level patterns – those found at the regional or even intercontinental level. Our greatest lack of understanding is at the intermediate level, i.e. within collections of organisms that we choose to label communities. Part of that ignorance no doubt stems from a failure to decide what a community really is but it may be partly due to our current inability to understand how ecological and evolutionary processes might interact.

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The Evolutionary Biology of Insect Hearing

James H. Fullard and Jayne E. Yack

Few areas of science have experienced such a blending of laboratory and field perspectives as the study of hearing. The disciplines of sensory ecology and neuroethology interpret the morphology and physiology of ears in the adaptive context in which this sense organ functions. Insects, with their enormous diversity, are valuable candidates for the study of how tympanal ears have evolved and how they operate today in different habitats.

Insect tympanal ears (i.e. those using a tympanic membrane or 'eardrum') are specialized organs designed to detect distant, faint sounds transmitted through air or water. Tympanal ears (the only type covered here) are located in at least ten different places in a diversity of insect taxa (Fig. 1a) – this strongly suggests polyphyletic origins. Some ears, such as the abdominal organ of the grasshopper and the tibial organ of the cricket, have been well described in the literature, because they are conspicuous and belong to insects with well-known acoustic behaviours. Other, more obscure ears, such as the 'cyclopean' ear of the praying mantid[1] and the prosternal (thoracic) ear of the parasitoid fly[2,3], have only been described recently with the aid of modern techniques. Considering that tympana have been identified in only 5% of all insect orders, we expect that many more insect ears await discovery.

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Morphological evidence of auditory evolution

Why have tympanal ears evolved independently so many times, and in such different locations? Although it has long been thought that insect ears evolved from internal proprioceptors[4] (sensory structures detecting body movements), it is only recently that this hypothesis has been examined experimentally. Comparative studies suggest that the invertebrate nervous system has been conservative in its evolution – homologous neurons exhibit few interspecific differences compared to peripheral, nonneural structures[5,6]. Such conservatism is useful for testing evolutionary hypotheses regarding the insect nervous system.

One way of studying the evolutionary origins of the insect auditory system is by examining the tympanal organ homologues of earless taxa and assuming that these species represent the ancestral deaf

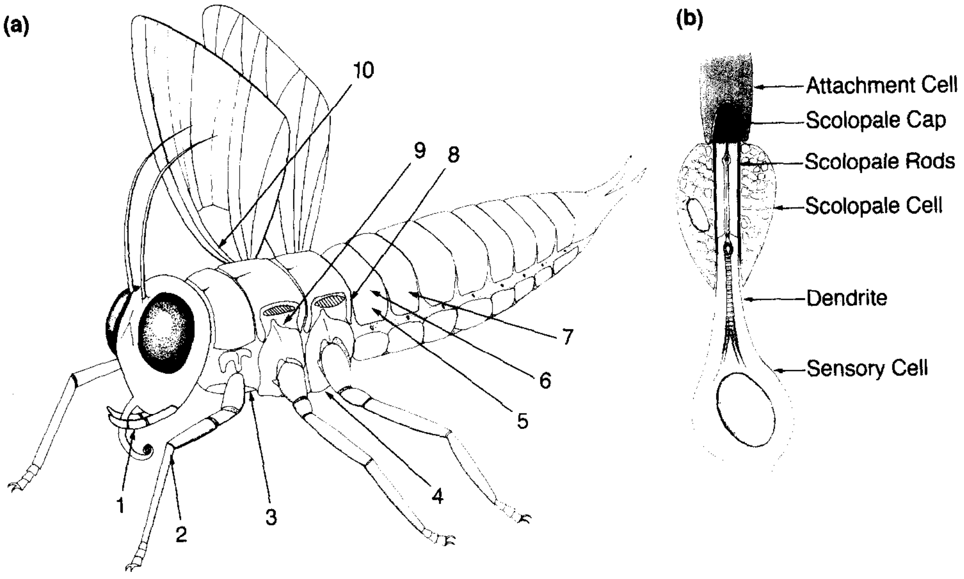


Fig. 1. (a) The ten regions where tympanal organs have evolved within insect groups. There is diversity in both the locations and complexities (from the single-celled notodontid moth ear, to that of the cicada, which possesses over 1000 auditory neurons). Despite this, all are fundamentally alike: each is comprised of a thinned region of cuticle (tympanal membrane), an air sac which allows the membrane to resonate to sound-induced pressure changes, and a chordotonal organ (CO). COs are a type of insect mechanoreceptor which are widely distributed throughout the body where they may function as either sound or body-movement detectors. Each CO consists of one to several hundred structural units called scolopidia. Each scolopidium in turn consists of an assemblage of three cell types: 1–3 sensory neurons; a scolopale cell with an extracellular cap or tube located at the distal end of the dendrite; and one or several attachment cells. Numbers refer to ears described on insect bodies: 1. Lepidoptera; Sphingoidea; 2. Orthoptera: Ensifera; 3. Diptera: Tachinidae; 4. Mantodea: Mantidae; 5. Lepidoptera: Geometroidea and Pyraloidea; 6. Orthoptera: Acrididae; 7. Hemiptera: Cicadidae; 8. Lepidoptera: Noctuoidea; 9. Hemiptera: Corixidae; 10. Neuroptera: Chrysopidae. (b) A typical tympanal scolopidium, characterized by only one sensory cell per scolopidium (monodynal), and a distal dendritic segment which is tightly associated with a scolopale cap (mononematic).

condition. Moths offer a special opportunity for this method: members of the superfamily Noctuoidea possess metathoracic tympanal ears (used for the detection of the echolocation calls of hunting bats), which are presumably derived from the atympanate condition represented by extant earless Lepidoptera (e.g. Saturniidae). Sensory cells (Fig. 1b) homologous to those in the noctuoid ear have been identified in several atympanate Lepidoptera[7,8]. These nonauditory neurons are in the same region as the noctuid moth ear sensilla, near the metathoracic wing-hinge, and appear to act as proprioceptors monitoring movements of the hind wing during flight and preflight warm-up. Structural comparisons between the auditory chordotonal organ (CO) and its proprioceptor homologue reveal few differences[9], and the proprioceptor even responds to intense, low-frequency sounds[7]. The major differences between the two organs exist in nonneural structures: enlarged respiratory chambers (the tympanic air sac), thinned cuticle (the tympanic membrane) and mechanical isolation from body movements (the tympanic frame).

Similar comparisons of tympanal ear prototypes have been made in other atympanate taxa. These include the prosternal proprioceptive CO of *Drosophila* spp., a proposed homologue of the tachinid fly tympanal organ[2], the pleural CO of the primitively atympanate grasshopper, *Heide amiculi*, proposed homologue of the abdominal grasshopper tympanal organ[10], and possibly the 'crista acustica' of *Phasmodes ranatriformis*, the proposed evolutionary prototype of the ensiferan tibial tympanal organ[11].

In addition to comparing tympanal organ homologues between taxa, we can examine the ear homologues of atympanate body segments of the same animal (serial homology). Comparative developmental studies[10] indicate that the abdominal ear of short-horned grasshoppers (Acrididae) is homologous to the proprioceptive pleural COs of the six other abdominal segments as well as the wing-hinge COs of the thoracic segments. It also appears that the tibial ear of crickets and katydids (bushcrickets) is homologous to mechanoreceptive units in these insects' meso- and metathoracic legs. The comparative neuroanatomical data described above suggest that insect tympanal organs have evolved from proprioceptors, and that the transition between the two forms involved minimal neural changes. Insect ears, apparently, are easy to make. Since proprioceptive COs are widely dispersed throughout the insect integument (Fig. 1), this may account for the diversity of positions in which tympanal organs are found in insects.

When considering why a tympanal organ evolved in a particular region, we can again use comparative data. It is likely that only the nerve cells of those proprioceptive COs whose primitive function preadapted them for high sensitivity were good candidates to evolve into auditory receptors. For example, in crickets and katydids, the present-day auditory homologues of the meso- and metathoracic legs are very sensitive to faint substrate vibrations[12], suggesting that these types of COs were more easily converted into auditory receptors than detectors of large amplitude leg movements. Similarly, if the pre-auditory function of the ancestral moth wing-hinge CO was to detect small-amplitude wing vibrations, such as those produced during flight warm-up, it may have been easily converted into a detector of high-frequency sounds once echolocating bats became a potent selective force.

Another factor influencing which CO proprioceptors evolved into

Glossary

dB: decibel, the logarithmic unit describing the intensity of sounds usually stated in terms of a ratio with reference to some arbitrary value (e.g. minimum human auditory threshold = 0 dB = 20 μPascals)

kHz: kilohertz (1000 cycles/second), the commonly used unit describing the frequency (pitch) of a sound, especially for human ultrasonics (> 20 kHz)

BF (best frequency): the frequency that an animal (or part of its auditory system) hears with the minimum intensity

PF (peak frequency): the frequency of a complex sound that contains the most power

Auditory receptor (*sensillum*): the nerve cell that acoustic energy first encounters and the one responsible for encoding the sound into action potentials to be interpreted by the central nervous system

Proprioceptor: a sensory organ or cell designed to monitor body movements (e.g. joint positions) tympanal receptors was the organization of their neurons within the ancestral central nervous system (CNS). Sensory cells send their axons into the CNS where they communicate with interneurons and motor neurons to produce behaviour. The conservative organization of the CNS has resulted in auditory sensory projections of such widely diverse insects as katydids, cicadas and moths sharing the same anatomical regions[13]. The CNS projections of ancestral receptors may have influenced their evolutionary potential as auditory cells depending upon their proximity to the neurons responsible for eliciting the derived adaptive behaviour. For example, the noctuid moth uses its metathoracic ear to rapidly trigger a series of evasive flight manoeuvres; a thoracic CO that already communicated with flight motor neurons would have been a better auditory candidate than an abdominal CO whose receptor endings were further from flight control centres.

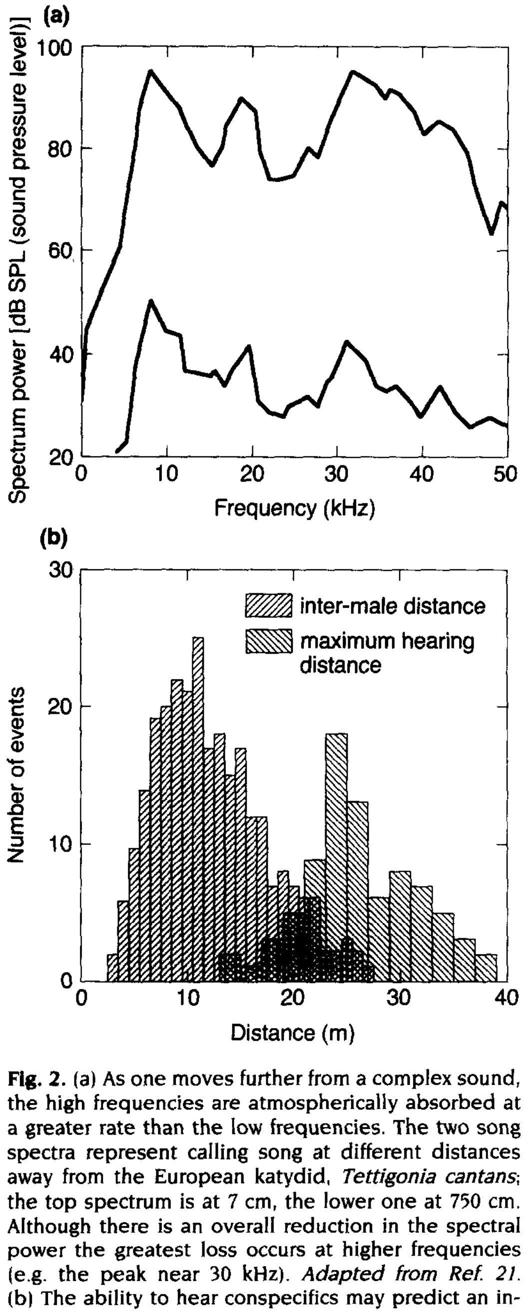


Fig. 2. (a) As one moves further from a complex sound, the high frequencies are atmospherically absorbed at a greater rate than the low frequencies. The two song spectra represent calling song at different distances away from the European katydid, *Tettigonia cantans*; the top spectrum is at 7 cm, the lower one at 750 cm. Although there is an overall reduction in the spectral power the greatest loss occurs at higher frequencies (e.g. the peak near 30 kHz). *Adapted from Ref. 21.* (b) The ability to hear conspecifics may predict an individual's spacing behaviour. The inter-male distance is that of the singing Australian katydid, *Mygalopsis marki*. The maximum hearing distance refers to the point at which one of this katydid's CNS neurons no longer detects conspecific calls. The inter-male distance is less than the maximum hearing distance, suggesting that it is the high frequencies of the call that determines male spacing behaviour. Whether it is this neuron alone that sets the male's spacing is unknown but examinations of the physiological hardware underlying an animal's mating behaviour can provide valuable insights into the mechanisms that govern that behaviour. *Adapted from Ref. 20.*

Adaptive function of hearing

Sounds provide the opportunity for animals that can detect them (the receivers) to make long-range decisions about the origins of those sounds (the senders) without actually contacting them. For short-lived organisms like insects with their plethora of potential predators, selection should favour those individuals who minimize their time and energy expenses with ears that can accurately determine the position, distance and identity of a sound's sender. Whether the physiological reality of insects' ears has lived up to their theoretical expectations, however, remains an open question (See Box 1).

Where are the sounds?

Mammals locate sounds by comparing the side-to-side differences of their intensity (i.e. body shadowing), time of arrival and/or waveform phases; such acoustic cues are severely compromised by the small size of most insects' bodies. While orthopterans have evolved adaptations that manipulate the physical properties of sound waves to enhance binaural differences[14], other location cues exist in the patterns of sounds. Many insects listen for the echolocation calls of bats[15] and as this predator homes in on its target, it increases the pulse repetition rate of its calls. This cue indicates a very close bat and triggers defences in tiger moths[16] and praying mantids[17]. Insects may have specific sensitivities to pulse repetition rate cues[18,19] to which some bats, in turn, may have evolved acoustic counter-manoeuvres (e.g. reducing the intensity of their close-range calls or eliminating them altogether).

Cues about the position and distance of a sound's origin also exist in its frequency structure. Since high frequencies attenuate more than low frequencies over distance (Fig. 2a), an ear equipped with a template of a sound's entire spectrum should be able to estimate the sender's distance independent of its intensity. Recent field studies suggest that katydids can physiologically determine the distance of singing males[20,21] (Fig. 2b) but experiments also suggest that the high-frequency information in those sounds might be limited at long distances[22,23]. This would have the effect of forcing receivers (e.g. receptive females) to move about more to get a 'fix' on the sounds, thereby increasing their conspicuousness to predators[24]. An example of such a threat are the insectivorous bats that, rather than attacking their prey in the air, locate them on the ground or vegetation (surface gleaning) by listening for their mating or movement sounds. In Panamá, the eared insects that surface-gleaning bats prey heavily upon, such as katydids, do not appear to hear the echolocation calls of the bats as they attack[25]. Similarly, a North American bat, *Myotis septentrionalis*, when surface gleaning, emits echolocation calls that are almost completely inaudible to sitting moths[26]. Although surface gleaning may impart a sizable predation pressure, its relative rarity within bat communities appears to have resulted in an insufficient selective force to cause auditory adaptations in insects. Instead, insects have responded with indirect ('passive') defences such as refined acoustic location of conspecifics[23] (thus reducing the receiver's requirement to move), the use of nonacoustic forms of calling[25] and a reduction in movement or the restriction of it to areas or times separated from potential predators (compare with the defences of earless moths[27]).

What are the sounds?

Interspecific recognition. It is expected that eared insects identify the sounds they encounter for survival (e.g. predator versus prey) and reproductive (e.g. conspecific versus heterospecific) purposes. Hypotheses about the neural hardware of conspecific recognition in crickets range from relatively coarse identification abilities to refined, genetically determined recognition circuits[28]. These studies further demonstrate the importance of time-structure cues for species recognition[29,30]; animals competing with background noise (e.g. leaves rustling) or the sounds of heterospecifics should exploit this parameter to improve the efficacy of their own sounds[22]. Male meadow katydids (*Conocephalus nigropleurum*) sing in aggregations with heterospecifics; in this environment, the temporal patterns of individual songs are obscured at long distance. Female *C. nigropleurum* may find their mates by initially approaching any source of high frequency sound – even one that is not temporally patterned – but once within the mixed-species cluster, they recognize conspecific songs and reject those of the heterospecifics[31].

Parasitoids constitute another selective force in insect mating systems. Certain female tachinid flies use male orthopterans as hosts for their larvae and track their mating calls to find them[32]. The tachinid's ear was recently described simultaneously for a European species, *Therobia leonidei*[2] and a North American species, *Ormia ochracea*[3]. The flies' ears are geographically matched to their hosts' songs: the European species' ears are tuned to the 25–35 kHz calls of katydids while those of the North American species listen for the 4–6 kHz calls of crickets (Fig. 3). The broad species diversity in the frequencies of orthopteran calls combined with the physiological constraint of evolving an infinitely sensitive ear suggests that the parasitoid makes an evolutionary 'choice' as to which end of the acoustic spectrum to tune itself to. Whereas low frequencies carry further, high frequencies are more easily located. Once the fly's ear is tuned to its host (or its assemblage[33] of hosts), it is probably unable to exploit others. However, finding hosts is not the only auditory requirement of these nocturnal flies and the high-frequency sensitivity of *O. ochracea* suggests it could also detect hunting bats (R. Hoy, pers. commun.). As with gleaning bats, parasitoids have influenced the acoustic component of insect mating systems and may have selected for alternative reproductive strategies (e.g. nonsinging males). Since singing persists in host species, questions arise about the details of this relationship. Do males assess parasitoid risks before singing? Can males detect approaching flies? Do parasitized males have any reproductive success? Can females recognize the songs of parasitized males?

Intraspecies recognition. When male insects sing, they are often competing with other males to attract females. Songs could either act as transmitters of detailed information (e.g. male vigour) over long distances or they could simply be beacons drawing in females to a point where their other senses actually determine the male's quality. The answer to this question lies, in part, with the physiological capacity of ears to decode the information provided to them while in the signal-degrading conditions of natural environments. Although studies have confirmed that females will discriminate songs[34], it is unclear whether she uses the song to predict the quality of males since correlations between song parameters and male physical attributes (e.g. body mass) have been difficult to interpret[35,36]. Females may 'choose' particular songs but these could simply be those of the closest male. Although the costs of making mistakes about a potential mate seem high, the physiological constraints of insect auditory systems may render most (but probably not all) of these animals incapable of receiving sufficiently unambiguous long-range acoustic information about a singing male's quality.

Secondary changes in ears

Although insects have primary uses for their ears, examples exist of supplemental functions. Certain crickets possess high-frequency sensitivity[15] that should enable them to avoid echolocating bats while, conversely, attraction to social sounds, although rare, exists in some moths[37]. The question arises as to how these insects have changed their presumably primitive auditory responses (e.g. attraction in the cricket and evasion in the moth) to the opposite taxes. The cricket may use specific neurons for tasks like bat-detection but moths, with their simpler systems, are more constrained. The ear of the Australian whistling moth (*Hecatesia thyridion*) although used for the detection of conspecific social sounds, resembles a typical bat-detecting ear[38]. This moth may have secondarily adapted its ears, ancestrally tuned for bat calls, to detecting conspecific males who, in turn, emit bat-like signals. To deal with bats, this moth appears to have become diurnal.

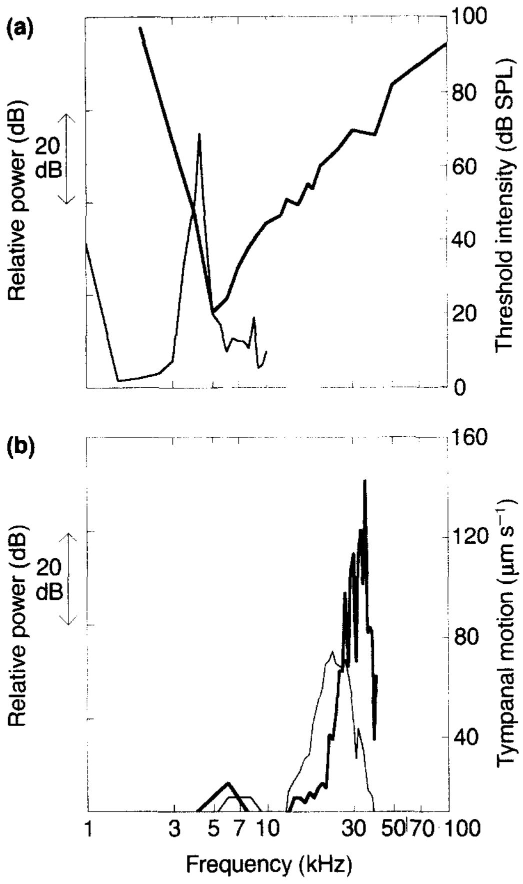
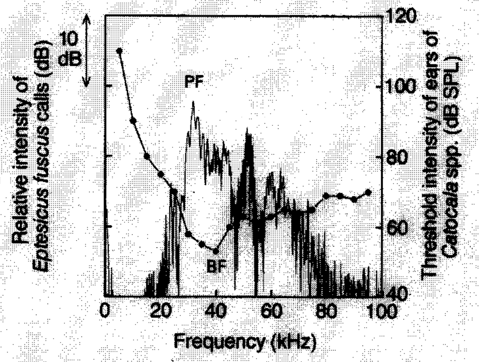


Fig. 3. Two species of tachinid fly have ears matched to the song frequencies of their hosts. (a) In North America, egg-laden females of *Ormia ochracea* with threshold intensities (thick line) have ears sensitive to the 4–5 kHz calls of the field cricket *Gryllus rubens* (thinner line) while (b) the ear of the European *Therobia leonidei* responds (thick line) to the 25–35 kHz calls of the katydid *Poecilimon veluchianus* (thinner line). The *T. leonidei* ears were measured by examining the vibration of the eardrum at different frequencies. In both cases, the matching of the tachinid ears to the fast Fourier transforms of the hosts' songs is not exact, which cautions against assuming single ear–sound evolutionary relationships. Both flies probably listen for an assemblage of hosts, each with slightly different song spectra. *(a) Adapted from Ref. 3; (b) adapted from Ref. 2.*

Box 1. Matching ears to sounds

One way of determining if an animal is adapted to detect certain sounds is by comparing its ear's auditory threshold curve (audiogram) to the frequency spectra of those sounds. Audiograms are derived by playing pure tones to animals at different frequencies and intensities (in human-referenced dBs). The intensity of the tone at a particular frequency that just elicits the desired response (e.g. neural firing) is arbitrarily defined as the auditory threshold for that frequency. The audiogram displays all of the thresholds including the ear's best frequency (BF). BF, combined with the bandwidth of the audiogram, describes the frequency domain of the auditory system under investigation. It may or may not, however, define the animal's adaptive auditory capability since different levels of the system contribute their own sensitivity biases.



To the audiogram, one compares the frequency spectra of those sounds suspected to form part of the animal's sensory environment. In the figure above, the frequency spectrum of the echolocation calls of the big brown bat (*Eptesicus fuscus*) (oscillating line), is superimposed upon the audiogram of underwing moths (*Catocala* spp.)[26] (filled circles). A commonly used frequency analysis is the fast Fourier transform (FFT), a mathematical breakdown of the various frequencies within a complex sound. The FFT describes the relative power of each of the frequencies within the sounds and defines the peak frequency (PF; that containing the most power) and the bandwidth of the spectrum. Whether the match (or lack of) between the FFT and the audiogram is adaptive or coincidental requires a field understanding of the animal's acoustic natural history beyond that which can be measured in the laboratory.

Sexual dimorphism in insect ears occurs as a result of the different life histories of the sexes. Female gypsy moths (*Lymantria dispar*) do not fly and have no need to detect bats, but males fly throughout the night. Compared to males, the ears of females appear degenerated in their loss of high-frequency sensitivity[39]. More dramatic examples exist in female moths with completely degenerate wings and ears[40]. A correlated reduction of wings and ears also exists in praying mantids[41] suggesting a genetic link between these two structures.

Conclusions

Insect hearing, although conservative in its cellular morphology, exhibits a broad range of adaptive modifications. We should, on one hand, appreciate the physiological constraints that exist when speculating on what insects can do with their ears, but on the other, be aware that insects represent one of the most diverse animal groups in the world and the majority of their ears remain unstudied. Understanding how ears function for these 'simple' animals in their natural environments will undoubtedly reveal new adaptations and may ultimately demonstrate the details of insect hearing to be as complex as this heterogenous taxon itself.

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