Accessory gills in mayflies (Ephemeroptera)

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Abstract

Thread-like or finger-like accessory gills have been found on the maxillae, labia, coxae, and ventral thoracic surfaces of various lineages of mayflies (Ephemeroptera). Representative members of the seven families known to have accessory gills were examined and compared. From the regular distribution of accessory gills, usually associated with coxal segments, a hypothesis concerning their origin is postulated. The fact that these are found only in some members of the more plesiomorphic families would imply that the ability to develop a coxal gill has been retained and is displayed in some extant taxa of some ancient lineages. The possible functions of accessory gills include respiration and filtration.

Keywords: Ephemeroptera, accessory gill, origin, function.

Zusammenfassung

Bei Eintagsfliegen verschiedener Abstammungslinien lassen sich an Maxillen, Labium, Hüften und der Ventralseite des Thorax faden- oder fingerförmige akzessorische Kiemen feststellen. Charakteristische Vertreter der sieben Familien, bei denen derartige akzessorische Kiemen bekannt geworden sind, werden vergleichend untersucht. Ausgehend von der Verbreitung dieser akzessorischen Kiemen, die normalerweise mit coxalen Segmenten assoziiert sind, wird eine Hypothese zu ihrem Ursprung aufgestellt. Da Coxal-Kiemen nur bei Vertretern ursprünglicher Familien gefunden werden, liegt die Vermutung nahe, dass die Fähigkeit zur Bildung solcher Kiemen in einigen rezenten Taxa alter Entwicklungslinien erhalten geblieben ist. Mögliche Funktionen von akzessorischen Kiemen sind Atmung und Filtrierung.

Contents

1 Introduction

Mayflies (Ephemeroptera) are aquatic insects with immature stages living in freshwater habitats. Consequently, they are morphologically adapted to the aquatic environment, and their gill adaptations (shape, number, structure and position) can be used for classification and identification (NEEDHAM et al. 1935, EDMUNDS et al. 1963, PETERS & CAMPBELL 1991). KUKALOVÁ-PECK (1978), based on fossil evidence, suggested that the mayfly imaginal wings are homologous with the larval abdominal gill plates, a conclusion supported by KLUGE (1989), based on morphology and comparison of living species.

The gills of mayflies can be divided into two kinds: the plate-like abdominal gills (or tergaliae of KLUGE et al. 1995) and the accessory gills (located on head or/and thorax) (ŠTYS & SOLDÁN 1980). The abdominal gills have been studied in detail, and a variety of functions have been documented: respiration (MORGAN & GRIERSON 1932, BEAVER 1990, ERIKSEN & MAEUR 1990); osmoregulation (WICHARD 1979; WICHARD et al. 1972, 2002); locomotion (swimming, KLUGE et al. 1984); water circulation (driving currents over the tracheated surfaces, EASTHAM 1932, NOTESTINE 1994); protection (gill cover in Caenidae and Neoephemeridae, NOTESTINE 1994); maintaining the position of the body (such as the adhesive disc of some species of *Rhithrogena* and *Epeorus*, WICHARD et al. 2002, ZHOU et al. 2003, DITSCHE-KURU & KOOP 2009).

In addition to the functional abdominal gills, accessory gills have been found in several families (NEEDHAM et al. 1935, ŠTYS & SOLDÁN 1980, MÜLLER-LIEBENAU 1985, PETERS & CAMPBELL 1991, WUILLOT & GILLIES 1994, ZHOU & PETERS 2003). Their origin and function are less clearly understood. Seven families are known to have accessory gills (Baetidae, Coloburiscidae, Isonychiidae, Nesameletidae, Oligoneuriidae, Rallidentidae, and Siphluriscidae). ŠTYS & SOLDÁN (1980) stated that because most of those taxa belong to the most ancestral evolutionary line of the order, this seemed to suggest that their presence is a plesiomorphic character; on the other hand, common sense and a comparison with other insect orders suggest that accessory gills have evolved as secondary structures supporting the function of abdominal gills. The origin of accessory gills is unclear. In this paper, I examine some typical representatives of mayflies with accessory gills and suggest a hypothesis concerning their origin and discuss their function.

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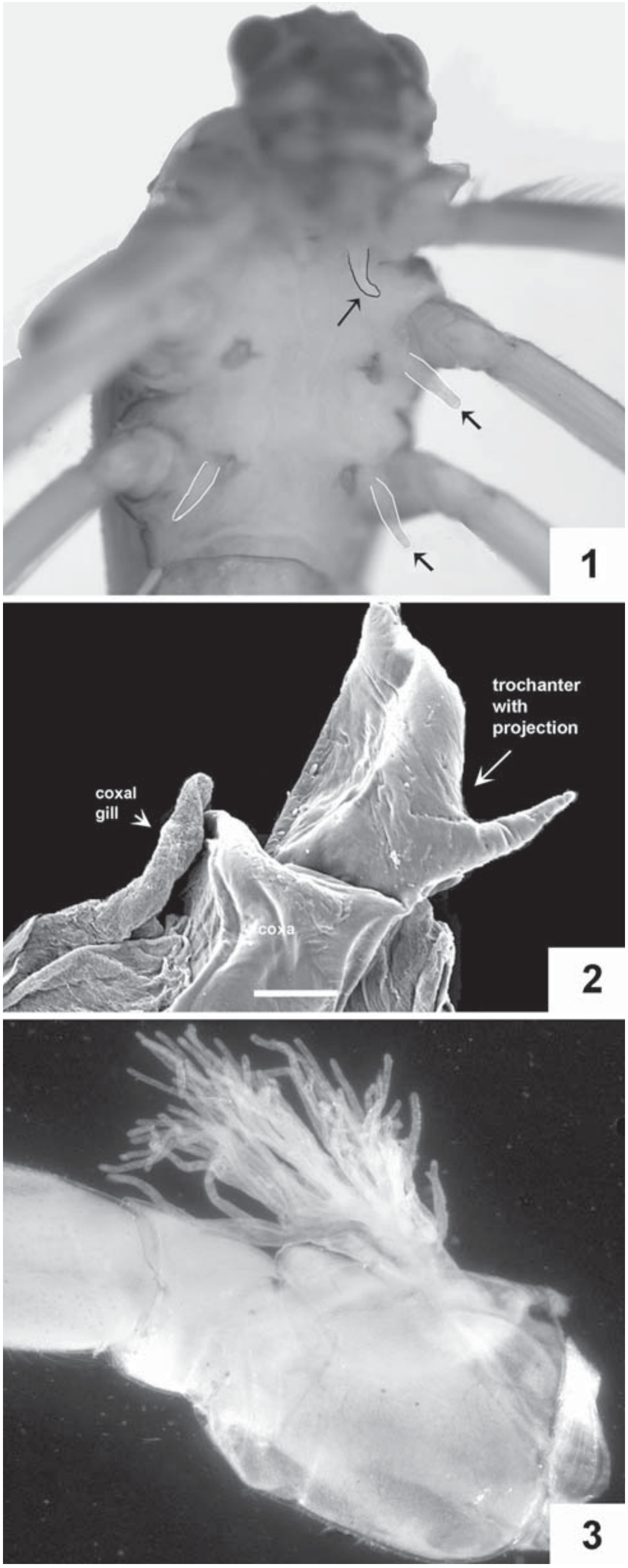
2 Results

The results of a comparative examination of accessory gills are given in Tab. 1 and more detailed pictures are provided by Staniczek (2010) in this issue. A few species need further comment. In the original description of the species later named *Afrobaetodes berneri* by Demoulin (1970), Kimmins (1955) reported that the nymphs had maxillary and sternal gills. After examining one type specimen and two nymphs collected in Guinea in 1994, the gills are located actually between the sternal sclerite and the coxae, and could be interpreted as having a coxal origin (Fig. 7).

In previous literature (like Štys & Soldán 1980), *Murphyella needhami* Lestage was reported to have gills on maxillae, labium, and forecoxae, with a single sternal gill located at the middle of each thoracic sternum. Here we can see that in *Murphyella*, accessory gills of the mouthparts are located in positions similar to those of *Siphluriscus chinensis* Ulmer (Zhou & Peters 2003), and those of the forecoxae are similar in position to those of *Baetiella bispinosa* (Gose) (Figs. 1–2, 4) and *Isonychia georgiae* McDunnough (Fig. 10). A common origin for the forecoxal

Tab. 1. Position of accessory gills in species examined.

Family: Species	Specimens examined from	Accessory gills associated with coxae or thoracic sterna	Accessory gills associated with mouthparts
Baetidae: *Baetiella bispinosa* (Gose, 1980)	China, Japan	At base of coxae in membrane between coxae and sterna on all legs (Figs. 1–2, 4)	No
Baetidae: *Baetodes huaico* Nieto, 2003	Argentina	Double gill (common base) at apex of coxae in membrane between coxae and trochanters (Fig. 5)	No
Baetidae: *Dicentroptilum papillosum* Wuillot, 1994	Mali	Double gill (apparently with common base) at base of coxae in membrane between coxae and sterna (Fig. 6)	No
Baetidae: *Heterocloeon petersi* (Müller-Liebenau, 1974)	USA (Georgia)	Single gill only on forecoxae in membrane between coxae and sterna	No
Baetidae: *Afrobaetodes berneri* Demoulin, 1970	Guinea	Single gill on each side of prosternum in membrane between coxae and sterna (Fig. 7)	Single gill at apex of basal segment of maxillary palp (Fig. 8)
Siphluriscidae: *Siphluriscus chinensis* Ulmer, 1920	China (Zhejiang)	Gill tufts at base of forecoxae and mesothoracic coxae in membrane between coxae and sterna (Figs. 3, 9)	One gill tuft near inner base of stipes on maxilla and a smaller gill tuft between stipes and cardo; gill tufts laterally on mentum of labial postmentum
Nesameletidae: *Nesameletus ornatus* (Eaton, 1883)	New Zealand	No	Single short gill laterally between stipes and cardo (maxilla)
Rallidentidae: *Rallidens macfarlanei* Penniket, 1956	New Zealand	No	Single short gill laterally between stipes and cardo (maxilla)
Isonychiidae: *Isonychia sayi* Burks, 1953	USA (Florida)	Gill tuft at base of forecoxae in membrane between forecoxae and prosternum	Gill tuft at medial base of stipes in membrane between stipes and cardo (maxilla)
Isonychiidae: *Isonychia georgiae* McDunnough, 1931	USA (Georgia)	Single gill at base of forecoxae in membrane between forecoxae and prosternum (Fig. 10)	Gill tuft at medial base of stipes in membrane between stipes and cardo (maxilla)
Coloburiscidae: *Coloburiscoides* sp.	Australia (Victoria)	No	Single long gill at base of stipes in membrane between stipes and cardo (maxilla); shorter finger-like gill on each side near apex of postmentum (labium)
Coloburiscidae: *Murphyella needhami* Lestage, 1931	Chile	Single gill in membrane between procoxae and prosternum; single median gill on each segment of thoracic sterna, median gill on prosternum in membranous area anterior to small, prosternal sclerite (Fig. 11)	Large double gill at base of stipes in membrane between stipes and cardo (maxilla); single gill on each side near apex of postmentum (labium)
Oligoneuriidae: *Lachlania dominguezi* Pereira, 1989	Argentina	No	Large gill tuft in membrane ventrally between stipes and cardo (maxilla)



Figs. 1–3. Forebody in ventral view (1) and foreleg bases (2–3). – **1–2**. *Baetiella bispinosa*. **3**. *Siphluriscus chinensis*. – 1, 3 = digital photos, 2 = SEM; the arrows in Fig. 1 indicate the gills: scale (of Fig. 2): 50 µm.

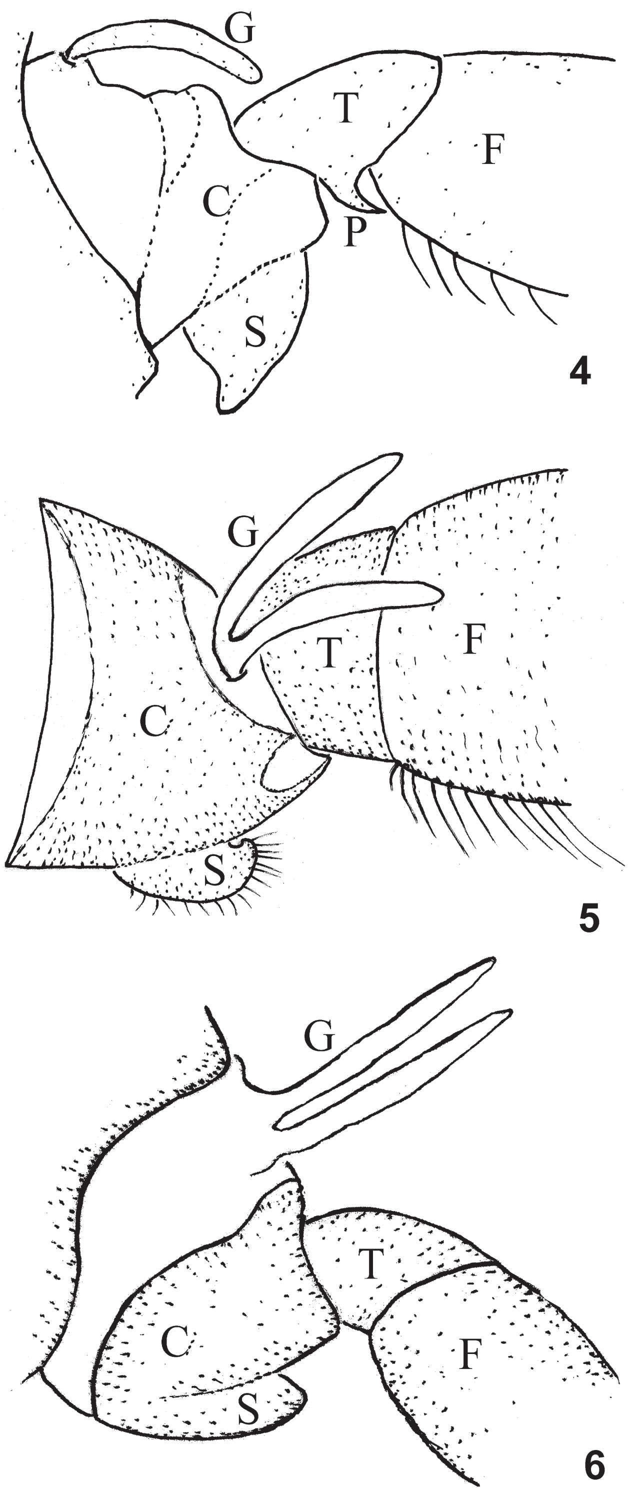
gills of *Isonychia* and *Murphyella* is supported by the common position of the tracheae (LANDA 1969). However, the gills on the sterna of *Murphyella* seem to be a unique derivation, with unique tracheation (LANDA 1969) although the tracheae supplying the sternal gills of *Murphyella* do come from tracheal branches with the same stem as the coxal gills. The thoracic prosternum of *Murphyella needhami* is very small in contrast to the procoxae and the membranous bases of the procoxae are enlarged, so there is a large membranous area between the coxae and the sternum. The gills of the procoxae are located near the coxal bases (Fig. 11), and other gills are located medially on each thoracic sternum.

3 Conclusions and Discussion

DEMOULIN (1969) suggested that maxillary gills are synapomorphic characters of Rallidentidae + Isonychiidae/ Coloburiscidae/Oligoneuriidae (as *Chromarcys*), the latter three families representing the Eusetisura of KLUGE (1998); DEMOULIN also considered their origin to lie with the family now treated as Nesameletidae. Later, KLUGE (2004) grouped the Siphluriscidae, Nesameletidae, Rallidentidae, and Baetidae in a plesiomorphic grouping termed “Tridentiseta” without clarifying the arrangement of the families within this group; the remaining families (Coloburiscidae, Isonychiidae, and Oligoneuriidae) form a monophyletic group Eusetisura within “Bidentiseta”, the presence of accessory gills on the mouthparts being considered a shared apomorphy within this group. These arguments seem to imply that maxillary gills (or all accessory gills) are derived characters having evolved independently, and this view is also clearly stated by STANICZEK (2010).

However, this argument can not explain why there are no accessory gills in other positions as are often found in other aquatic orders, e. g. like filaments on trichopteran or dipteran larval abdomen. Although gills of mouthparts are a character of Eusetisura, their existence is not necessarily apomorphic. I would suggest that the presence of accessory gills may be a plesiomorphic condition in Ephemeroptera, probably arising from coxal rami (exites or endites). That those structures existed on some insect legs of fossil insects seems indisputable (KUKALOVÁ-PECK 1983, 1991, 1997). The question is whether or not they could be modified as accessory gills in mouthparts and legs. The fact that these are found only in some members of the more plesiomorphic families would imply that the ability to develop a coxal gill has been retained and is displayed in some extant taxa of the most ancient lineages.

In the recent consideration of mayfly relationships, OGDEN et al. (2009) provided several possible trees on this issue. Except POY topology, all other trees including summary hypothesis tree (OGDEN et al. 2009: fig. 7) show that the Siphluriscidae (*Siphluriscus chinensis*) is the



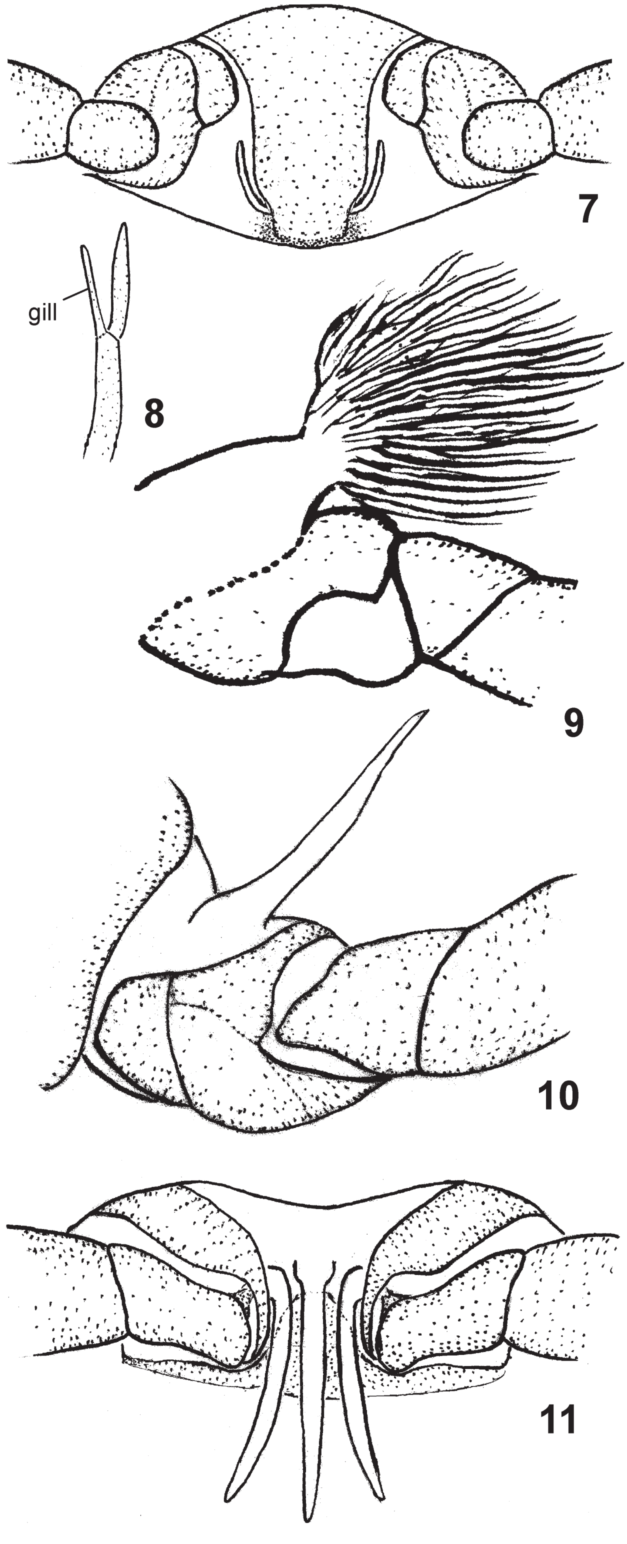
Figs. 4–6. Coxal gills of Baetidae. – **4**. *Baetiella bispinosa*. **5**. *Baetodes huaico*. **6**. *Dicentroptilum papillosum*. – C = Coxa, F = Femur, G = Gill, P = Process, S = dorsal sclerite of coxa, T = Trochanter.

sister group of all other mayflies. Morphologically, this family has most plesiomorphic characters among mayflies. At the same time, it holds the largest number of accessory gills as well, such as two pairs of coxal gills on thoracic forelegs and midlegs. In addition the Baetidae, which have several lineages with accessory gills, also diverged very early from other mayflies in those trees. Another interesting fact is that Gondwanan mayflies usually have more accessory gills on their head and/or thorax.

Exceptions are the sternal gills of *Murphyella* and possibly the gill on the maxillary palp of *Afrobaetodes*. Furthermore, most genera of Baetidae lack accessory gills, and the genera cited here appear to be derived for differing ecological situations. In *Baetodes*, for example, some species have a double gill, some a single, and other species have no accessory gills (Nieto 2003). *Baetodes* differs from other genera of Baetidae in that the gills are in a distal position on the coxa in the membrane between coxa and trochanter (Fig. 5), but all other Baetidae examined have basal coxal gills (membrane between coxae and sterna). Gills of *Afrobaetodes berneri* Demoulin are located closer to the prosternum than to the procoxae (Fig. 7). In both of these cases, these accessory gills can still be homologized with those of other Baetidae by the fact that all have a coxal origin. Even abdominal gills of mayflies are located in differing positions (anterior, posterior, dorsal, ventral) supporting the conclusion that the location of gills with similar origins can change dramatically. In more derived families or groups of families sometimes treated as infraorders, such gills are never found in spite of similar ecological requirements.

Most mayfly accessory gills have the following six characteristics. First, they are thread-like or finger-like filaments or tufts, never plate-like. Second, they are situated on head and/or thorax, never on the abdomen. These two points show that they have a different origin from the abdominal gills. Third, they are arranged segmentally. Fourth, they are usually located on the coxae or the mouthpart homologs of the coxae. These two points infer that they are sub-structures of the legs. Fifth, they are located on membranous areas of the body; and finally, they occur in several mayfly lineages, not a single or rare clade. The latter two points indicate they are likely plesiomorphic structures, although their presence in some Baetidae may be apomorphic. Unfortunately, relationships within Baetidae are poorly understood.

I would suggest that the accessory gills in Ephemeroptera probably arose from original appendages of legs, but have maintained the capacity to persist only in selected families. However, more study of the development of these structures including a detailed comparison with other insect orders is needed.



Figs. 7–11. Accessory gills of Ephemeroptera. – **7–8**. *Afrobaetodes berneri*, prothorax, ventral view (7), maxillary palp (8). **9**. *Siphluriscus chinensis*, forecoxal gill. **10**. *Isonychia georgiae*, forecoxal gill. **11**. *Murphyella needhami*, prothorax, ventral view.

Possible functions of accessory gills

The functions of the accessory gills have only been studied in a most general sense and are believed to be used in respiration. The possibilities of other functions have not been examined, but I might propose a possible filtering function as a subject for further study.

R e s p i r a t i o n . Štys & Soldán (1980), based on anatomical work of Landa (1969), reported that accessory gills (for example in *Isonychia* and *Murphyella*) are connected by their tracheae with both the lateral tracheal trunks and the cephalic gills with the cephalic tracheae. Staniczek (2010) also clearly shows this kind of connection which indicates a respiratory function.

O s m o r e g u l a t i o n . According to Staniczek (2010) this may be another function of the accessory gills.

F i l t r a t i o n o r h e l p i n f i l t e r i n g . The larvae of Coloburiscidae, Isonychiidae, and Oligoneuriidae (Eusetisura) have long and dense hair on their forelegs and mouthparts, and they use them to filter tiny organic materials in the water (Elpers & Tomka 1995, Wallace & O'Hop 1979, Wallace & Merritt 1980). These families also have gills on the forecoxae or on the maxillae which may aid in filtration. The presence of coxal gill tufts and other cephalic gills may have a direct or indirect effect in food filtering, like detaining bigger particles or changing the water current etc. With the exception of Siphluriscidae, the accessory gills of the other families are too small to be used for such a function. Although Siphluriscidae have accessory gills on mouthparts and coxae, they are probably not filterers based on the presence of a scraping type of mandible (Zhou & Peters 2003). Unfortunately, the ecology of *Siphluriscus* is unknown and needs further research.

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