1991) avenues. Furthermore, phylogenetic tests of adaptation (e.g., correlations between form and function or between form and environment) and the evolution of development are greatly strengthened where multiple independent contrasts (Felsenstein 1985) provided by parallel or convergent evolution are possible (Palmer 2004).

Less well appreciated is how patterns of parallel evolution may shed valuable light on the evolutionary origin of key innovations. (We use the term ''key innovation'' in the sense of Mayr (1960): a functionally significant synapomorphy associated with and presumed to have facilitated a major adaptive radiation.) Darwin, like many others since (e.g., Mayr 1960; Nitecki 1990; Müller and Wagner 1991), was troubled by how novel forms arise: ''Why . . . should there be so much variety and so little real novelty?'' (Darwin 1872,

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p. 156). One recurring hurdle to our understanding of how key innovations arise evolutionarily is their rarity: often, they arise only once within a clade (Vermeij 2006) so the only clues about origins lie in fossils or living descendents of taxa immediately ancestral to the clade defined by the key innovation. Therefore, multiple independent origins of putative precursor states—structurally or functionally intermediate preadaptations—permit more rigorous tests of the ecological correlates of key innovations.

Here we describe a pattern that offers promise for understanding the evolutionary origin of key innovations: parallel preadaptation. This term refers to the multiple independent evolutionary origins of precursors (preadaptations) to what ultimately became a key innovation (adaptation) with a wholly new function in one or a few clades. We illustrate this phenomenon with a phylogenetic study of alpheid shrimps, a spectacularly diverse clade of caridean shrimps within which an undeniable key innovation evolved: the snapping claw.

Alpheid Ecological Diversity

The caridean shrimp family Alpheidae, which includes over 600 species in 36+ genera, is an abundant and ecologically diverse group of decapod crustaceans. Most alpheids inhabit marine, shallow tropical and subtropical waters (e.g., Chace 1988), although some live in cool-temperate waters (e.g., Anker and Jeng 2002; Anker and Komai 2004; Fig. 1i). A few have colonized oligohaline or freshwater habitats (e.g., Powell 1979; Yeo and Ng 1996), whereas others are stygobitic or stygophilic (e.g., Hobbs 1973; Anker and Iliffe 2000). Alpheids also live in mangroves and estuarine areas (e.g., Anker 2003a,b), and in the deep sea (e.g., Chace 1988). All are strictly benthic, and rarely if ever leave the bottom to swim. Some heavily calcified forms (e.g., Alpheus) resemble mini-lobsters more than typical shrimps, and so have a ''reptantian life style'' (Coutière 1899). On marine hard and soft substrates, alpheids are among the most frequently encountered shrimps, and sometimes the dominant decapods (except maybe for brachyuran crabs) both in number of species and individuals (A. Anker, pers. obs.). Endolithic species are also major bioeroders of corals and other hard substrata (e.g., Fischer and Meyer 1985; Kropp 1987).

Many alpheids live in permanent symbiosis with other organisms, including sponges, cnidarians, molluscs, echinoderms, other crustaceans, echiurans, and gobiid fishes (Bruce 1976; Karplus 1987; Dworschak et al. 2000; Anker et al. 2001, 2005; Marin et al. 2005). Many aspects of these associations, such as interspecific communication (Vannini 1985; Karplus 1987), protandric hermaphroditism (Nakashima 1987; Gherardi and Calloni 1993), host protection (Glynn 1983), and eusociality (Duffy et al. 2000) make alpheids particularly interesting to field and behavioral biologists.

Alpheid Snapping Claws and Morphological Diversity

Alpheid chelipeds (claw-bearing legs) come in a remarkable variety of forms. Some are small, unspecialized, symmetrical forms (e.g., Figs. 1a, 4o; see also Fig. S1 in the Supplementary Material available online only at http://dx.doi.org/10.1554/05-486.1.s1) that differ little from those of other caridean shrimp (cf. Fig. 4n). Others are greatly enlarged (Figs. 1c,j–o,r–t; 3d,f–j; online Fig. S2a,b,f), often highly asymmetrical (Figs. 1j,n,s,t; 3d,f–j; online Figs. S2i, S3), and sometimes specialized and oddly shaped (see Fig. 4p,t,v,x; online Fig. S3b). Cheliped polymorphism and sexual dimorphism occur in many genera (e.g., Banner and Banner 1982; Anker et al. 2001; Anker 2003b, see also online Fig. S3).

In the most diverse alpheid clade (*Alpheus* + *Synalpheus* + derivative genera), one of the first pereiopods (chelipeds) bears a voluminous claw with a complex snapping mechanism on the fingers: the snapping claw (Fig. 5g–i). The snapping claw is a powerful, multifunctional tool used for defense and aggression in interspecific and agonistic interactions (e.g., Hazlett and Winn 1962; Schultz et al. 1998; Schmitz and Herberholz 1998; Duffy et al. 2002). The loud snap, one of the most audible and familiar of underwater noises, is detectable as far away as one kilometer (M. Chitre, pers. comm.). The crackling noise produced by numerous snapping shrimps may interfere with submarine sonar system, and it prompted extensive investigations following World War II (Johnson et al. 1947) to the present day (e.g., Chitre 2005).

Most early workers who studied snapping in *Alpheus* and *Synalpheus* believed impact of the dactylus (movable finger) on the pollex (fixed finger) caused the snap (e.g., Coutière 1899; Volz 1938; Knowlton and Moulton 1963; Ritzmann 1974). However, dramatic evidence from *Alpheus heterochaelis* (Versluis et al. 2000) revealed that the snap results from implosion of a cavitation bubble caused by water rapidly ejected from a socket in the fixed finger by a plunger (specialized tooth) on the dactylus (Fig. 6a). Dactylus closure is among the most rapid movements in the animal kingdom (Schmitz 2001). The snapping mechanism of *Synalpheus* and most other *Alpheus* remains to be investigated.

The alpheid frontal region is also unique among decapod crustaceans (see Fig. 4a–m; online Fig. S4). In most species, eyes are covered dorsally by anterior projections of the carapace, the so-called orbital hoods. Orbital hoods vary among groups and bear important taxonomic characters. The immense diversity of orbital hoods and chelipeds (e.g., Banner and Banner 1982) likely facilitated diversification of snapping alpheids, especially *Alpheus* (see Discussion).

Alpheid Evolutionary Relationships

The taxonomy of the Alpheidae is challenging. Despite extensive effort (e.g., Banner and Banner 1973, 1975, 1982; Chace 1988; Christoffersen 1979), all larger genera await revision. Cryptic species occur in many genera, notably in the two most speciose genera, *Alpheus* (>400 species) and *Synalpheus* (>150 species) (e.g., Knowlton and Keller 1985; Knowlton and Mills 1992; Duffy 1996; Anker 2001a; Nomura and Anker 2005), and most cryptic species complexes remain unresolved (Anker 2001a).

Surprisingly, given their ecological significance and interesting adaptations, phylogenetic studies of alpheids are rare. Only Coutière (1899) advanced a hypothesis of intergeneric relationships of 14 recognized alpheid genera. Although his ''evolutionary tree'' (Fig. 2) is outdated, Coutière provided detailed information on morphology, analyzed nu-

merous morphological characters, and discussed relations among alpheid genera and their affinities with other caridean families. Coutière (1899, 1905) also subdivided *Alpheus* into seven informal species groups that have guided subsequent workers (e.g., Banner and Banner 1982; Kim and Abele 1988; Anker 2001a). His subdivision of *Synalpheus* into seven species groups (Coutière 1909) was less well received as only three remain in use (Banner and Banner 1975).

Christoffersen (1987, 1990) advanced the first family-level phylogeny of caridean shrimps based on a cladistic analysis of morphological characters and proposed several new families, including the Pterocarididae for the peculiar monotypic genus *Pterocaris*. Christoffersen (1990) was unable to satisfyingly place another odd monotypic genus, *Yagerocaris*, which Chace and Kensley (1992) eventually transferred from the Hippolytidae to the Alpheidae.

Pioneering studies of internal relationships of *Alpheus* using protein and DNA variation revealed numerous cryptic *Alpheus* species across the Isthmus of Panama (Knowlton et al. 1993; Knowlton and Weigt 1998) and in the Indo-Pacific (Williams et al. 1999). Williams et al. (2001) proposed a first phylogenetic hypothesis for *Alpheus*, based on molecular data. Unfortunately, their analysis was biased toward Atlantic and eastern Pacific species, and many key Indo-West Pacific taxa were not considered. Furthermore, the discovery of pseudogenes prompted a reinvestigation (Williams and Knowlton 2001). Nevertheless, these studies were important first steps toward an alpheid phylogeny, and revealed the long suspected polyphyletic status of some *Alpheus* species groups (Anker 2001a; Williams et al. 2001). *Synalpheus*—the second most diverse alpheid genus—has also received some attention. Duffy et al. (2000) and Morrison et al. (2004) used both molecular and morphological data to assess the relation between eusociality and speciation among some western Atlantic *Synalpheus*.

We present here the first comprehensive cladistic analysis of the Alpheidae. This generic-level analysis of morphological data aims to test the monophyly of the Alpheidae and some speciose and heterogenous genera (e.g., *Alpheus*, *Athanas*); to investigate alpheid morphological evolution, including key innovations like snapping claws and orbital hoods; and to test Coutière's (1899) hypotheses of alpheid phylogeny and his ideas about parallel evolution of the snapping claw and coevolution of the snapping claw and orbital hoods.

MATERIALS AND METHODS

Ingroup Taxa

All 36 currently recognized alpheid genera were used as terminals, in most cases represented by their type species. Some genera were represented by several species, especially where significant morphological variation was present (e.g., *Alpheus*) or where nonmonophyly was suspected (e.g., *Alpheopsis*, *Automate*, *Alpheus*). For instance, each of Coutière's (1899; 1905) seven *Alpheus* species groups was represented by at least one species. Of about 200 species examined, 56 were included in the analysis (Appendix S1, available online only in the Supplementary Material).

All body regions and appendages were searched for characters, and all character states were scored by A. Anker from specimens deposited in collections held by national and other museums (see online Appendix S1 for full details) or collected by A. Anker.

Outgroup Taxa

Because the sister group to the Alpheidae is controversial (cf. Thompson 1967; Christoffersen 1987), we used four outgroups to root our analyses: *Pandalopsis* (Pandalidae, Pandaloidea), *Ambidexter* (Processidae, Processoidea), *Ogyrides* (Ogyrididae, Alpheoidea), and *Lysmata* (Hippolytidae, Alpheoidea). Representatives of the two alpheoid families were included to test for alpheid monophyly. Outgroup characters were scored from detailed descriptions of *Lysmata vittata*, *Ogyrides orientalis* (Bruce 1990), *Pandalopsis lamelligera* (Komai 1997), and *Ambidexter symmetricus* (Manning and Chace 1971) and direct observation of specimens of *Lysmata*, *Ogyrides*, *Pandalus*, and *Processa*.

Cladistic Analysis

We scored 122 characters (Appendix 1) for all 60 terminal taxa, and a data matrix (Appendix 2) was constructed in MacClade 4.0 (Maddison and Maddison 2000). All characters were unordered and weighted equally, missing data were scored unknown, and polymorphisms were scored as such rather than assuming a plesiomorphic state. Since characters were unordered, the score for each state (i.e., 0, 1, 2) implies nothing about polarity or order. Coding of character 42 (mandibular palp distal article) applies only to terminal taxa bearing a mandibular palp and cannot be meaningfully scored for taxa lacking the palp. To avoid potential problems created by the inappropriate coding of "inapplicable" states (Maddison 1993; Platnick et al. 1991), inapplicables were scored "?" but are indicated as "-" in Appendix 2 to distinguish them from unknowns.

Trees were generated in PAUP* 4.0b10 (Swofford 2002) under the heuristic search (MULPARS, tree-bisection-reconnection, 100 replications with random input order). Relative stability of clades was assessed using jackknifing as implemented in PAUP* (500 pseudoreplicates, 33% character deletion).

Optimizations

Selected morphological characters were optimized onto a minimal length tree with topology equivalent to the 50% majority rule consensus simplified to genus level. If a genus was paraphyletic or polyphyletic in the original tree, a "genus group" was included as a separate terminal in the condensed tree. For example, *Athanas* was found to comprise two groups, *Athanas* 1 (sensu stricto, which included *A. nitescens*, the type species, and *A. dimorphus*) and *Athanas* 2 (*A. squillophilus*). In the Discussion, the minimum number of character state changes was inferred using only nodes with greater than 50% jackknife support (Fig. 3) and the maximum number of character state changes was inferred using all nodes in Figure 4.

RESULTS

The PAUP analysis yielded 62 minimal length topologies (tree length 523, CI 0.36, HI 0.64, RI 0.66). However, the
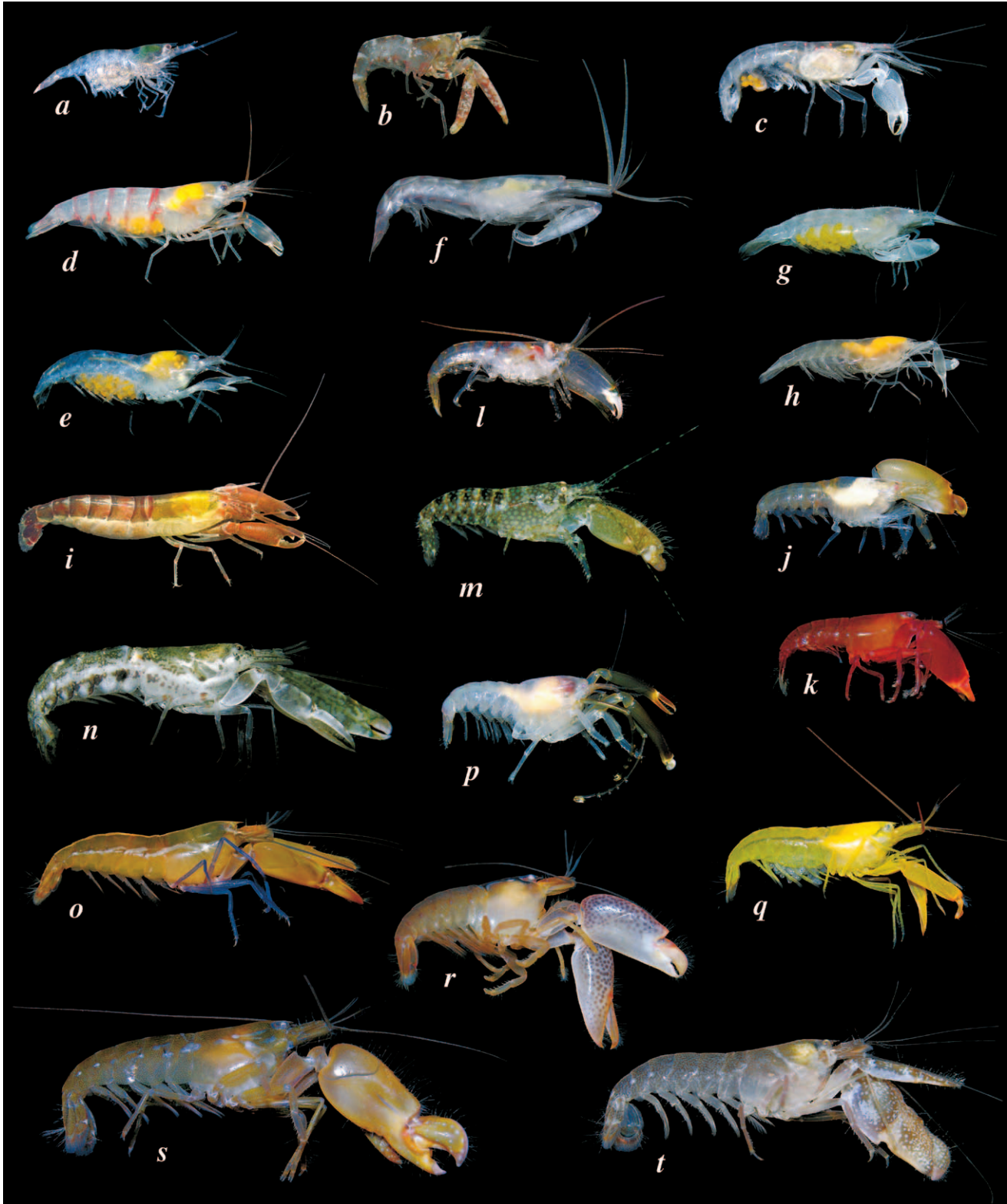
FIG. 1. Alpheid shrimp diversity: (a) *Potamalpheops johnsoni*, 10 mm total length (TL), free living under wood logs in mangrove mud, Singapore; (b) *Athanas* cf. *nitescens*, 12 mm TL, free living under rocks, São Tomé; (c) *Automate* n. sp. aff. *evermanni*, 16 mm TL, free living under rocks on sand, Las Perlas, Panama (Pacific); (d) *Parabetaeus* cf. *hummelincki*, TL 18 mm, free living under rocks, São Tomé; (e) *Alpheopsis labis*, TL 12 mm, free living under rocks, Isla Grande, Panama (Caribbean); (f) *Leptalpheus forceps*, TL 18 mm, commensal in burrows of callianassid ghost shrimps, Cahuita, Costa Rica (Caribbean); (g) *Salmoneus ortmanni*, TL 13 mm, free living on silt, under rocks, Isla Grande, Panama (Caribbean); (h) *Salmoneus* n. sp. aff. *caboverdensis*, TL 12 mm, commensal in burrows of callianassid ghost shrimps, Isla Grande, Panama (Caribbean); (i) *Betaeus harrimani*, TL 24 mm, commensal in burrows of upogebiid
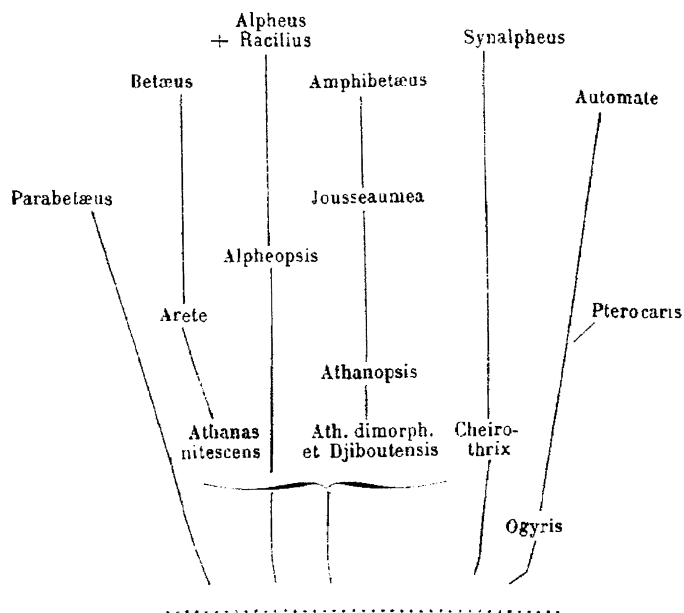
FIG. 2. Evolutionary tree of the Alpheidae (+ *Ogyrides* later transferred to its own family, Ogyrididae) proposed by Coutière (1899). *Cheirothrix* was subsequently replaced by *Batella*; *Ogyris* was replaced by *Ogyrides* and placed in the family Ogyrididae (see Holthuis 1993 cited in Supplementary Material available online). Reproduced from Coutière (1899).

overall tree topology was almost fully resolved, with ambiguity restricted to three species within *Leptalpheus* and *Fenneralpheus* (*L. axianassae*, *L. forceps*, *F. chacei*) and three species of *Alpheus* (*A. edwardsii*, *A. macrocheles*, *A. sulcatus*) (Fig. 3). Consequently, the strict consensus and 50% majority-rule consensus were quite similar at the genus level (ambiguous nodes are labeled § in Fig. 3). Most in-group branches were supported by at least two character-state changes (43 of 55, Fig. 3; see also Appendix S2, available online only in the Supplementary Material). Jackknife proportions also exceeded 50% for most in-group branches (32 of 55, Fig. 3).

Our analysis confirmed the monophyly of the Alpheidae (Fig. 3). Within the Alpheidae, *Yagerocaris* was sister group to all remaining alpheids, followed by clade PS and the enigmatic genus *Pterocaris*. The robust clade ABC was sister group to clade H ("higher" Alpheidae), containing all remaining genera. Clade H and its three major clades I, II, and III were unfortunately supported by few synapomorphies (e.g., orbital hoods concealing eyes; Fig. 3; see online Appendix S2). However, many smaller clades—SD, AP, BV, ALF, MB (excluding *Mohocaris*), APN, and the most speciose clade AS—were well supported (Fig. 3; online Appen-

dix S2). A more detailed analysis of relations among species of *Alpheus* and *Synalpheus* in clade AS will be required to confirm that *Synalpheus* is not derived from a basal branch within the hugely diverse genus *Alpheus*. Finally, some genera appear nonmonophyletic, including *Athanas*, *Arete*, *Leptalpheus*, *Betaeus*, *Alpheus*, and *Alpheopsis*, so revisions of these genera may be necessary.

Optimizations of evolutionarily significant characters are evaluated in detail in the Discussion. Other characters important to the delineation of alpheid genera—number of straplike epipods (mastigobranchs) on the pereiopods, the presence/absence of a triangular articulated plate on the sixth abdominal somite, and frontal margin of the carapace—are discussed in detail in the Supplementary Material available online (under Evolution of Other Characters and Their Validity for Taxonomy).

Discussion

Evolutionary Relationships of the Alpheidae

Monophyly of the Alpheidae

Our analysis revealed the Alpheidae—morphologically the most heterogenous caridean shrimp family—to be monophyletic. Several characters define the family (Fig. 3; Appendix 1 and online Appendix S2), including the cardiac notch (char. 19); stout, more or less parallel and juxtaposed eyestalks (char. 31); absence (loss) of antennal tooth (char. 25); and first pereiopods (chelipeds) more robust than second (char. 72). The highly derived Ogyrididae appear to be sister group to the Alpheidae (see also Christoffersen 1987).

Tree topology

Many crown groups are well supported by five or more characters, including clades ABC, AP, SD, BV, ALF, and AS (Fig. 3). *Yagerocaris*, *Potamalpheops*, and *Stenalpheops* appear to be the least derived alpheid genera. *Yagerocaris* exhibits numerous plesiomorphies (including some "hippolytid" features) and some odd autapomorphies, explaining its original placement in the Hippolytidae (Kensley 1988). Miya (1997) suggested *Stenalpheops* and *Potamalpheops* were closely related, which our analysis also confirms. The position of clade ABC, as sister group to the "higher" Alpheidae (clade H), reflects the morphology of its constituent genera. *Automate*, *Coronalpheus*, and *Bermudacaris* all possess plesiomorphies such as dorsally completely exposed eyestalks (Fig. 4d; online Fig. S4c) and enlarged, but relatively unspecialized claws (Figs. 1c and 4q).

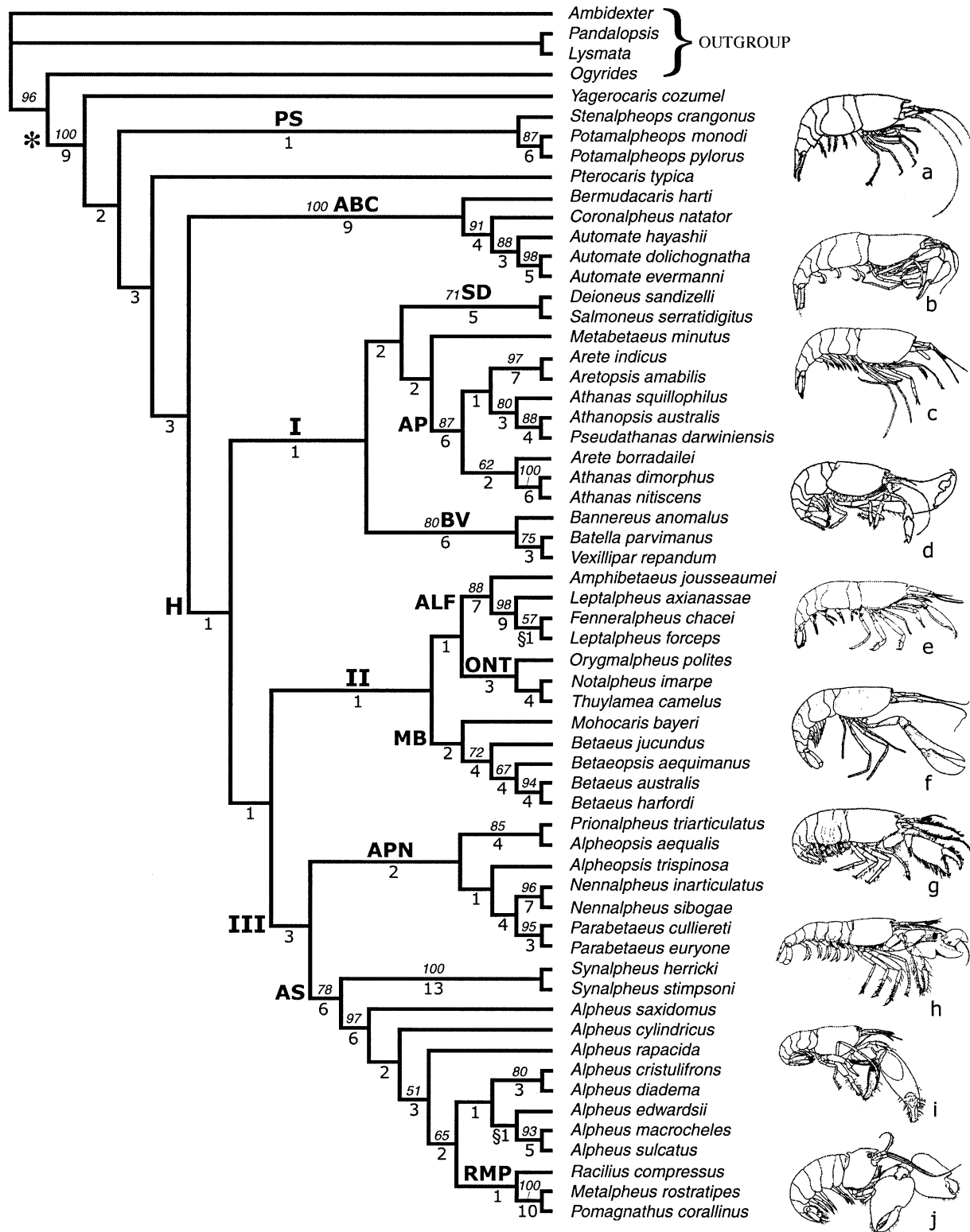As with many morphological phylogenetic analyses of this

FIG. 3. One of 62 most parsimonious topologies (length 523, CI 0.36, RI 0.66). § indicates unresolved branches in the strict consensus with the upper recovered in 58% and lower in 65% of trees respectively; all remaining branches were recovered in 100% of most parsimonious topologies. Asterisk indicates the ingroup node. Labels in bold indicate clades referred to in the text, numbers above branches indicate jackknife proportion, and numbers below branches indicate the number of unambiguous changes supporting that branch (for complete listing of character state changes, see Appendix S2 in the Supplementary Material available online). Figures of alpheid body form include: (a) *Yagerocaris cozumel*; (b) *Deioneus sandizelli*; (c) *Metabetaeus minutus*; (d) *Aretopsis amabilis*; (e) *Fenneralpheus chacei*; (f) *Notalpheus imarpe*; (g) *Prionalpheus sulu*; (h) *Alpheus* aff. *richardsoni*; (i) *Alpheus alcyone*; (j) *Racilius compressus*. Adapted from various sources.

scale, uncertainties remain. Although our results suggest that the enigmatic *Pterocaris* is a highly derived alpheoid shrimp, which supports earlier suggestions (Coutière 1899; Anker and Dworschak 2001), its position within the family remains questionable due to insufficient data (e.g., unknown male) and numerous autapomorphies of this peculiar ''hairy'' shrimp (see Anker and Dworschak 2001). The topology of some clades, as well as the position of some taxa, requires further scrutiny (for a detailed discussion of clades BV, AP, ONT and the position of *Metabetaeus* see Taxonomic Commentary in the Supplementary Material available online). Within the hyperdiverse genus *Alpheus*, the position of *A. cylindricus* and some other species (Fig. 3) may not reflect true relationships, because many *Alpheus*-specific characters are not applicable to a family-wide analysis, and because more *Alpheus* species are required to accurately recover relations within this genus. The present topology is also not congruent with molecular studies of selected *Alpheus* species (Williams et al. 2001), so a separate morphological analysis of *Alpheus* is still needed. Finally, *Synalpheus* and *Alpheus* are linked together mainly by features of the snapping claw and orbital hoods. However, both structures differ somewhat between these genera (see below, The alpheid snapping claw), so they may not actually be homologous.

Comparison with Coutière's hypothesis on alpheid evolution

Our analysis supports some features of Coutière's (1899) alpheid evolutionary tree (Fig. 2), including affinities between *Arete* and *Athanas nitescens* (clade AP), *Alpheopsis* and *Alpheus* (clade III), *Athanopsis* and *Athanas dimorphus* (clade AP), and *Pterocaris* and *Automate* (basal position). However, our analysis reveals some important differences. For instance, we found clade SD, containing *Salmoneus*, to be distant from clade ALF, containing *Amphibetaeus* and *Leptalpheus* (Fig. 3), and *Betaeus* and *Betaeopsis* (Coutière's *Betaeus* included *Betaeopsis*) to be not closely related to *Arete*. Our results also suggest that *Parabetaeus*, which Coutière (1899) had difficulty placing, lies near *Alpheopsis* and *Nennalpheus*.

Coutière (1899) also placed *Synalpheus* near *Batella* (*Cheirothrix* in Coutière's tree), but our results placed *Batella* closer to *Bannereus* and *Vexillipar* in the well-supported clade BV, which is not closely related to *Synalpheus* + *Alpheus* (our clade AS). Coutière (1899) noted some ''hippolytid'' (likely primitive) features of *Synalpheus*, such as a crown of strong spines on the tip of the third maxilliped and doubled fingertips of the minor claw. However, the third maxilliped is distally unarmed in some *Synalpheus* species (e.g., *S. stimpsoni*), and the fingertips are not doubled in many others.

Paraphyly or polyphyly of some alpheid genera

The apparent nonmonophyly of several alpheid genera is not surprising, and was suspected earlier (for detailed discussion of *Alpheopsis*, *Arete*, *Athanas*, *Betaeus*, and *Leptalpheus* see Paraphyly or Polyphyly of Some Alpheid Genera in the Supplementary Material available online). The paraphyletic status of *Alpheus*—the largest and most complex decapod genus—requires comment. Our results suggest that the minor clade RMP (Fig. 3) lies within *Alpheus*. *Racilius*,

Metalpheus, and *Pomagnathus* bear a ''derived *Alpheus*'' appearance. Although they differ from *Alpheus* (for details see Paraphyly or Polyphyly of Some Alpheid Genera in the Supplementary Material available online), these differences seem insignificant on a broader phylogenetic scale. Interestingly, both *Pomagnathus* and *Racilius* are obligate symbionts of pocilloporid and galaxiid corals, respectively, and *Metalpheus* species occasionally associate with living coral; this symbiotic lifestyle may explain their specialized body form. That such a large and diverse clade as *Alpheus* should have spawned a new, morphologically distinct clade is not surprising and does not challenge *Alpheus* as a valid genus. However, if the diverse genus *Synalpheus* derives from within *Alpheus*, the limits to *Alpheus* may need to be redefined.

Parallel Evolution and Morphological Versatility

Many morphological features of alpheid shrimp exhibit parallel evolution (Fig. 4; online Fig. S6; online Appendix S2), suggesting that great potential versatility of form is a prerequisite to adaptive radiation, as in other hyperdiverse groups like cichlid fishes, passerine birds and placental mammals (Vermeij 1973). We focus here on features of the chelipeds (the claw-bearing leg) because of their great functional and ecological significance (e.g., Fischer and Meyer 1985; Schultz et al. 1998; Schmitz 2001; Duffy et al. 2002). Widespread parallel evolution in cheliped features suggests that they are adaptive (Futuyma 1998) and may have been facilitated by similar genetic (Schluter et al. 2004) or developmental (Nijhout 1991) pathways.

Cheliped enlargement and orientation

Modified-enlarged chelipeds, folded chelipeds, and inverted chelipeds all evolved multiple times in the Alpheidae (Fig. 4). Most derived taxa possess enlarged chelipeds (Fig. 4), a trend seen in many other crustacean groups (Vermeij 1987). The enlargement of claws probably started early in alpheid history (Fig. 4), but proceeded independently in different groups. In basal taxa, like *Yagerocaris* and most *Potamalpheops* species, chelipeds are not particularly enlarged. In the basal *Stenalpheops*, the chelipeds are elongate and robust, but with fingers bent strongly backwards in males so the pollex fuses with the palm and forms a peculiar subchela (Fig. 4p; see also Anker et al. 2001). So even early branches exhibit specialized chelipeds (Anker 2001b).

Alpheid shrimp carry their chelipeds in many ways, and cheliped folding appears to have evolved independently four to six times (Fig. 4). Most carry them extended forward (e.g., Figs. 1e,i,m–t; 3a,c–j), whereas others fold them (e.g., Fig. 1f,g) with the propodus (palm + fixed finger of claw) held against the merus (second leg segment). Methods of folding, however, often differ. For instance, both chelipeds may be folded, with the propodus accommodated by a deep excavation of the ventral side of the broadened merus (jackknife system), as in many *Athanas* and *Athanopsis* species (Fig. 4r; online Fig. S2d,e). Alternatively, the carpus (third leg segment) rather than the merus may be excavated, as in *Arete borradailei* (online Fig. S3f). Finally, the system may be reversed altogether: the merus may be slender and fit into a shallow depression on the propodus (online Fig. S2h), as in
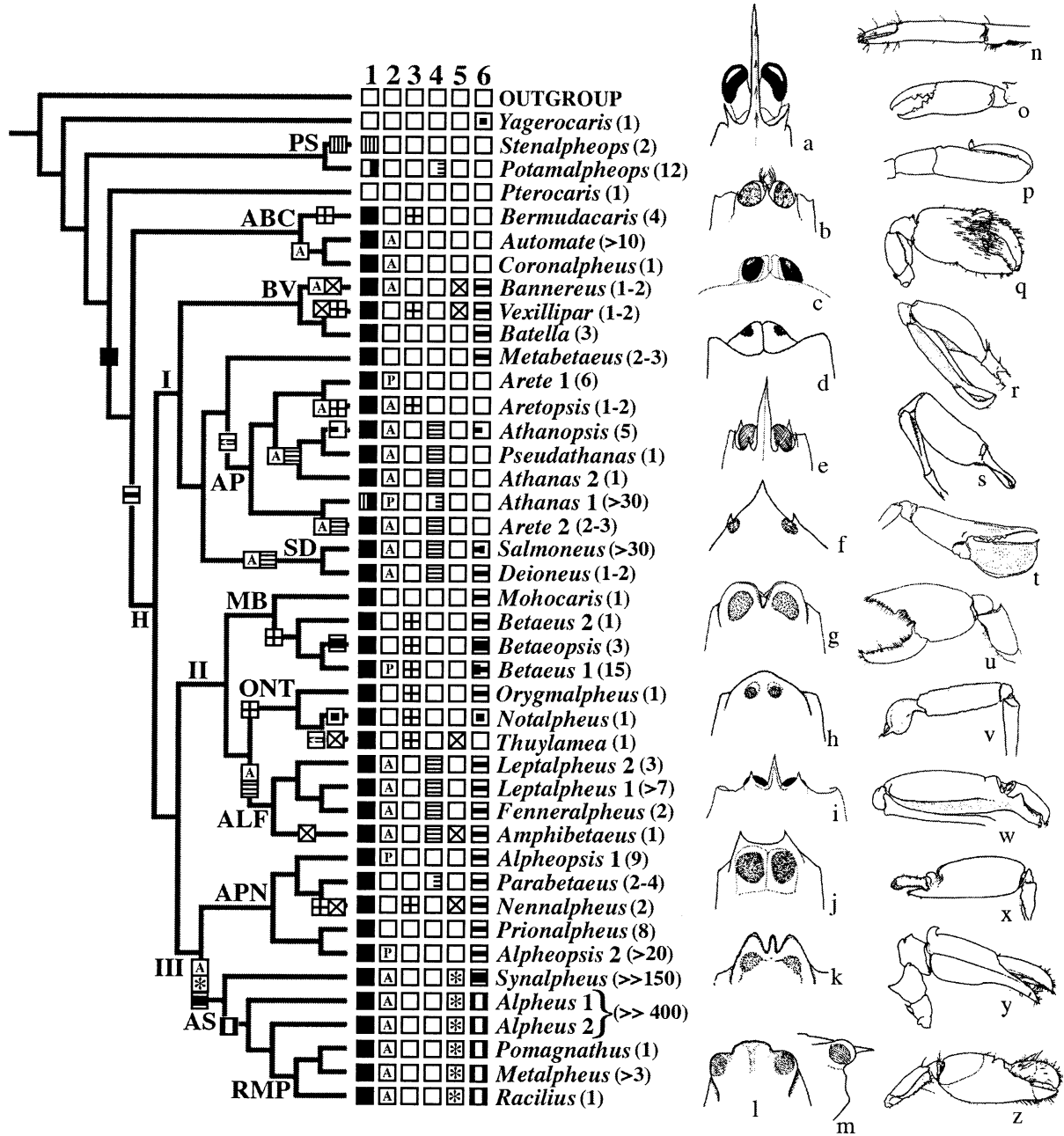
1. Cheliped enlargement: □ - chelipeds not enlarged; ■ - one or both chelipeds enlarged (compared to second pereiopods); ▥ - chelipeds enlarged only in males; ▯ ▥ - polymorphic within genus.

2. Cheliped asymmetry: □ - symmetrical or subsymmetrical; Ⓐ - asymmetrical; ℗ - polymorphic within genus.

3. Claw inversion: □ - claw not inverted, dactylus in lateral or dorsal position; ⊞ - claw inverted, dactylus in ventral or ventro-lateral position.

4. Cheliped folding: □ - chelipeds carried extended; ▤ - chelipeds carried folded (may be folded in different manners); ▤ - polymorphic within genus.

5. Tooth-cavity systems on claw fingers: □ - absent; ⊠ - present on one or both chelipeds, not functional (no snapping), not homologous; ⊞ - present on one cheliped, functional (snapping mechanism).

6. Orbital hood: □ - absent, eyes exposed; ▣ - weakly developed, eyes mostly concealed; ▤ - moderately developed, not inflated, eyes concealed (▤ indicates probable reversal); ■ - well developed, slightly inflated, eyes concealed; ▯ - highly developed, usually swollen, eyes completely concealed; ▤ - polymorphic within genus.

Amphibetaeus and most *Leptalpheus* and *Salmoneus* (Fig. 4s,w). These cheliped folding systems are extremely unusual among caridean shrimps, although an even more complex one exists in *Leontocaris* (Leontocarididae) with its extraordinary double-folded chelipeds (Fransen 2001). In alpheids, cheliped folding is not related to claw size—many species with large chelipeds (e.g., *Alpheus* and *Synalpheus*) do not fold them, yet some with small claws carry them folded (e.g., some *Athanas*). The cheliped may even fold in different ways within the same genus (e.g., *Salmoneus*, online Fig. S2j,k).

Orientation of the dactylus (movable finger) also varies among genera. The complete or almost complete inversion of the dactylus, from the typical lateral or dorsal position (Figs. 3g–j, 4o,q, w–z; online Fig. S2a) to ventral or almost ventral position (Figs. 1i, 3d,f, 4t,u), likely evolved five to six times (Fig. 4). This quasi-complete dactylus inversion in some alpheids (e.g., *Betaeus*, *Aretopsis*) resembles the contrast between the anomuran families Porcellanidae and Galatheidae (dactylus in ''inner'' position) and brachyuran crabs (dactylus in ''outer'' position).

Cheliped asymmetry

As in many decapod crustaceans (Mariappan et al. 2000), conspicuously asymmetrical chelipeds—those that differ between the right and left sides in shape, size, armature of the fingers, presence of a specific feature, and so on (online Fig. S3)—evolved multiple times in alpheid shrimps (Fig. 4; for details see Cheliped Asymmetry, Reversed Asymmetry, and Abnormal Symmetry in the Supplementary Material available online). In addition, conspicuous asymmetries evolved in other appendages as well, including the mandible in *Prionalpheus* species, second pereiopods in some *Alpheus* and *Stenalpheops crangonus* (see Anker 2001b).

Handedness has not been studied statistically for any alpheid species, but in *Alpheus*, *Synalpheus*, *Metalpheus*, *Racilius*, *Salmoneus*, and *Leptalpheus*, direction of asymmetry appears to be random (Coutière 1899; Nouvel 1944; Shin-Ike 1956; A. Anker, pers. obs.; I. Marin, pers. obs.). Therefore, most (if not all) Alpheidae with asymmetrical chelipeds exhibit antisymmetry (dextral and sinistral forms equally common), which strongly suggests that direction of asymmetry is not inherited (Palmer 2004). Cheliped directional asymmetry is rare among caridean shrimps, although it does occur in most processid shrimps (Nouvel 1944; Manning and Chace 1971) and some pandalid shrimps (Butler 1980). Interestingly, in contrast to lobsters and male fiddler crabs, in which direction of asymmetry is fixed early in development, the alpheid minor cheliped retains the potential to develop

into a major cheliped, and symmetric chelipeds in normally asymmetrical alpheid taxa are extremely rare (for details see Cheliped Asymmetry, Reversed Asymmetry, and Abnormal Symmetry in the Supplementary Material available online).

Conspicuously asymmetrical chelipeds evolved seven to nine times in alpheid shrimps (Fig. 4). In some cases, closely related taxa differ in cheliped asymmetry, for example, *Vexillipar* (symmetrical)–*Bannereus* (asymmetrical); *Alpheopsis trispinosa* (subsymmetrical)–*A. africana* (asymmetrical); *Alpheopsis aequalis* (subsymmetrical)–*A. labis* (asymmetrical). The same phenomenon occurs in the enlarged second chelipeds of some pontoniine shrimps, as in the closely related genera *Coralliocaris* (symmetrical chelipeds), *Harpiliopsis*, and *Jocaste* (asymmetrical chelipeds) (Bruce 1994). Cheliped asymmetry may therefore evolve rapidly.

In many alpheids, asymmetry consists merely of differences in claw size or finger armature. Functional asymmetry, where two chelipeds become specialized in different ways, appears only in a few groups, like: *Athanas ornithorhynchus*, with a specialized platypus-bill-shaped minor cheliped (see Marin et al. 2005); *Amphibetaeus*, with a primitive tooth-cavity system on the major cheliped; and clade AS, where the major cheliped possesses a true snapping mechanism (see below, The alpheid snapping claw).

Cheliped sexual dimorphism

Cheliped sexual dimorphism has also evolved at least seven times within the Alpheidae (online Appendix S2) and is even more complex than asymmetry. It may involve size and/or shape of the major claw (e.g., many *Synalpheus* and *Alpheus*), finger armature on one or both claws (e.g., *Athanas*, *Betaeus*), and rows of unique balaeniceps setae on the minor claw (many *Alpheus*). Asymmetry may also be sexually dimorphic, as in *Athanas djiboutensis*, where it is more pronounced in females (online Fig. S3c). *Athanas* is notorious for sex- and age-related cheliped polymorphism (Miya and Miyake 1968; Banner and Banner 1983; Anker 2003a), although a case of yet unexplained cheliped polymorphism was also reported in one species of *Salmoneus* (Anker 2003b). Within clade AP, sexual dimorphism, asymmetry and eventually polymorphism evolved several times, resulting in much complexity (online Fig. S3). Similarly, sexual dimorphism likely evolved multiple times within *Alpheus*, where it especially involves major claw size and shape and features on the minor claw fingers.

Given the rich diversity of features involved, and the numerous independent evolutionary origins, alpheid shrimps

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FIG. 4. Optimization of five cheliped features (1–5) and one feature of the carapace frontal margin (6) on a cladogram (Fig. 3) condensed to genera. Figures in the left column (a–m) show frontal regions of the carapace in dorsal (a–l) and lateral (m) views: (a) *Lysmata* sp. (outgroup), with typical caridean features (e.g., long dentate rostrum and divergent eyes); (b) *Potamalpheops monodi*; (c) *Stenalpheops anacanthus*; (d) *Automate evermanni*; (e) *Athanas* [1] *djiboutensis*; (f) *Salmoneus teres*; (g) *Betaeopsis aequimanus*; (h) *Leptalpheus* n. sp. aff. *forceps*; (i) *Alpheopsis* [1] cf. *trispinosa*; (j) *Parabetaeus culliereti*; (k) *Synalpheus pachymeris*; (l) *Alpheus frontalis*; (m) *Alpheus sibogae*. Figures in the right column (n–z) show chelipeds (P1): (n) *Lysmata* sp. (outgroup), typical nonspecialized caridean P1; (o) *Potamalpheops pylorus*, male P1; (p) *Stenalpheops crangonus*, male P1; (q) *Automate anacanthopus*, major P1; (r) *Athanas* [1] *djiboutensis*, major P1; (s) *Salmoneus ortmanni*, major P1; (t) *Notalpheus imarpe*; (u) *Betaeus harfordi*; (v) *Mohocaris bayeri*; (w) *Leptalpheus pacificus*, major P1; (x) *Alpheopsis* [1] *diabolus*; (y) *Alpheopsis* [2] *trigona*, major P1; (z) *Alpheus savuensis*, major (snapping) P1. Most figures original, some adapted from various sources.

offer many opportunities to study the ecological correlates and evolutionary consequences of sexual dimorphism.

Parallel Preadaptation and the Evolutionary Origin of Key Innovations

The evolutionary origins of key innovations (Mayr 1960) are often enigmatic (Nitecki 1990). First, they typically have qualitatively new functions so functional intermediates may not be obvious (Futuyma 1998). Second, they are often rare events, which suggests that unique conditions promoted them (Vermeij 2006) and limits clues to immediate relatives (either living or fossil) of the clade exhibiting the innovation. Alpheid shrimp offer a valuable window on how a key innovation, the snapping claw, evolved because, like so many other characteristics of alpheid chelipeds (previous section), putative precursors to functional snapping claws also exhibit parallel evolution. We refer to this phenomenon as *parallel preadaptation* and suggest that a search for examples in other taxa would be rewarding.

The alpheid snapping claw

The large and powerful snapping claw is perhaps the most famous feature of alpheid shrimps, hence the popular names ''snapping shrimps,'' ''pistol shrimps,'' or ''cracker shrimps,'' even though not all alpheids snap. It clearly qualifies as a key innovation (sensu Mayr 1960) because it is structurally unique (Fig. 5); it evolved once at the base of a hyperdiverse clade (>550 species; nearly 75% of alpheid species; Fig. 4); and it performs many functions, including prey capture (MacGinitie and MacGinitie 1968), defense (Reaka 1987; Duffy et al. 2002), intra- and interspecific signaling (Hazlett and Winn 1962; Schultz et al. 1998; Schmitz 2001; Duffy et al. 2002; Tóth and Duffy 2005), rock boring (Fischer and Meyer 1985; Werding 1990), and excavation of soft sediments (Magnus 1967).

Snapping claw evolution appears tightly related to claw finger armature. The cutting edges of alpheid claw fingers may be unarmed, or bear teeth that take many forms (e.g., Fig. 4l,u,w; for more details see Cheliped Tooth Variation in the Supplementary Material available online). Most teeth do not insert into cavities on the opposing fingers. Significantly, tooth-cavity systems—projections on one finger that insert into a cavity on the opposing finger (Fig. 5) and that are a prerequisite for snapping—evolved four to six times in alpheids (Fig. 4). Therefore, tooth-cavity systems in nonsnapping clades legitimately represent extant preadaptations because some form like them must have arisen before true snapping evolved.

In all alpheid tooth-cavity systems, a projection on the dactylus (movable finger) inserts in a cavity on the pollex (fixed finger). However, nonsnapping tooth-cavity systems take several forms. In *Thuylamea* (symmetrical claws; clade ONT, Fig. 4) a small, triangular tooth inserts into a small depression (Fig. 5a). In the unrelated *Nennalpheus* (symmetrical claws; clade ANP, Fig. 4) a broad, flattened tooth fits into a shallow cavity (Fig. 5e). In both *Vexillipar* (symmetrical claws) and *Bannereus* (asymmetrical claws; clade BV, Fig. 4), claws possess a broad bulge that fits into a deep groove (Fig. 5b–d; for more commentary see Cheliped Tooth Variation in the Supplementary Material available online). Finally, in *Amphibetaeus* (asymmetrical claws; clade ALF, Fig. 4), the voluminous major claw has a stout, flattened tooth that fits into a relatively deep cavity (Fig. 5f). This configuration resembles the true snapping claw, but *Amphibetaeus* does not snap (Coutière 1899).

The true snapping claw (Figs. 5g–i, 6a–c) apparently evolved only once in the Alpheidae (clade AS, Fig. 4), in contrast to Coutière's (1899) hypothesis that it evolved separately in *Alpheus* and *Synalpheus*. However, the snapping claw of *Synalpheus* (Figs. 5g, 6c) does differ from that of *Alpheus* by lacking linea impressa (molt suture, see Gordon 1957); adhesive plaques; and stiff, anteriorly curved setae on the distal surface of the plunger, the ''stamen-shaped sensilla'' (Fig. 5i) of Sullivan and Schmitz (1997), which are absent only in species of *Alpheus* with a secondarily reduced plunger (A. Anker, pers. obs.). Snapping claws in the minor clade RMP (derived from *Alpheus*) closely resemble those of *Alpheus* (Figs. 1l, 5h).

Adhesive plaques or discs (a term coined by Coutière 1899) are another intriguing feature of alpheid claws that have evolved multiple times (four to six times; online Appendix S2). They are polished, rounded discs on the dorsodistal palm margin and the nearby base of the dactylus (Figs. 5h, 6b) that enhance claw cocking. In the fully opened (cocked) position (Fig. 6a) these discs adhere strongly to each other (Ritzmann 1973), likely by Stefan adhesion, a peculiar property of liquids, which resist shear when confined to extremely narrow spaces (Denny 1988). This adhesion stores energy when the powerful closer muscles begin to contract, which enhances dactylus closing speed (Ritzmann 1973).

Curiously, adhesive plaques evolved in both snapping and nonsnapping alpheids. They are conspicuous (Figs. 5h,i; 6b) in the most diverse clade of snapping alpheids (*Alpheus*) but are notably absent in the less diverse clade (*Synalpheus*, Figs. 5g, 6c). Thus, adhesive plaques may have facilitated the greater diversification in *Alpheus* (>400 species vs. >150 species in *Synalpheus*, Fig. 4) by enhancing energy storage in the cocked claw (Fig. 6a). The importance of effective claw cocking is seen in some derived *Alpheus* that have evolved a cocking system not seen in any other Crustacea: accessory internal apodemes (tendons) in the palm. Taxa with accessory cocking tendons (e.g., *A. californiensis* of the *A. edwardsii* group, Fig. 5i) have apparently more powerful snaps, even though they have reduced adhesive plaques (Fig. 5i), compared to taxa without cocking tendons (e.g., *A. clamator* of the *A. macrocheles* group) that have well-developed adhesive plaques (Ritzmann 1974). Dactylar retention mechanisms of other *Alpheus* groups, as well as *Racilius*, *Metalpheus*, *Pomagnathus*, and *Synalpheus*, require investigation and could provide valuable new phylogenetic characters. Significantly, *Synalpheus* snap very powerfully, despite lacking adhesive plaques (A. Anker, pers. obs.), so they may possess an as yet undiscovered cocking aid. On the other hand, *Alpheus* with greatly reduced dactylar plungers, for example, *A. crockeri* (Fig. 1q), can still snap (A. Anker, pers. obs.). These two facts remain unexplained. Interestingly, well-developed adhesive plaques on the major claw also evolved at least once in the common ancestor of one nonsnapping clade
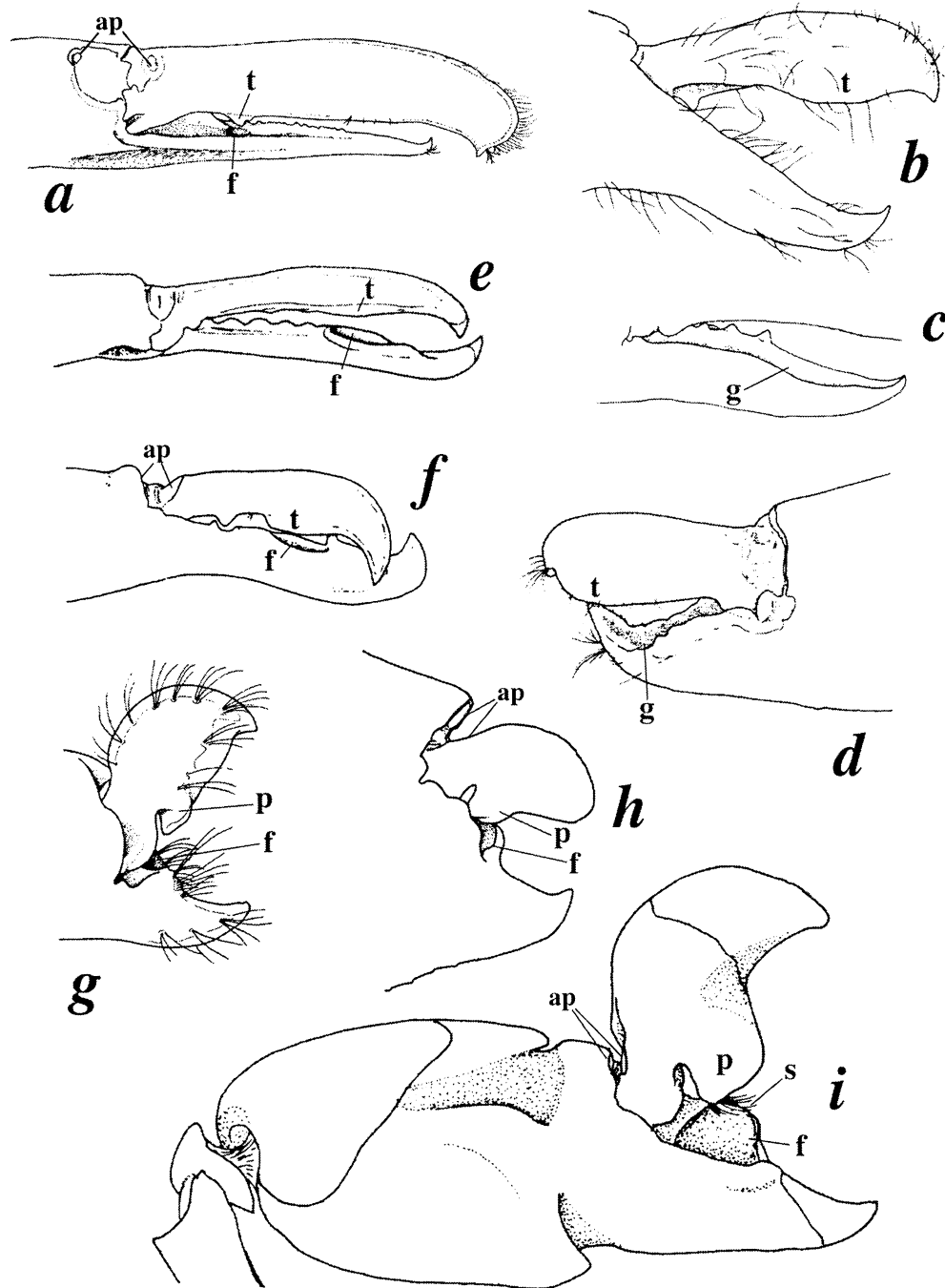
FIG. 5. Tooth-cavity systems on chela fingers of various Alpheidae: (a) *Thuylamea camelus*; (b,c) *Vexillipar repandum*; (d) *Bannereus anomalus*; (e) *Nennalpheus sibogae*; (f) *Amphibetaeus jousseaumei*, major claw; (g) *Synalpheus dorae*, major claw; (h) *Racilius compressus*, major claw; (i) *Alpheus edwardsii*, major claw. Abbreviations: ap, adhesive plaques; f, fossa (more or less deep cavity); g, groove; p, plunger; s, stamen-shaped sensillae; t, tooth (in a,f) or thickening/bulge (b–e). (a–f,h,i) Adapted from Anker (2001b); (g) adapted from Bruce (1988b).

(*Amphibetaeus*, cf. Fig. 5f, and some *Leptalpheus*, cf. Fig. 4w), and rudimentary adhesive plaques occur on both claws in three other nonsnapping clades (*Orygmalpheus*, *Thuylamea*, *Nennalpheus* + *Parabetaeus*), which further reinforces the impression of widespread parallel evolution of alpheid cheliped features.

Bruce (1988a) suggested the bulge-groove system in *Ban-nereus* may reflect the primitive condition for the plunger-fossa-type snapping mechanism in *Synalpheus*. However, our results do not support a close relationship between *Bannereus* (clade BV) and *Synalpheus* (clade AS) (Fig. 4). These two structures are rather dissimilar (cf. Fig. 5g) and furthermore, in *Synalpheus*, the plunger-fossa evolved on the major claw only, as opposed to both claws in *Bannereus*.
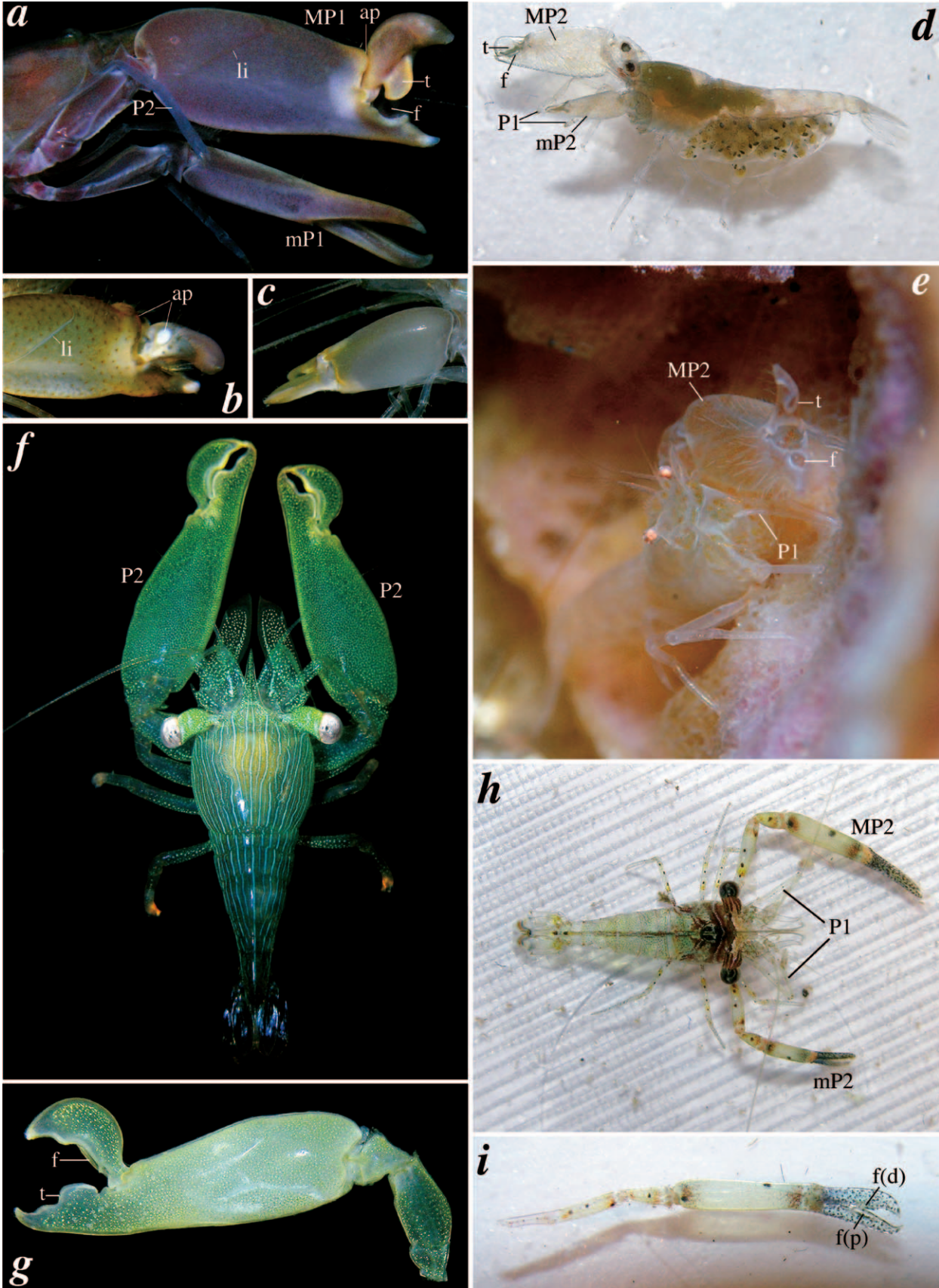
Orbital hoods and the evolution of snapping

Orbital hoods—anterior or anterolateral extensions of the carapace that partially or completely cover the eyes (Fig. 4; online Fig. S4)—are a unique and widespread character in alpheid shrimps. Our results support Coutière's (1899) hypothesis that orbital hoods evolved in concert with, and perhaps facilitated the evolution of, snapping claws. Eyestalks became short, stout, and juxtaposed early in alpheid evolution, and the frontal carapace naturally tended to conceal them. Even in *Yagerocaris*, the most basal alpheid, the eyes are partly concealed (Kensley 1988). In some alpheids (e.g., *Potamalpheops*, *Athanas*) eyes remain dorsally exposed or are partly concealed laterally or dorsolaterally by acute projections, called ''extra-orbital'' and ''infra-orbital'' teeth by Coutière (1899; Fig. 4e,f; online Fig. S4b,g,j). In most alpheids, the eyes are completely covered by the carapace and visible in dorsal view only through the quasi-transparent orbital hoods (e.g., Fig. 4g,h,j,k,l; online Fig. S4e–j,n,q). Orbital hoods attain the greatest development and morphological diversity in clade AS (*Synalpheus*, and especially in *Alpheus*; Fig. S4o–q, see also Banner and Banner 1975, 1982; Kim and Abele 1988), supporting Coutière's (1899) belief that more complex and sophisticated orbital hoods evolved in concert with snapping claws.

Orbital hoods are functionally significant for snapping alpheids. The snapping claw is commonly used in agonistic behavior: a snap close to the head could damage the eyes. Indeed, orbital hoods may provide some protection from an individual shrimp's own snap. Interestingly, in experiments with *Alpheus heterochaelis*, a species with a powerful snapping claw, Schmitz and Herberholz (1998) did not observe injuries among antagonists because intraspecific fights are largely ritualized. However, interspecific encounters often result in serious injuries, including loss of chelipeds or other appendages (A. Anker, pers. obs.) and possibly eye injuries. The great elaboration of orbital hoods in snapping alpheids suggests they are an essential accessory for effective snapping. The evolution of moderately developed orbital hoods in clade H, well before the origin of snapping claws (clade AS, Fig. 4), further suggests that they may actually have facilitated the evolution of the snapping behavior.

Snapping claws in other caridean shrimps

Snapping claws also evolved in the palaemonid subfamily Pontoniinae (Bruce 1976). The tooth-cavity systems of *Periclimenaeus*, which has over 50 mostly sponge- and tunicate-dwelling species, and a related genus (*Paraclimenaeus*) resemble alpheid snapping claws, except that they occur on the major second pereiopod (Bruce 1994; Fig. 6d,e), not the first as in alpheids. A snap by *Periclimenaeus* is weak compared to *Alpheus* or *Synalpheus* (A. Anker, pers. obs.). A different tooth-cavity system evolved on both second pereiopods in some *Coralliocaris* (Fig. 6f,g), which can snap with both claws simultaneously (A. Anker, pers. obs.). Even more remarkable, in *Coralliocaris*, the system is reversed compared to snapping alpheids and to *Periclimenaeus*: the tooth is on the pollex and the fossa on the dactylus (Fig. 6f,g). Yet another sound-producing mechanism occurs in *Periclimenella*. For example, *P. spinifera* possesses ''sound-producing fossae'' (Bruce 1994) on the major second cheliped (Fig. 6h,i); its snap is weak but audible (A. Anker, pers. obs.). A double-fossa system also occurs on the major second cheliped of *Climeniperaeus* (Bruce 1994), but whether this shrimp can snap is unknown.

In contrast to the single origin in alpheids (see above, The Alpheid Snapping Claw), parallel preadaptations in pontoniine shrimps yielded full-fledged adaptations for snapping in at least three distant lineages (*Coralliocaris*, *Periclimenella*, and *Periclimenaeus*, and perhaps also in *Paraclimenaeus* and *Climeniperaeus*). Notably, the evolution of snapping mechanisms in the Pontoniinae was not accompanied by protection of the eyes, which remain fully exposed (cf. Fig. 6d,f,h), as in most Caridea. A phylogenetic study of pontoniine shrimps would provide an independent test of the pattern of parallel preadaptation described above for alpheids (Fig. 4). In addition, studies of the physics of snap generation in pontoniine shrimp would provide some fascinating insights into the evolution of sound production by crustacean claws (Schmitz 2001).

Evolutionary significance of parallel preadaptation

Parallel preadaptation is merely a pattern of variation observed within a clade: multiple independent evolutionary origins of precursors (preadaptations) to what ultimately became a key innovation (adaptation) with a wholly new function in one or more clades. Thus, parallel preadaptation can only be recognized in clades in which a key innovation exists, and searches for other examples would therefore be most productive in these taxa (Nitecki 1990).

The causes of parallel preadaptation are presumably similar to those of parallel evolution, although debate continues over what these might be. Parallel evolution may be facilitated by (1) a tendency to evolve along genetic lines of least resistance, as often occurs with adaptive radiations (Schluter

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FIG. 6. Snapping mechanisms in Caridea: (a) *Alpheus formosus* (Alpheidae), Caribbean coast of Panama; major and minor chelipeds (first pereiopods); major chela cocked, exposing a large tooth (plunger) on the dactylus and a deep fossa (socket) on the pollex; (b) *Alpheus rugimanus* (Alpheidae), São Tomé, major cheliped showing adhesive plaques and linea impressa; (c) *Synalpheus recessus* (Alpheidae), Pacific coast of Panama, major chela, note absence of adhesive plaques and linea impressa; (d) *Periclimenaeus* sp. (Palaemonidae, Pontoniinae), Fiji; note *Synalpheus*-like facies; (e) *Periclimenaeus gorgonidarum* (Palaemonidae, Pontoniinae), Japan; chela of major second pereiopod widely opened exposing fossa on pollex and tooth on dactylus; (f) *Coralliocaris graminea* (Palaemonidae, Pontoniinae), Fiji; (g) same, second pereiopod with tooth on pollex and fossa on dactylus; (h) *Periclimenella spinifera* (Palaemonidae, Pontoniinae), Fiji; (i) same, major second pereiopod with fossae on both dactylus and pollex. Abbreviations: ap, adhesive plaques; d, dactylus; f, fossa; li, linea impressa; mP1, minor first pereiopod; MP1, major first pereiopod; mP2, minor second pereiopod; MP2, major second pereiopod; p, pollex; P1, first pereiopod; P2, second pereiopod. Photographs by (a–c) A. Anker and D. Poddoubtchenko, (d,f–i) A. Anker, and (e) S. Yamamoto (Izuzuki Diver 1998–2005).

1996); (2) a tendency to evolve in an analogous way along developmental lines of least resistance, in which significant phenotypic variants arise predictably and easily from minor genetic variants due to idiosyncrasies of development (Nijhout 1991; West-Eberhard 2003); or (3) developmental constraints (Wake 1991), where potential forms are limited by a paucity of workable genetic or developmental pathways.

The concept of parallel preadaptation suggests a potentially valuable test for a connection between two disparate evolutionary phenomena: key innovations and parallel evolution. If both arise from the same genetic/developmental processes, then parallel evolution (character convergence) should be more common in clades that exhibit key innovations. However, if key innovations reflect unique or contingent events (Vermeij 2006), then clades within which they have arisen should be no more likely to exhibit parallel evolution than other clades. Some tantalizing hints of parallel preadaptation exist for other key innovations, such as adhesive toe pads in arboreal geckos and anolis lizards (Russell 2002) and avian feathers (i.e., repeated evolution of featherlike branched structures in preavian reptiles; Prum and Brush 2002).

Perhaps the most important observation of all is that parallel preadaptation provides strong evidence that the precursors of key innovations, such as tooth cavity systems and (to a lesser extent) adhesive plaques in alpheid claws, are also adaptive. In clades that exhibit this pattern, putative preadaptations may be studied directly, which, in turn, should yield a better understanding of how key innovations evolve.

Future Studies

As with most phylogenetic analyses of this scope, uncertainties remain, and our hypothesis of alpheid relations would benefit from tests with independent larval or molecular data. Species of 15 of the 36 described genera could be collected easily. Unfortunately, some enigmatic genera, such as *Yagerocaris*, *Mohocaris*, and *Bannereus* are known only from a few specimens from relatively inaccessible habitats (e.g., submarine caves, deep-water hexactinellid sponges), so more specimens of them would be most valuable. In addition, seven new alpheid genera were unavailable at the time of our analysis. Two, *Coutieralpheus* and *Leslibetaeus*, appear to be relatively basal but their affinities remain obscure (Anker and Felder 2005; Anker et al. 2006). All of these new genera need to be considered in future studies. More detailed phylogenetic studies of relations within the two hyperdiverse genera, *Alpheus* and *Synalpheus*, are also needed, as are investigations of *Athanas*, *Leptalpheus*, *Betaeus*, *Automate*, and *Alpheopsis*, all of which were nonmonophyletic in our analysis. Our proposed sister-group relation of *Alpheus* and *Synalpheus* requires confirmation, especially in view of differences in orbital hood and snapping claw form between them (see Discussion, Tree topology, above).

Finally, several questions regarding key innovations deserve attention. First, what is the function of tooth-cavity systems in nonsnapping alpheids? Are they used for defense and prey subjugation, like the teeth on brachyuran crab claws (Vermeij 1987), or are they used to create jets of water? Water jetting would be a natural precursor to true snapping. Second, what function, if any, do adhesive plaques have in nonsnap-

ping alpheids? Do they enhance dactylus closing speed, as in snapping *Alpheus* (Ritzmann 1973), or do they have another function? Third, how often have the unique accessory cocking tendons (Ritzmann 1974) evolved in the snapping claws of different *Alpheus* lineages, and do they affect claw performance (e.g., higher sound pressure) or diversification (greater diversity in clades with accessory tendons)? If accessory cocking tendons affect performance and diversification, they may also qualify as key innovations. Finally, how widespread is parallel preadaptation in other groups? Other examples would offer further opportunity to study the functional significance of preadaptations.

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NOTE ADDED IN PROOF: Two new genera, *Acanthanas* and *Richalpheus*, appear to be closely related to *Athanas* and *Amphibetaeus*, respectively (Anker et al. 2006; Anker and Jeng 2006), and one of the two presently known species (A. Anker, pers. obs.), *R. palmeri*, also has a tooth-cavity system similar to that of *Amphibetaeus*, which would add yet another independently evolved tooth-cavity system to the above-discussed cases.

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APPENDIX 1

Characters used in the phylogenetic analysis of the Alpheidae. Abbreviations: A1, antennule; A2, antenna; AbdI-VI, first to sixth abdominal somite; AI, appendix interna; AM, appendix masculina; Md, mandible; Mx1, maxillile; Mx2, maxilla; Mxp1–3, first to third maxilliped; P1–5, first to fifth pereiopods, Pl, pleopod; T, telson; Ur, uropod.

1. Articulated, posteroventral plate on AbdVI: absent (0); present (1). 2. Posteroventral angle of AbdV: pointed (0); rounded (1). 3. Abdominal pleura length: covering bases of Pls (0); not covering bases of Pls (1). 4. AbdVI relative to other AbdI-V: distinctly elongated (0); not distinctly elongated (1). 5. Telson, anal tubercles: absent (0); present (1). 6. Preanal plate on sternum of AbdVI: acutely produced (0); rounded (1), bearing two acute teeth (2). 7. AbdVI, posterior projection: acute (0); rounded (1). 8. Mediosternal portion of AbdVI: not particularly depressed (0); depressed (1). 9. AM:

present in males, absent in females (0); present in males and in some females (1); present invariably in all males and females (2); absent in both males and females (3). Remarks: Several taxa, e.g., *Automate hayashii*, *Orygmalpheus polites*, and *Pterocaris typica* are presently known only from females. The presence of AM in ovigerous specimens is related to protandrous hermaphroditism in *Arete* and presumably also in *Aretopsis* and some species of *Athanas*. The situation appears to be different in *Salmoneus*, in which all specimens invariably bear AM. 10. Posterior margin of T: narrow triangular or medially pointed (0); slightly convex, not protruding (1); truncate (2); protruding rounded (3); with broad triangular median piece (4); with small median notch (5); with subrectangular median piece (6). 11. Mesial portion of transverse suture (diaeresis) of Ur exopod: forming deep cleft and with large tooth proximal to mesial margin (1); without these features (0). 12. Lateral tooth of transverse suture (diaeresis) of Ur exopod proximal to lateral spine: feebly developed, usually blunt, or absent (0); relatively large, projecting and acute (1). 13. Small spines on posterior margin of T: absent (0); present (1). 14. Transverse suture (diaeresis) of Ur exopod: unarmed (0); with minute subtriangular teeth from lateral margin to about midlength of exopod (1); with small rounded teeth from lateral margin to about midlength of exopod (2); with 3–7 large, triangular teeth proximal to lateral margin (3); with large, rounded teeth from lateral to mesial margin of exopod (4); with alternating larger and smaller spines (5); with two rounded or subacute lobes (6). 15. Small distal spines on Ur exopod: absent (0); present (1). 16. Ur exopod posterior margin: truncate (0); rounded (1). 17. Ur protopod: with one tooth or rounded lobe (0); with two distal teeth (1). 18. Carapace, anterolateral longitudinal suture (starting from anterior margin proximal to base of A2): absent (0); present (1). 19. Carapace, cardiac notch: absent (0); well developed (1); feebly developed (2). Remarks: Important alpheid synapomorphy (Chace and Kensley 1992). 20. Posterior margin of carapace below cardiac notch: straight or rounded (0); oblique (1). 21. Rostrum: well developed, distinctly delimited from frontal margin (0); small, not conspicuous (1); absent (2). 22. Deep concavity on frontal carapace margin exposing most of eyestalks: absent (0); present (1). 23. Orbitorostral process ventral to rostral region: absent (0); present (1). 24. Orbital hoods: absent (major portion of eyestalks remaining exposed dorsally) (0); present, partially covering eyestalks (anterior portion of eyes remaining visible) dorsally, but not anteriorly (1); present, completely covering eyestalks dorsally, but not anteriorly (2); present, inflated, completely covering eyes dorsally and partly anteriorly (3). Remarks: The degree of the development of the orbital hoods varies considerably among the genera. Furthermore, their derivation remains unclear. Coutière (1899) believed that the orbital hoods formed by the orbital projections sometimes bearing acute distal teeth (extracorneal teeth, see character 26 below) on their anterior margin. The orbital hoods of *Metalpheus* and *Racilius* are usually regarded as ''incomplete'' (imperfect compared to those of *Alpheus*); however, they are still better developed than the orbital hoods of other genera, such as *Synalpheus*, *Mohocaris*, and *Betaeus*. 25. Carapace, antennal tooth: present (0); absent (1). 26. Extracorneal teeth (acute or subacute, sometimes rounded projections on anterolateral margin of carapace, above eyestalks): absent (0); present (1). Remarks: Coutière (1899) believed that the extracorneal teeth participated in the formation of the orbital hoods and were secondarily reduced or lost in many taxa. The extracorneal teeth of *Athanas*, *Arete*, and *Potamalpheops* occupy a somewhat different position: they are situated more laterally to the eyes and therefore may be not homologous to the extracorneal projections of other taxa, which situated more proximally to the mediodorsal line, above the eyes. 27. Infracorneal teeth (acute projections of anterolateral margin of carapace, lateral to eyes): absent (0); present (1). Remarks: In *Arete* species the projections seen as infracorneal teeth could be homologous with extracorneal teeth (see also Coutière 1899). 28. Infracorneal region: straight, not projecting anteriorly (0); broadly rounded, sometimes convex, projecting anteriorly (1). 29. Long setae on anteromesial margin of eyestalks: absent (0); present (1). 30. Anteromesial margin of eyestalk: unarmed (0); with broadly rounded projection, extending beyond anterior margin of cornea (1); with triangular or lanceolate tooth (2). 31. Eyestalk: elongated and/or divergent (0); stout, subparallel, not juxtaposed

mesially (1); stout, parallel, juxtaposed mesially (2). 32. Ocellar beak: feebly developed or absent, not projecting (0); well developed, projecting between eyes (1). 33. Epistomial sclerite: unarmed (0); with small acute or subacute tooth (1), long, curved, acute tooth (2). 34. Tubercle of antennal gland: slightly protruding (0); strongly protruding (1). 35. Anteroventral margin of carapace: smooth, unmodified (0); with pronounced lip above anterior pereiopods (1). 36. Ur distolateral spine: situated approximately between 2/3 and 3/4 of exopod, not reaching beyond distal margin of exopod (0); inserted posteriorly, reaching to or beyond distal margin of exopod (1); inserted anteriorly, almost at midlength of exopod (2). 37. Mxp3 arthrobranch: present (0); absent (1). 38. Mxp2 podobranch: present (0); absent (1). 39. Number of mastigobranchs (straplike epipods) on P coxae: four: P1–4 (0); three: P1–3 (1); two: P1–2 (2); none (3). Remarks: The plesiomorphic state for all Caridea is a complete set of straplike epipods (Mxp3-P4) and setobranchs (P1-5). However, in some Alpheidae, as in some Hippolytidae (Bauer 1984), multiple independent reductions of epipods have occurred. 40. Small dorsal lobe (rudimentary exopod?) on basis of P1: absent (0); present (1). Remarks. All higher Caridea are characterized by the absence of exopods on P1–5. The small lobes present in several alpheid genera, and supporting the monophyly of the clade around *Athanas*, are possibly ''neoformed'' exopods. 41. Md palp: present (0); absent (1). Remarks: Contrary to Chace's (1988) statement, all examined specimens of *Aretopsis* had a mandibular palp. 42. Md palp distal article: not expanded (0); expanded (1). Remarks: ''?'' was assigned to all taxa lacking mandibular palp. 43. Md molar process: robust, subequal to incisor process (0); reduced or much smaller than incisor process (1); absent (2). 44. Md incisor process: not particularly expanded or reduced, usually with <10 small to medium-sized teeth (0); conspicuously expanded, distally with >20 minute teeth (1); somewhat expanded, distally with about 10–15 small teeth (2); not expanded, distally without or with reduced teeth (3); conspicuously expanded, asymmetrical, with elongated or distally truncate teeth (4); absent (5). Remarks: Some outgroup taxa lack Md incisor process. 45. Md incisor process, row of small lamellar teeth on distal margin: absent (0); present (1). Remarks: These teeth are present in *Thuylamea*, *Amphibetaeus* (cf. Coutière 1899), and apparently in *Leptalpheus* and *Fenneralpheus*; however, their microstructure and homology remain uncertain. 46. Mx1, ventral endite: not expanded (0); distally expanded (1). 47. Mx2, dorsal endite: divided in two halves by deep cleft (0); with small notch on distal margin (1); without any notch (2); reduced (3). 48. Mxp1 endopod (palp): not expanded (0); expanded (1). 49. Caridean lobe of Mxp1: very broad (0); rather narrow (1). 50. Mxp2 epipod: more or less rounded or oval shaped (0); elongated (1); absent (2). 51. Mxp2, endopod propodus: with lateral transverse suture (1); unadorned (0). Remark: This suture is often very inconspicuous and difficult to observe. 52. Mxp3 ultimate segment: with at least three terminal and subterminal spines, irregular or arranged in rows (0); distally unarmed (1); with one or two small terminal spines (2); with ring of strong terminal spines (3). 53. Paired strong spines along dorsal margin of Mxp3 ultimate segment: absent (0); present (1). 54. Mxp3 ultimate segment: subequal or shorter than penultimate segment (0); distinctly longer than antepenultimate segment (1); slightly longer than antepenultimate segment (2). 55. Mxp3, antepenultimate segment: slender, pediform, not covering underlying mouthparts (0); operculate, partly covering underlying mouthparts (1). 56. Mxp3 antepenultimate segment: unarmed (0); with triangular distodorsal projection (1). 57. Lateral plate on Mxp3 coxa: acute distally (0); reduced or poorly developed (1); elongated, acute or subacute distally (2); rounded (3); oval shaped (4). 58. Mxp3 exopod: absent or short, reaching at most to middle of antepenultimate segment (0); long, reaching at least to distal third (often beyond distal margin) of antepenultimate segment (1). 59. Long flexible setae on dorsal margin of Mxp3 exopod: absent (0); present (1). Remarks: A feature probably present in most Alpheidae. 60. Mxp3 penultimate segment: distinctly longer than wide (0); as long as or only slightly longer than wide (1). 61. Thickened, distally blunt setae on Mxp3 ultimate segment: absent (0); present (1). 62. Mxp3 antepenultimate segment: entire (0); subdivided by distinct subproximal suture (1). 63. Stylocerite length: not reaching middle of first segment of antennular peduncle (0); clearly exceeding distal

margin of first segment of antennular peduncle, sometimes reaching beyond second segment (1); reaching to but not exceeding distal margin of first segment of antennular peduncle (2); reaching only to middle of first segment of antennular peduncle (3). 64. Stylocerite: not pressed against A1 first segment, laterally more or less convex (0); tightly pressed against A1 first segment, laterally not convex (1). 65. A1 lateral flagellum: without distinct accessory ramus (0); with accessory ramus composed of more than two segments (1), with accessory ramus composed of more than two segments (2). Remarks: The apparent absence of accessory ramus in *Alpheus obesomanus* group, *Arete borradailei*, *Automate*, and *Metalpheus* could be due either to its ancestral absence or to its partial fusion with the main ramus. 66. A1 lateral flagellum divided into main ramus and accessory ramus: distally to third segment (0); at first to third segment (1). Remarks: In all taxa lacking accessory branch (cf. character 65), the aesthetascs are situated distally to the third segment; therefore, the character state for these taxa was scored as 0. 67. A2 flagellum in cross-section: not particularly robust or compressed, cylindrical (0); robust, flattened (1). 68. Ventromesial carina of A1 first segment: with (0), without (1) variously shaped acute or blunt tooth. 69. Dorsomesial carina of A1 first segment without (0), with (1) row of small spines. 70. A2 basicerite: not particularly enlarged or stout (0); enlarged, stout (1). 71. A2 scaphocerite blade: well developed, with at most small incision proximal to distolateral spine (0); well developed, with deep cleft (1); reduced (2). 72. P1: not enlarged in either sex (0); enlarged in both sexes, much more robust compared to P2 (1); enlarged in males, slightly enlarged or not enlarged in females (2). 73. Right-left P1 symmetry: P1 equal or subequal in size, symmetrical or subsymmetrical in shape (0); strongly asymmetrical in shape and very unequal in size, with major cheliped much longer and more robust than minor cheliped (1); strongly asymmetrical in shape and very unequal in size, with minor cheliped less robust but equal in length or longer than major cheliped (2). Remarks: P1 polymorphism and sexual dimorphism are common in the genus *Athanas*. In many taxa the asymmetry is very slight, for example, restricted to differences in armature of chelal fingers (state 0). 74. Major P1 (or one of P1) palm: laterally compressed, bluntly projecting anteriorly, overhanging propododactylar articulation (1); without these features (0). 75. P1 chela, adhesive plaques: absent (0); well developed on both P1 (1); well developed on one (major) P1, absent on minor P1 (2); feebly developed (sometimes inconspicuous) on both P1 (3). 76. Cheliped palm: not excavated (0); ventrally excavated or depressed on one (major) P1 (1). 77. P1 merus, ventral excavation or depression: absent, at most flattened (0); present (1). 78. P1 orientation: not inverted, dactylus in dorsal or lateral position (0); inverted, dactylus in ventral or ventrolateral position (1). 79. Mesial rows of grooming setae on P1 carpus: present (0); absent (1). 80. Flattened mesial subtriangular projection on P1 coxa: absent (0); present (1). 81. Cutting margin of P1 fingers: unarmed or with simple armature (0); with molar-shaped tooth (plunger) on dactylus + deep rounded depression (fossa or socket) on pollex present on one (major cheliped), no other armature on cutting edges (1); subdistal truncate tooth on dactylus + deep rounded depression on pollex present on one (major cheliped), along with some proximal teeth (2); distal thickening on dactylus + shallow rounded depression on pollex present on both chelipeds, along with some proximal teeth (3); distal thickening on dactylus + deep groove along cutting edge of pollex present on both chelipeds, no other armature on cutting edges (4). 82. Stamen-shaped sensillae (setae on distal margin of plunger of major chela): absent (0); present (1). Remarks. These setae are present in the vast majority of *Alpheus* (except those with a reduced plunger), *Metalpheus*, *Pomagnathus*, and *Racilius*, but are absent in *Synalpheus*. All taxa lacking dactylus plunger were exceptionally coded with 0 to avoid too much influence of the ''lacking data.'' 83. Teeth armature on cutting edges of P1 fingers: absent or feebly developed (0); consisting of proximal serration on one (major or minor) cheliped (1), serration along almost entire margin on one (major) cheliped (2), irregular teeth on both chelipeds (3), large teeth, often with hiatus on one (major or minor) cheliped (4). 84. Major (or one of) P1, longitudinal groove extending laterally from dactylar articulation to about middle of palm: absent (0); present (1). 85. P1 palm, slight longitudinal depressions laterally and

mesially: absent (0); present (1). 86. Linea impressa (oval-shaped suture on proximodorsal portion of cheliped palm): absent (0); present (1). Remarks: The linea impressa is well developed only in *Alpheus*, *Metalpheus*, *Pomagnathus*, and *Racilius*, and is only indicated in some species of *Arete* and *Synalpheus* (Coutière 1899). 87. P1 carpus: elongated, cylindrical in both chelipeds (0); short and stout, more or less cup shaped in both chelipeds (1), short, cup shaped in major cheliped; elongated, subcylindrical in minor cheliped (2). Remarks: Strong sexual dimorphism and polymorphism in some species of *Athanas* and *Salmoneus*. 88. P1 carpus, shape: not subrectangular (0); both subrectangular, with subacute processes (1). 89. Major P1 palm, transverse groove on inferior margin, proximal to pollex: absent (0); present (1). 90. P1 palm ornamentation: without transverse grooves or depressions on superior margin (0); major cheliped with transverse groove on superior margin, proximal to propodo-dactylar articulation connecting lateral and mesial groove (1); major P1 with transverse groove on superior margin, proximal to propodo-dactylar articulation, not connecting lateral and mesial grooves (2); both P1 with deep transverse groove, slightly more distant from propododactylar articulation (3). 91. P1 merus: not or only slightly projecting, blunt (0); distodorsally projecting, acute (1). 92. P1 ischium, dorsal rows of spines: absent (0); present (1). Remarks: These spines are sometimes situated on blunt projections, for example, in *Arete*, *Athanas*, *Alpheopsis*, and *Automate*. 93. Cheliped fingers: not balaeniceps (0); balaeniceps (1). Remarks: The balaeniceps or sub-balaeniceps condition of P1 fingers evolved independently in several *Alpheus* lineages and is also subject of sexual dimorphism. 94. P1 dactylus shape: not compressed or expanded (0); laterally compressed and dorsally expanded (1); laterally expanded, dorsally compressed (2). Remarks. State 1 is possibly a homoplasy between two species of *Alpheopsis* sensu lato (*A. cortesiana* and *A. harperi*, both not in ingroup), *Notalpheus imarpe*, and to lesser extent *Thuylamea camelus*. 95. Chelae of both P1 with minute, flattened and rounded granules: absent (0); present (1). 96. Ventral margin of palm of one (major) or both P1 with one or several tubercles: absent (0); present (1). 97. P1 ischium mesially with stout blunt or subacute projection: absent (0); present (1). 98. P1 finger tips: mostly calcareous (0); large portion corneous, amber colored (1), Remarks: Synapomorphy of *Synalpheus*, occurs also in some other taxa (some *Alpheopsis*). 99. P2 chela: propodus not elongated, at most twice as long as fingers (0); considerably elongated, more than 3 times as long as fingers (1); moderately elongated, about 2.5 times as long as fingers (2). 100. P2 dactylus and propodus: distally simple, acute (0); distally bearing strong, hooks (1). 101. P2 dactylus and propodus: with tufts of simple, distally curved setae (0); with several tufts of stiff, elongated setae (1); with tufts of elongated setae near finger tips, some arranged in fans (2). 102. P2, second carpal segment: shorter or subequal to first segment (0); longer than first segment (1). 103. P3 merus: with 2 or more spines (0); ventrally unarmed (1); with 1 spine (2). 104. P3 dactylus: ventrally armed with spines (0); biunguiculate or triunguiculate, distal portion bearing ventrally secondary unguis not separated from main article (1); multiunguiculate, with distal portion separated from main article by suture, distal portion unarmed, proximal portion ventrally serrated with several small secondary unguis (2); multiunguiculate, with distal portion separated from basal portion by suture, distal portion with larger secondary unguis, proximal portion ventrally serrated with several small secondary unguis (3); simple, with ventral margin unarmed (4). Remarks: The dactylus is highly specialized in one of the outgroups (coded with ''?''). 105. P3 dactylus, proximoventral small hinge sclerite: absent (0); present (1). 106. P3 propodus: with more than 2 strong spines (0); unarmed or with 1 or 2 small spines (1). 107. P3 carpus, distoventral spine: absent (0); present (1). 108. P3 ischium: with at least 1 ventral spine (0); unarmed (1). 109. P5 propodus: without grooming brush (0); distolaterally with grooming brush composed of more than 4 rows of stiff setae (1); with grooming brush composed of at most 3 rows of stiff setae (2). 110. Conspicuous but concealed projection, situated laterally to basis of eyestalks: absent (0); present (1). Remarks: As pointed out by Coutière (1899) this concealed projection appears to be present in all alpheids, and is more conspicuous in some taxa, such as *Amphibetaeus*. 111. Mxp1 palp (endopod): segmented (0); entire (1). 112. Rounded elevation on transverse suture (diaeresis) of Ur exopod: present (0); absent or with very feebly developed (1). 113. A2 scaphocerite, distolateral tooth: well-developed (0); small, inconspicuous (1); reduced (2). 114. Ventral rugosities and small spines on palm of at least one (major) P1: absent (0); present (1). 115. Anterodorsal region of carapace: not delimited (0); well delimited from rest of carapace (1). 116. P1 merus, acute distomesial tooth: absent (0); present (1). 117. P3 merus, acute distoventral tooth: absent (0); present (1). 118. Carapace surface: glabrous (0); with pubescence formed by dense or scarce erect setae (1); with pubescence formed by fine, hairlike, elongated setae (2). 119. Ur exopod length: subequal or only slightly shorter than endopod (0); distinctly shorter than endopod (1). 120. T lateral constriction: absent (0); present (1). 121. A2 carpocerite: short, not reaching distal third of scaphocerite (0); slightly exceeding or subequal to scaphocerite (1); distinctly exceeding scaphocerite (2). 122. P1 fingers distally: acute (0); bifid, with small subdistal tooth (1). Remarks: Bifid finger tips characterize most *Potamalpheops* species and *Yagerocaris*, but also the minor P1 of many *Synalpheus* species (coded with ''0'').

APPENDIX 2. Character matrix used to conduct the phylogenetic analysis of the Alpheidae. Unknowns indicated by "?"; inapplicables indicated by "-"; polymorphisms indicated in brackets, for example, (01).

Alpheopsis aequalis
110101100101000010100002100000112100(01)10000000000010020000110011011100000100000100000000001400001111100000(01)0010

Alpheopsis trispinosa
1101011001010000101000011100001110000000000001001000001100101100101100000100300000000000001400101111100000020

Alpheus cristulifrons
0101111001011100001010131000001100010000000000000100100000111010001011000110001000000001140000111100011100020

Alpheus cylindricus
0101111001001001010010031000001100000100000000010100000111010001011010110020000000001100111100010000010

Alpheus diadema
01011110011010100010001310000011000000100000020000100010000011101202000001110100011100011101000000001400001110001110010

Alpheus edwardsii
01011110010000000010013100000110000010000000000000100010000011101202000001110100011100011101000000001400001110001110010

Alpheus macrocheles
01011110011010001000131100021100010100002000001100100000110100011101202000001110100011100011101000000001400001110100010

Alpheus rapacida
01011110011000000010003100000110000010000000110000111101202000001110100011100011101000000114000011100010010010

Alpheus saxidomus
010101100201000000020(12)0031000001100010100000000001001000001100130000000211010001011010110000000000000011400011110010000020

Alpheus sulcatus
010111100110000000100013110002110000100000000001001002020000011101000010110100010101010000000001400001110011010010

Amphibetaeus jousseaumei
0101111010000000010200210000110?????0010000001000??100000011021001020000010000000000001400111?1?100000010

Arete indicus
11011010110000000010000011000001000001121000200101000000001011011010100000100000001000(34)00010000100001000001100102111000000000000

Arete borradailei
10010110010000010100001110000001310101001010010000011101100010101000000140112112110000000010

Aretopsis amabilis
11011110110000001000001000010001210002001010010010111101101010000011000011000400010000000110001111100000000010

Athanas dimorphus
1001011001000000010000011100010000011111000000010020000011001101000002000010100030000(01)000010000000000014000110100000010000

Athanas nitescens
100101100100000010000011100010000111100000010000111100010110100010002000001100110100000020000001100300000(01)000010000000001400001101000010000

Athanas squillophilus
11010100010000000100000110000100000111100000110001001010000011001101110000011001101000000000001400100111000000000020

Athanopsis australis
110101100100000010100011100001000001111000000110010010000011001101110000110000024001010100000000010

Automate dolichognatha
0111011032006000101100100000200000000000000010000110040010210001100110000010004000100001140000100000000000120

Automate evermanni
01110110320000000010111001000002000000000000000100011000100401021000110011000000100004000100001000000001140100010000000001120

Automate hayashii
011101107?10006000010000010000120000001000000000010001100400100120000010001140000110000000120

Bannereus anomalus
0101011001000000001020021000010000000130100000110030200010001201000000110000010400000100000000000212013000111111000001010

Batella parvimanus
0001010100000000011000211000010100001301030001200020011100110110100001000000100030001000000000011201200001111000000000

Bermudacaris harti
01110110010000000102000100000000000000000000010001100401001200000011101010100101000001140000111100000011020

Betaeopsis aequimanus
0100001001000000001020021000020120000000011101010101010000000011000011211000000020

Betaeus australis
110111110300020010020021000021100000100000000110010101000110001000001100030001000000000024001111110000000010

APPENDIX 2. Continued.

Betaeus harfordi
1101111103000200101020020002110000110000000001001000001101010100011001101010100011000011003000100010000000000210111110000001020

Betaeus jucundus
110101110100000000001020021000001000001100000000000011101101010001110101010001100001100000024001011110000000010

Coronalpheus natator
0111011001000600000100000010000110000000000000001100110040100120000010011000001140000111400000001020

Deioneus sandizelli
10010011010000000110000211000010000000001100000020011001101100000120010010000(24)0001000000000001400011010000000000

Fenneralpheus chacei
1101111110310000111102002100001100010000000010000010000211010010211010021110100011001001100200010002000100000000000001400011111000001020

Leptalpheus axianassae
110101(01)10310000111102002100001100010000100001000011000002110011201010000001102100100000000000001400101111000000020

Leptalpheus forceps
1101011103100001111020020000011000100010000100100000021101121101000011000011001001001000010000000001400101111000001020

Metabetaeus minutus
000001100201000000100002110000100000110000000001001101000000100000010000000010000000000001400011111000000010

Metalpheus rostratipes
0101111001010010001000130000011000110011010010010011110002020000111111000010101100010000000110001110011000010

Mohocaris bayeri
01000100010000000010200210000010100000100000000010010000110001001002010000010000002400000110000000020

Nennalpheus inarticulatus
01010101010000000100001110000100000001000010000011001200100000000140001030100011000000000140100111100000001020

Nennalpheus sibogae
100101010100000000010000211000010100000000010000001000011001200100000000140100111100000000020

Notalpheus imarpe
11010100010000000100001110000100000010000000100120100000010100000001401001011000000001400101111000000020

Orygmalpheus polites
010101100100000000102002100000100001000000000001100000011010000010100000001401001100000000020

Parabetaeus culliereti
10010100040000000010(02)00021100000100000000010011010000000100110100000001003000100030001000000011100000000000

Parabetaeus euryone
1101010004000000000100002110000101000001000000110010110000001003010100(23)0001000100000000000004000011110000000000

Pomagnathus corallinus
01011110010010002000131000001100010130011110100010101111010202000111011000010101100010000000011100011011100000010

Potamalpheops monodi
110001000100010001000001101110100000010100000001001101000000000000004000011010000000001

Potamalpheops pylorus
11010110010000010000011011010100001101100000110110101101100000011000000100030001000000040000110100000000011

Prionalpheus triarticulatus
110101000101030000100002100000112100013012400301201000011010101101110000011000111011101000010010

Pseudathanas darwiniensis
110101000100050000100000110000100000130000000110110000201100400010000100010000001400101010000000010

Pterocaris typica
0101011001000000000010010000000013000001300000200010010000011101202000000111110001011000101100011000000010

Racilius compressus
0101111001010000000(12)000131000001100000100000020000100000000311001101110000110000010020000000000001400001111000000010

Salmoneus serratidigitus
00010101250000001110000211000010000001000000021100000021100011010000100000000000000001400001101000010000

Stenalpheops crangonus
110011111010004100010100010000100000130000000101010101010010021100000101000002000100000201000011100011100000100000020

Synalpheus herricki
0101011030101000000100012110000110000130000000010110100100210000100100101011001111000010000020

Synalpheus stimpsoni
0101011103101000000100002110000113000000130000000001002000000101011100010011110001112100001000010000020

APPENDIX 2. Continued.

Thuylamea camelus
0110110103000000010(02)00(02)10000010000001000010100000110012110000001000100010101000001100000001401001100000000020

Vexillipar repandum
0101011001000000001100021100010000000110103000110000200111001201000000100000112022000111100000000010

Yagerocaris cozumel
00000201260000000001000001000021100000100000000001100000000100011010000000000000000000000024000011100000010001

Lysmata
00000000000000000000000000000000000001000000000010500000000000000000000000000000000000000100000000000000001

Ambidexter
010000100000000000000000000000000100010500000000000000000000000000000000000000000000000000000

Pandalopsis
00000000000000000000000000000000000000001000000000000000000000000001000000000000000000000200000000000000000

Ogyrides
010001100000000000000000010000000000113000000000000001000000100000000010000000000000000001?00000000000000000000