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Niche shift: a tool for expanding range? The case of *Ocladius* (Coleoptera: Curculionoidea: Brachyceridae)

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SUMMARY

The distribution and ecology of the genus *Ocladius* (Coleoptera, Curculionoidea, Brachyceridae) are considered. The majority of the species live in tropical and subtropical Africa and Madagascar, with a few species in the Mediterranean region and in central and western Asia. The southern African species whose biology is known are associated with several plant families, both Dicotyledons and Monocotyledons; the Mediterranean and Asian species are monophagous on Chenopodiaceae. Also based on the available data on phylogeny and diversification of the Chenopodiaceae it is hypothesized that some taxa of *Ocladius*, possibly in eastern Africa during the Miocene, underwent a niche shift to the chenopods, and that this event triggered an adaptive radiation, resulting in the expansion of the genus to Mediterranean and Asian habitats.

Ocladius is a genus of small Curculionoidea presently placed in the family Brachyceridae (Alonso Zarazaga and Lyal, 1999), an attribution originally based on morphology, mainly on the structure of the genitalia (Thompson, 1992). *Ocladius* is part of a subfamily, Ocladiinae Lacordaire, 1866, that also includes *Desmidophorus* Dejean 1835, a genus with a disjunct Afro-Indomalayan distribution. Marvaldi (2000) did not recognize the splitting of the Curculionidae in several families. Based on larval characters, the author confirmed the close relationships between the Brachycerinae and Ocladiinae and placed the latter in phylogenetic sequence after the Brachycerinae, thus always among the more primitive taxa. A study on phylogenetic relationships among Brachyceridae taxa, again based on larval morphology, confirmed monophyly of the group and suggested that *Ocladius* and *Desmidophorus* are sister taxa (Morimoto and Kojima, 2006).

The genus *Ocladius* includes about 90 described species (listed in Tab. I). Knowledge of its taxonomy is incomplete, and no key to all the species has ever been proposed. Synopses to the Palaearctic species were compiled by Pic (1894) and Vauloger (1899). Descriptions of new species followed throughout the 20th century for the Palaearctic and, mainly, the African fauna; Hustache (1936) compiled a catalogue of the species of the genus and Osella et al. (1998) presented lists of the *Ocladius* species of the Mediterranean Region and southern Africa. Meregalli and Colonnelli (2006) revised the Arabian species. No taxonomic analysis of the whole genus was ever carried out, no phylogenetic analysis is available and no character matrix has been compiled so far.

Morphologically, the species of *Ocladius* share a synapomorphy in elytral suture, which has a special locking structure, described by Meregalli and Colonnelli (2006). Perhaps not casually, also *Desmidophorus* has a peculiar locking structure, although completely different from that seen in *Ocladius*. It is an enlargement present in both elytra, near the apex, with the right elytron expansion overlapping that of the left. In *Ocladius variabilis* Fähræus, 1871, a species which approaches *Desmidophorus* in some traits, a minute expansion of the suture near the elytra apex is visible at high magnification.

The genus is distributed throughout tropical as well as subtropical Africa, Madagascar, the Arabian peninsula, northern Africa, the coasts of southern Spain, and desert areas of western Asia up to Turkestan (Fig. 1). It includes several differentiated species groups. The list of the species with their range is shown in Tab. 1.

Two thirds of the species (58) are native to tropical Africa, which become 71 if Madagascar is added; this fauna is very varied, and several species-groups can be recognized. Most of the species have a restricted range. Although geographical subdivisions of this region are partly arbitrary, half of these species have a southern African range; the number of species is progressively reduced towards central Africa (Angola and Congo): this region represents the northernmost limit of the southern African taxa. Only 13 species have been recorded so far for eastern Africa; nevertheless, nearly all of the species-groups are comprised in this area. This pattern changes drastically for the Arabian and Palaearctic faunas, found along the coasts of the Red Sea, the Arabo-Mediterranean region, and central Asia. Although several species are present (10 species along the Red Sea and in Arabia, 5 in the Mediterranean region and western Morocco, and 2 in Asia), only a few groups are represented. Most of the species present along the Red Sea coasts, in Sinai and the Arabian Peninsula are part of the *O. barani* group, a complex endemic to this region and morphologically similar to southern African taxa; the others are part of the *O. bifasciatus* group. All the Mediterranean species belong to only one

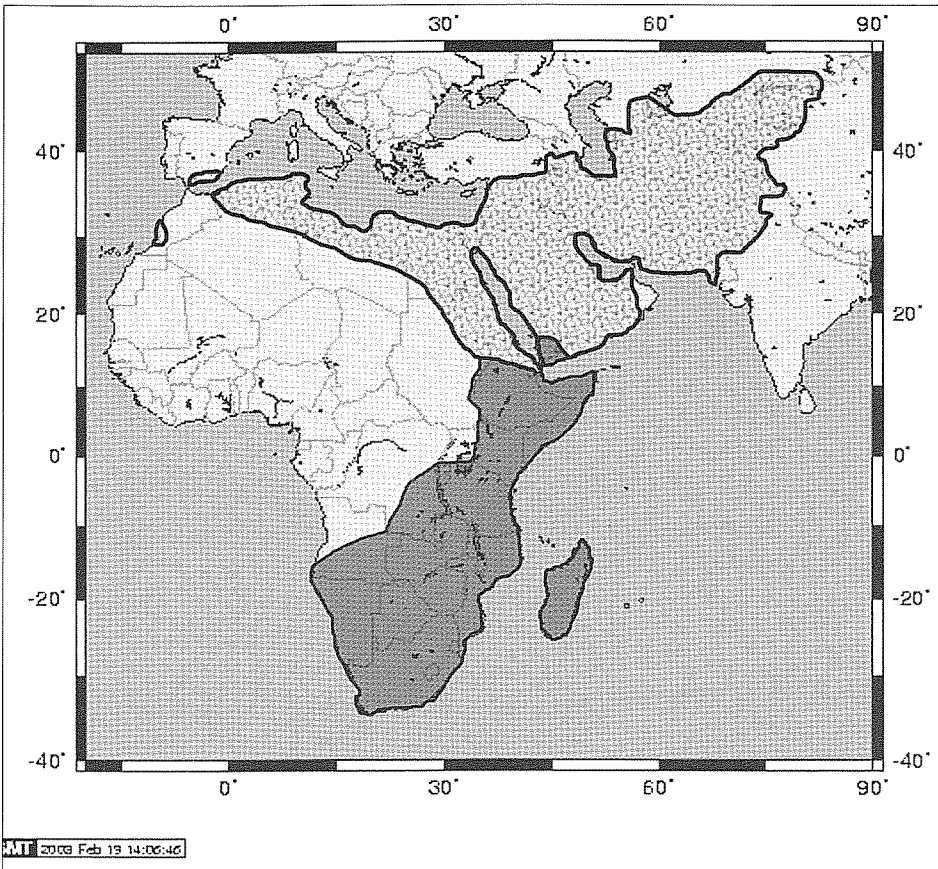


Fig. 1 - Distribution of the genus *Ocladius*. Solid grey: distribution of the polyphagous species-group. Shaded grey: distribution of the Chenopodiaceae-associated species (Map created with OMC, http://www.aquarius.geomar.de/omc/omc_intro.html).

species group, which seems to be native to this region and expands to Asia with one species, *O. engelhardi* Pic, 1894. The second central Asian species is *O. salicorniae* (Olivier, 1807), an arabo-turanian taxon, probably related to the *O. bifasciatus* group. Only in the extreme south-western part of the Arabian Peninsula do two species belonging to tropical African groups appear (*O. balkis* Meregalli and Colonnelli, 2006 and *O. rufithorax* Pic, 1894, both vicariants of Somalian species). On a biogeographic point of view, these species determine the north-eastern limit of the Afrotropical fauna for this genus (Meregalli and Colonnelli, 2006).

The biology and ecology is only known for a minority of species. Those from tropical Africa seem to have a broad spectrum of host-plants and are found in arid as well as mesophilous habitats (Meregalli, personal observations

Tab. I - Checklist of the genus *Ocladius*.

SPECIES	DISTRIBUTION
<i>Ocladius abdeldayemi</i> Meregalli & Colonnelli, 2006	Sinai
<i>Ocladius abyssinicus</i> Pic, 1900	Eastern Africa
<i>Ocladius aegyptiacus</i> Tournier, 1875	Ethiopia
<i>Ocladius aidhabensis</i> Meregalli & Colonnelli, 2006	Egypt
<i>Ocladius allaudi</i> Fairmaire, 1900	Madagascar
<i>Ocladius ambaricus</i> Meregalli & Colonnelli, 2006	Ethiopia
<i>Ocladius assercularicollis</i> Boheman, 1838	Southern Africa
<i>Ocladius baccicollis</i> Boheman, 1838	Southern Africa
<i>Ocladius balkis</i> Meregalli & Colonnelli, 2006	Yemen
<i>Ocladius barani</i> Pascoe, 1874	Arabia
<i>Ocladius basalis</i> Fähræus, 1871	Southern Africa
<i>Ocladius basimaculatus</i> Voss, 19860	Namibia
<i>Ocladius bifasciatus</i> Tournier, 1875	Arabia, Red Sea coasts
<i>Ocladius bimaculatus</i> Hesse, 1928	Southern Africa
<i>Ocladius bufo</i> Vauloger, 1899	Tunisia
<i>Ocladius camelus</i> Pic, 1909	Madagascar
<i>Ocladius caroli</i> Hartmann, 1906	Southern Africa
<i>Ocladius castaneipennis</i> Fähræus, 1871	Southern Africa
<i>Ocladius coccus</i> Fähræus, 1871	Southern Africa
<i>Ocladius coquereli</i> Fairmaire, 1871	Madagascar
<i>Ocladius costicollis</i> Bohemann, 1838	Southern Africa
<i>Ocladius costiger</i> Boheman, 1845	Southern Africa
<i>Ocladius costulipennis</i> Fairmaire, 1886	Madagascar
<i>Ocladius cratiger</i> Marshall, 1959	Namibia
<i>Ocladius cyanipennis</i> Hustache, 1935	Angola
<i>Ocladius dianthi</i> Marshall, 1937	Southern Africa
<i>Ocladius diversepunctatus</i> Pic, 1909	Kenya
<i>Ocladius diversesculptus</i> Pic, 1921	Madagascar
<i>Ocladius diversesculatus</i> Pic, 1921	Madagascar
<i>Ocladius engelhardi</i> Pic, 1894	Central Asia
<i>Ocladius eorum</i> Meregalli & Colonnelli, 2006	South-western Arabia
<i>Ocladius fasciculatus</i> Pic, 1915	Madagascar
<i>Ocladius foveatus</i> Boheman, 1838	Southern Africa
<i>Ocladius frontalis</i> Fairmaire, 1897	Madagascar
<i>Ocladius glomeris</i> Schoenherr, 1826	Southern Africa
<i>Ocladius goudoti</i> Hustache, 1922	Madagascar
<i>Ocladius grandii</i> Osella & Meregalli, 1986	Spain
<i>Ocladius granosus</i> Fairmaire, 1899	Madagascar
<i>Ocladius hirtipennis conicollis</i> Voss, 1960	Tanzania
<i>Ocladius hirtipennis cordaticollis</i> Voss, 1960	Congo
<i>Ocladius hirtipennis hirtipennis</i> Hustache, 1924	Congo
<i>Ocladius hirtipennis intermedius</i> Voss, 1960	Congo
<i>Ocladius holomelas</i> Fairmaire, 1877	Algeria, Morocco
<i>Ocladius inaequalicollis</i> Bohemann, 1845	Southern Africa
<i>Ocladius interstitialis</i> Fähræus, 1871	Southern Africa
<i>Ocladius lacunatus</i> Boheman, 1838	Southern Africa
<i>Ocladius laevipennis</i> Hustache, 1922	Madagascar
<i>Ocladius lamii</i> Hustache, 1938	Angola
<i>Ocladius lenis</i> Marshall, 1959	Southern Africa
<i>Ocladius lobicollis</i> Hustache, 1938	Somalia
<i>Ocladius longepilosus</i> Aurivillius, 1926	Uganda
<i>Ocladius maculipes</i> Pic, 1909	Somalia
<i>Ocladius maculosus</i> Fairmaire, 1886	Madagascar

Tab. I - Checklist of the genus *Ocladius*.

SPECIES	DISTRIBUTION
<i>Ocladius madecassus</i> Pic, 1915	Madagascar
<i>Ocladius nitidus</i> Aurivillius, 1910	Kenya
<i>Ocladius nodifer</i> Marshall, 1935	Mozambique
<i>Ocladius obliquisetosus</i> Fähræus, 1871	Southern Africa
<i>Ocladius paucisquamis</i> Meregalli & Colonnelli, 2006	Jordan, Israel
<i>Ocladius perrieri</i> Fairmaire, 1899	Madagascar
<i>Ocladius pertusus</i> Schoenherr, 1826	Southern Africa
<i>Ocladius plicicollis</i> Fairmaire 1886	Madagascar
<i>Ocladius pusillus</i> Hustache, 1935	Angola
<i>Ocladius quadriseriatus</i> Hustache, 1935	Angola
<i>Ocladius rhodesianus</i> Pic, 1909	Zimbabwe
<i>Ocladius rubriventris</i> Hustache, 1923	Angola
<i>Ocladius ruficornis</i> Hustache, 1923	Madagascar
<i>Ocladius rufipes</i> Hustache, 1929	Kenya
<i>Ocladius rufithorax</i> Pic, 1894	Yemen
<i>Ocladius rugosipennis</i> Marshall, 1938	Somalia
<i>Ocladius rupicolus</i> Hesse, 1928	Southern Africa
<i>Ocladius russelli</i> Meregalli, Colonnelli & Borovec, 2001	Morocco
<i>Ocladius salicorniae</i> (Olivier, 1807)	Central and Western Asia
<i>Ocladius sapeti</i> Gestro, 1887	Eritrea
<i>Ocladius senex</i> Faust, 1899	Congo
<i>Ocladius senilis</i> Boheman, 1838	Southern Africa
<i>Ocladius seriatus</i> Faust, 1896	Eastern Africa
<i>Ocladius seriefoveatus</i> Fairmaire, 1901	Madagascar
<i>Ocladius serripes</i> Peringuey, 1893	Southern Africa
<i>Ocladius solarii</i> Caldara, 1976	Libya, Egypt
<i>Ocladius speculiferus</i> Fairmaire, 1898	Madagascar
<i>Ocladius subcarinatus</i> Boheman, 1838	Southern Africa
<i>Ocladius subelongatus</i> Pic, 1905	Sinai
<i>Ocladius subfasciatus</i> Boheman, 1845	Southern Africa
<i>Ocladius subtuberculatus</i> Pic, 1910	Mozambique
<i>Ocladius subundulatus</i> Fähræus, 1871	Southern Africa
<i>Ocladius sulcicollis</i> Fähræus, 1871	Southern Africa
<i>Ocladius sulcipes</i> Boheman, 1845	Southern Africa
<i>Ocladius textilis</i> Boheman, 1845	Southern Africa
<i>Ocladius tricarinatus</i> Aurivillius, 1912	Eastern Africa
<i>Ocladius tuberculatus</i> Aurivillius, 1910	Kenya
<i>Ocladius variabilis</i> Fähræus, 1871	Southern Africa
<i>Ocladius vani</i> Marshall, 1923	Southern Africa
<i>Ocladius ventriosus</i> Marshall, 1959	Southern Africa
<i>Ocladius walkei</i> Cameron, 1905	Perim Island (Red Sea)
<i>Ocladius ziczac</i> Marshall, 1928	Tanzania

Southern Africa 35 species
 Eastern Africa 16 species
 Madagascar 18 species
 Arabia 10 species
 Central Africa 9 species
 Mediterranean 5 species
 Central Asia 2 species

in western South Africa). Marshall (1937: 476), describing *O. dianthi* Marshall, 1937, noted that “The larvae of this species are reported by the Division of Entomology, Pretoria, as boring in the stems of carnations” (probably genus *Dianthus* L., Caryophyllaceae). Hustache (1938) named *O. lamii* Hustache, 1938, associated with *Lamium* L. Howden (1986) reported *O. obliquaetosus* Fåhraeus, 1871 sitting or mating on species of Liliales, and described feeding on the “spikelets” of four grass species (Poaceae) and oviposition in one of these grasses. The same author (Howden, 1995) gave further remarks about endophytic oviposition of the same species in stems. *Ocladius interstitialis* Fåhraeus, 1871 and *O. subundulatus* Fåhraeus 1871 were reported, on specimen labels, to be associated with *Indigofera daleoides* Benth. ex Harv. (Meregalli, personal observation on labels of Museum specimens). A so far undetermined species was found under Mesembryanthemaceae in sandy habitats in southwestern Africa, whereas others are commonly caught with sweep net on grasses (Meregalli, personal observation). Specimens of *O. rufithorax* Pic, 1894 were collected in Yemen at night on lucerne (*Medicago sativa* L., Fabaceae) (Meregalli and Colonnelli, 2006). Many of these entities belong to different species-groups, so it is impossible to determine whether host-plant relationships are characteristic of a single taxon or if they are typical of a phylogenetic lineage.

It can be noted that *O. interstitialis* and *O. rufithorax*, associated with Fabaceae, are part of the same species group; on the other hand, *O. subundulatus*, also reported to live on Fabaceae, belongs to the same species group as *O. dianthi*, associated with Caryophyllaceae. Moreover, it is not known if the southern African species are monophagous or polyphagous. According to Marvaldi et al. (2002) weevil lineages primarily associated with monocots have a basal phylogenetic position in the clade Curculionidae, and the authors included Ocladiini among these. However, it does not seem that in *Ocladius* this association is very significant, as it probably applies to only a few species, and indeed was documented only for *O. obliquaetosus*; all the other species whose host-plants are known develop on dicots. Also the sister taxon *Desmidophorus* is usually not associated with monocots, and some species are even broadly polyphagous on dicots [*Hibiscus mutabilis* L. for *D. crassus* (Morimoto and Kojima, 2006); *Hibiscus* ss. pp. (Chao and Chen, 1980), *Mangifera indica* L. (Lei and Zhou, 1998) and *Ailanthus altissima* (Miller) Swingle (USDA, 2006) for *D. hebes*; etc.].

In any case, even though there can be edaphic specialization at species rank, there is no host-plant specialization at genus rank for the tropical and subtropical species of *Ocladius*. It is thus remarkable that all the Arabian, the Mediterranean and the Asian species appear to be exclusively associated with

Chenopodiaceae of arid or desert habitats (Osella and Meregalli, 1986; Meregalli et al., 2001; Meregalli, personal observations in several sites of Morocco, Tunisia and Sinai). The goosefoot family plants often belong to the genera *Arthrocnemum* Moq. and *Haloxylon* Bunge.

The strict association of the Palaearctic *Ocladius* with the chenopods stimulates some thoughts on the onset of this host-plant association and on the possibility that this event triggered the secondary radiation and penetration of the genus into the Arabian, Mediterranean and central Asian habitats.

According to Kadereit et al. (2006) the Chenopodiaceae tribe Salicornioideae diversified in Eurasia during the Oligocene, along the northern margin of the Tethys Sea. By the Miocene all the major lineages had originated; also thanks to the onset of C₄ metabolism (P'yankov et al, 2001), these halophytes and hygrophalophytes enjoyed a very successful radiation in the most arid, often salty, habitats of the Mediterranean and Asian region, including coastal salty patches along the Red Sea, where they constitute the dominant, occasionally nearly exclusive, flora.

An interesting observation on the ecology of some southern African taxa of *Ocladius* indicates that at least some species take refuge under shrubs of Mesembrianthemaceae in sandy habitats. This is analogous to the *Arthrocnemetum* association seen in the Palaearctic region, where Chenopodiaceae offer the same ecological conditions in the vegetated patches of otherwise desert or semidesert coenoses.

A possible scenario to understand relationships among Mediterranean and southern African species of *Ocladius* is proposed, implicating an ecological shift towards chenopod host-plants. This niche shift possibility was discussed by Colonnelli and Osella (1998) to explain adaptation to a "new" host-plant in weevils usually associated with other plant species. The authors defined host-plants as plants upon which larval development takes place, whereas refuge plants are those used by the adult weevil as food, shelter and transport (Colonnelli and Osella, 1998: 192). The authors suggested that some taxa, in peculiar conditions of environmental stress, when the original host-plant became a limiting resource, shifted to the use of refuge plants as host-plants. Becerra and Venable (1999) discussed relevance of host metabolites in insect host-shift and suggested models explaining patterns of evolution of host use.

Available data suggest that *Ocladius* differentiated in Africa, apparently in sub-tropical warm habitats, an environment also typical of the sister genus *Desmidophorus*. A first radiation in central and southern Africa occurred, leading to the appearance of all the species-groups of the tropical *Ocladius* fauna. It shall be noted that the southern African taxa of *Ocladius* are broadly polyphagous, at least as a genus. During their evolution several host-plant shifts

may have occurred, leading to the diversification of the various groups of species and their association with distinct host-plants. Alternatively, of course, parts of an ancestral highly polyphagous stock may have specialized on distinct host-plants. In any case, *Ocladius* became associated with a broad spectrum of host-plants, including monocots as well as dicots.

During the Miocene climate cooled and became drier and in eastern Africa this led to the onset of dry grass vegetation or savannah (Retallack, 1992). In the driest and salty habitats along the Red Sea coasts, large patches of Chenopodiaceae became dominant, mainly thanks to the physiological shift to C4 metabolism (P'yankov et al, 2001). Ecologically, these plants reproduced the type of habitat still used by some southern African species of *Ocladius*, that take refuge during the warmer and driest periods of the year under large shrubs of mesembs. Several of the halophyte, and hygrophalophyte, chenopods have the advantage of being perennial and maintain leaves, usually succulent, for the whole year. In salty and desert habitats, particularly during the driest periods, they are often the only food and water source for herbivorous insects. It is thus possible that after using plants of the goosefoot family as a refuge, some oligophagous or polyphagous species of *Ocladius* shifted to the chenopods as exclusive host-plants.

There are two significant cases of apparent polyphagy in taxa native to the Arabian peninsula and the coasts of the Red Sea. *Ocladius bifasciatus* was found on *Reseda amblyocarpa* Freser (Resedaceae) in Aden (southern Yemen), while specimens from Gebel Elba, along the coasts of the Red Sea, slightly differentiated morphologically, are associated with a chenopod, *Salsola foetida* Del. (Meregalli and Colonnelli, 2006). The second case regards *O. eremorum* Meregalli and Colonnelli, 2006, a species from southern Arabia, and its sister taxon, the Turanian *O. salicorniae* (Olivier, 1807). The former appears to be associated with *Farsetia* Turra (Fabaceae) (Colonnelli, personal communication), whereas *O. salicorniae*, is associated with chenopods. The species that were not using plants of the goosefoot family as the hosts were probably disadvantaged in these dry and often salty habitats, widespread along the Red Sea coast; conversely, those that developed an exclusive host-plant association with the Chenopodiaceae had the chance of colonizing many of the regions dominated by this halophyte vegetation, probably via the arid eastern Africa corridor, that is, the coasts of the Red Sea, the Arabian Peninsula deserts, and, subsequently, the southern coasts of the Mediterranean region and the deserts of Central Asia. In the Mediterranean habitat the Messinian salinity crisis also allowed *Ocladius* to reach southern Spain. In northern Africa, along wadis and around internal salt lakes, these species also reached regions relatively distant from the sea, in the Sahara desert. It is well known that halophyte vegetation was never absent from the Sahara, although the territory occupied by the veg-

etation expanded and contracted several times after the Miocene, and up to a few thousands years ago (Geyh and Thiedig, 2008). There is an apparently isolated species of *Ocladius* in western Morocco, and again data on chenopod distribution and biogeographical history helps to understand the weevils' distribution. As explained by Akhani et al. (1997) there are close relationships between northwestern African and eastern Mediterranean-Turanian species of chenopods, so the presence in western Morocco of an *Ocladius* belonging to a southern Mediterranean species group is not surprising and confirms the effects of the exclusive host-plant association in determining adaptive radiation and spread of these weevils.

It should be added that several other groups of Curculionidae, among them many Lixinae, Baridinae, etc, show a specific host-plant association with Palaearctic halophytic Chenopodiaceae. Although, differently from *Ocladius*, these subfamilies include Palaearctic taxa associated with plants of other families, the relationships between insects and halophyte vegetation may have the same paleoecological origin. In *Ocladius*, but probably also in several other insects, the onset of the specific correlation with halophytes, allowing the occupation of a new ecological niche, boosted a very successful radiation along the Mediterranean coasts and the western and central Asia, where this typical insect-host-plant community developed.

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