polymorphs in the impact craters (*7*). As mentioned above, the water component of the impact's ejecta will partly evaporate and the rest will freeze on the surface, producing normal crystalline hexagonal ice. The vapor component will partly escape into space and partly condense as amorphous ice on the numerous solid ejecta and around the craters. Condensation on solid ejecta is very important because most meteorites, and thus most craters, are small, and it is the small craters for which more than half the ejecta are solid.

It appears that ice freshly formed on the surfaces of icy bodies by meteoritic bombardment should be partly crystalline and partly amorphous, the ratio of the two depending on the ratio of solidified liquid water to condensed water vapor and on the fraction of solid ejecta. In view of the various uncertainties discussed above, one can only say that less than 50 percent of the volume of the bombarded icy layer should be amorphous. This conclusion should be modified for the rings of Saturn because they are probably continuously recovered by condensation of water molecules sputtered from the outer edge of the A ring (*14*). The conclusion could be checked by observing the sun through the rings from a spacecraft: the ring particles collide and produce interparticle dust (*15*) that, in analogy to observations from the earth, should lead to a halo at 22° and 47° if the dust is crystalline and to no halos if it is amorphous.

It appears possible, in most cases, to distinguish between the various polymorphs of crystalline ice on satellites (*7*). On the other hand, the problem of identifying amorphous ice is difficult because the optical differences are usually limited to the shape of the reflection lines at 3 and 13 μm. In principle, amorphous ice on a satellite could be identified if, in analogy to the early studies of our moon, it were possible to deduce the thermal inertia $(k\rho c)^{1/2}$ of the satellite's surface by observing the rate of temperature change near the terminators (*16, 17*). The thermal conductivity of amorphous ice k at 20 K is 10^3 times and at 150 K more than 10 times lower than that of hexagonal ice (*3*), while the density ρ is essentially the same and the specific heat c in the pertinent range of temperatures should differ very little (*18*). It would be necessary, however, to ascertain first that the surface is not a loose aggregate of fine powders, and this may be a very difficult task.

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New Burgess Shale Fossil Sites Reveal Middle Cambrian Faunal Complex

Abstract. *Soft-bodied and lightly sclerotized Burgess shale fossils have been found at more than a dozen new localities in an area extending for 20 kilometers along the front of the Cathedral Escarpment in the Middle Cambrian Stephen Formation of the Canadian Rockies. Five different fossil assemblages from four stratigraphic levels have been recognized. These assemblages represent distinct penecontemporaneous marine communities that together make up a normal fore-reef faunal complex.*

The Burgess shale (~ 530 million years old) contains one of the most remarkable fossil faunas in the geological record (*1*). Among its well-preserved fossils are the earliest known representatives of many soft-bodied and lightly sclerotized animal groups (*1*) that together provide a remarkably complete picture of marine life in the Middle Cambrian following the first major radiation of the metazoans (*2*).

The Burgess shale is known essentially from one locality. In 1981 and 1982, new localities of soft-bodied and lightly sclerotized fossils, representing several distinct fossil assemblages, were found. The new localities are in outcrops of the Stephen Formation immediately adjacent to the Cathedral Escarpment. This escarpment is the near vertical margin of a massive dolomitized reef (*3*) that has been traced for 20 km southeast from the Burgess shale locality on Fossil Ridge (*4*). The outcrops are on six mountains: Fossil Ridge, Mount Field, Mount Stephen, Mount Odaray, Park Mountain, and Curtis Peak (Fig. 1).

Up to now, the Burgess shale fossils had been obtained from two levels on Fossil Ridge: the 2.3-m thick Phyllopod bed (*5*) quarried by Walcott between 1910 and 1917, which yielded over 95 percent of the known fossils, and another bed 23 m higher in the section quarried by Raymond in 1930 (*6*). Two communities have been identified in this bed: the benthic *Marrella-Ottoia* community and the poorly represented pelagic *Amiskwia-Odontogriphus* community (*7*). The Raymond quarry bed contains a sparser, less diverse, and less well-preserved assemblage, characterized by the arthropod *Leanchoilia*, the worms *Ottoia* and *Banffia*, and the enigmatic animal *Anomalocaris*.

Few fossils are present in beds closer to the escarpment or in between the quarries. Away from the escarpment, however, in lateral extension of the beds exposed in the Raymond quarry, *Ottoia* occurs in situ, while talus at about this level up to 200 m south of the quarry yielded the arthropods *Sidneyia* and *Leanchoilia* (locality 2, Fig. 1). Most significantly, a number of lightly sclerotized animals, including the arthropods *Proboscicaris*, *Tuzoia*, *Alalcomenaeus*, and the "appendage F" animal (*8*) were found, almost in situ, 65 m above the Walcott quarry, indicating that a fossil-bearing layer is also present at about this stratigraphic level (locality 1, Fig. 1). This level occurs in beds characterized by the trilobite *Ehmaniella burgessensis* (*9*).

The Cathedral Escarpment is most clearly exposed in outcrops on the south face of Mount Field (*4*), about 1.9 km south-southeast of the Walcott quarry (Fig. 1). Among the numerous soft-bodied, lightly sclerotized, and shelly fossils found in uncleaved shales about 30 m west from the reef front (locality 3, Fig. 1) were the rare echinoderm *Echmatocrinus*, which is regarded as the earliest crinoid, and a specimen of the trilobite *Olenoides* with preserved appendages. The presence of *Ottoia* and the sponge

Table 1. Stephen Formation fossil localities, excluding Burgess shale quarries.

	Arthropods																						Worms				Sponges								Algae			Other		
Locality	Appendage "F"	*Alalcomenaeus*	*Anomalocaris*	*Branchiocaris*	*Burgessia*	*Canadaspis*	*Ehmaniella burgessensis*	*Hurdia*	*Isoxys*	*Leanchoilia*	*Marrella*	*Mollisonia*	*Naraoia*	*Ogygopsis*	*Pagetia bootes*	*Perspicaris*	*Plenocaris*	*Priscansermarinus*	*Proboscicaris*	*Sidneyia*	*Tuzoia*	Indeterminant	*Ottoia*	*Selkirkia*	*Tubulella*	Indeterminant	*Chancelloria*	*Choia*	*Hazelia*	*Leptomitus*	*Pirania*	*Takakkawia*	*Vauxia*	*Wapkia*	*Margaretia*	*Marpolia*	*Morania*	*Pollingeria*	*Wiwaxia*	*Fasciculus*
Fossil Ridge																																								
65 m above Walcott quarry	x	x					x												x	x	x					x		x					x		x					
200 m south of quarries	x	x	x				x		x											x	x		x										x		x			x		
Mount Field																																								
South face, near escarpment	x		x			x	x		x	x					x						x	x	x	x	x	x	x		x			x	x		x	x		x		
South face, 50 to 250 m west	x				x	x	x				x				x			x		x			x			x							x		x	x				
South face, 300 to 350 m west	x	x	x			x	x		x			x	x		x			x		x	x	x		x	x	x						x	x		x	x		x		
Mount Stephen																																								
40 m above boundary limestone						x				x									x	x	x	x	x			x	x	x	x		x		x					x		
150 m above boundary limestone		x					x		x										x			x			x	x	x						x		x					
	x						x	x		x											x			x	x		x						x		x		x			
1500 m southwest	x	x		x			x	x				x	x				x			x		x			x		x	x		x			x		x					x
Ogygopsis shale	x		x			x		x	x		x	x		x		x			x	x				x	x	x	x	x	x		x					x			x	
Odaray Mountain																																								
Cirque						x	x								x	x										x				x			x		x					
South spur, lowest beds	x		x											x		x						x	x	x	x	x				x	x		x	x		x			x	
South spur, 8 m above limestone	x						x	x												x													x							
Park Mountain, north side							x								x							x	x			x	x			x			x			x		x	x	
Curtis Peak																																			x					

Vauxia in a 2-m thick layer of shale immediately above a tongue of limestone suggests that some of the fossils came from this band. The faunal content and the quality of preservation at this locality are similar to those at the Raymond quarry. The same strata yielded a few fossils, mainly algae and sponges, for about 100 m further west of the escarpment along the face of Mount Field. In the talus below the cliffs in this area (locality 4, Fig. 1) was a specimen of *Marrella*, the arthropod most abundant in the Phyllopod bed, and one of *Burgessia*, previously known from that source only, suggesting a possible extension of the Phyllopod bed away from the Walcott quarry. Both specimens have the preservation typical of the Phyllopod bed. Between 300 and 350 m west of the escarpment a patch of dark-gray talus (locality 5, Fig. 1) contained a few fossils, notably *Tuzoia*, *Alalcomenaeus*, and *Priscansermarinus*, a probable barnacle (*10*). The first two genera are characteristic of the uppermost fossiliferous layer on Fossil Ridge and may have come from the lateral extension of it on Mount Field.

After crossing the Kicking Horse valley, the Cathedral Escarpment crops out on the north shoulder of Mount Stephen and swings southward along the northwest face of the mountain (*4*). Stephen Formation shales in contact with the escarpment on the north shoulder overlie the boundary limestone (*11*), a thick limestone debris apron immediately in front of the escarpment (Fig. 2). In a 3-m thick band about 40 m above the boundary limestone and 2 to 15 m from the reef face (locality 6, Fig. 1) is a diverse assemblage, including *Ottoia* and *Leanchoilia* (Fig. 3A), with similar preservation and content to that of the Raymond quarry. For about 100 m above this band, talus near the escarpment (locality 7, Fig. 1) yielded shelly fossils, a few poorly preserved worms, and the lightly sclerotized arthropods *Alalcomenaeus* and *Proboscicaris*, forms characteristic of the highest fossiliferous layer on Fossil Ridge. Talus some 450 m west of the escarpment (locality 8, Fig. 1) contained a few algae, sponges, and arthropods, including genera characteristic of the Raymond quarry assemblage and the fossiliferous layer above it.

A new assemblage dominated by lightly sclerotized arthropods was discovered in a large slipped block about 1500 m southwest of the north shoulder of Mount Stephen and at about the same elevation (locality 9, Fig. 1). It occurs within a narrow strip of shale bounded by faults so that its distance from the escarpment is unknown. A thickness of about 40 cm of pale gray-blue siliceous shale has yielded a distinct assemblage with large numbers of two arthropods—*Alalcomenaeus* (Fig. 3B) (58 percent of specimens found), which is rare elsewhere (*12*), and *Branchiocaris* (Fig. 3C) (8 percent), a genus previously known from five Walcott quarry specimens (*13*). Other notable animals include the sponge *Leptomitus*, the arthropod *Plenocaris*, and *Fasciculus* (Fig. 4), a genus possibly related to the Cnidaria (*14*), which also bears a superficial resemblance to modern ctenophores. The presence of specimens of the index trilobites, *Pagetia bootes* and *E. burgessensis* in the talus, suggests that these strata are similar in age to those on Fossil Ridge (*9*).

The famous *Ogygopsis* trilobite beds on the west side of Mount Stephen (locality 10, Fig. 1), which were discovered before the Burgess shale (*15*), contain tens of thousands of this trilobite, as well as sponges such as *Pirania* and body fossils of the spongelike *Chancelloria*. Appendages of *Anomalocaris* are far more common here than in the Burgess shale (*16*). We found a few other lightly sclerotized genera, some for the first time, but these are rare (Table 1). There are also additional specimens of *Marrella* (*17*) and *Mollisonia* (*5*) and a partially complete *Wiwaxia*. *Ogygopsis* is absent in the Phyllopod bed and Raymond quarry assemblages; thus despite a few other species in common, it is clear that the *Ogygopsis* trilobite assemblage is different.

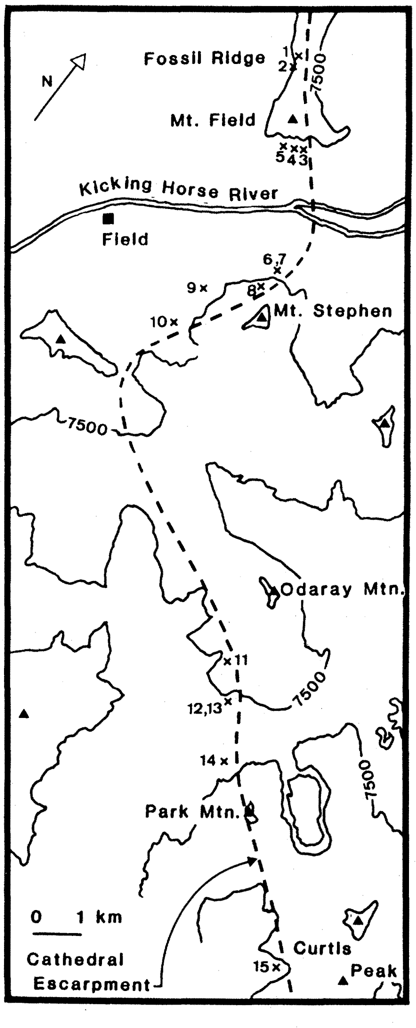

Fig. 1. Map of part of Yoho National Park around the town of Field, British Columbia, showing fossil localities along the reconstructed course of the Cathedral Escarpment (dashed line). Base map taken from Lake Louise topographic map (sheet 82 N/8 West, National Topographic System; 1:50,000), and the location of the Cathedral Escarpment from McIlreath (*4*). Contours are in feet.

The stratigraphic position of the *Ogygopsis* shale has proven difficult to determine (*9*). Results of 1982 fieldwork (*18*) indicate that the thin-bedded dolomite conformably underlying the *Ogygopsis* shale is probably dolomitized boundary limestone rather than Cathedral Formation, as has been suggested (*19*). This interpretation is based mostly on the occurrence of a thick bed of shale bearing *Glossopleura*, the trilobite characteristic of the basal Stephen Formation (*9*), passing with apparent conformity beneath the thin-bedded dolomite and in turn lying conformably on basinal Cathedral Formation.

South of Mount Stephen the escarpment cuts through a cirque flanked by two spurs on the southwest side of Odaray Mountain (*4*). Here the escarpment is followed for the most part by a normal fault. On the south spur in the cirque, a large block of Stephen Formation, triangular in cross section and lying in its original stratigraphic position on the escarpment side of the fault (locality 11, Fig. 1), yielded a few soft-bodied, lightly sclerotized and shelly fossils. The trilobites *P. bootes* and *E. burgessensis* indicate a stratigraphic interval similar to the beds on Fossil Ridge (*9*).

On the eastern flank of the south spur, outside the cirque, more than 150 m of relatively uncleaved Stephen Formation below the Eldon Formation are exposed. The lowest beds of the Stephen Formation lying conformably on thin-bedded dolomite consist of about 7 m of dark-gray shale lying beneath a bedded limestone 24 m thick. In addition to shelly fossils, including abundant specimens of the trilobite *Olenoides*, these beds (locality 12, Fig. 1) yielded a variety of soft-bodied and lightly sclerotized forms, notably *Ottoia*, *Anomalocaris*, *Marrella*, and *Perspicaris*. Lightly sclerotized fossils were also collected in situ about 8 m

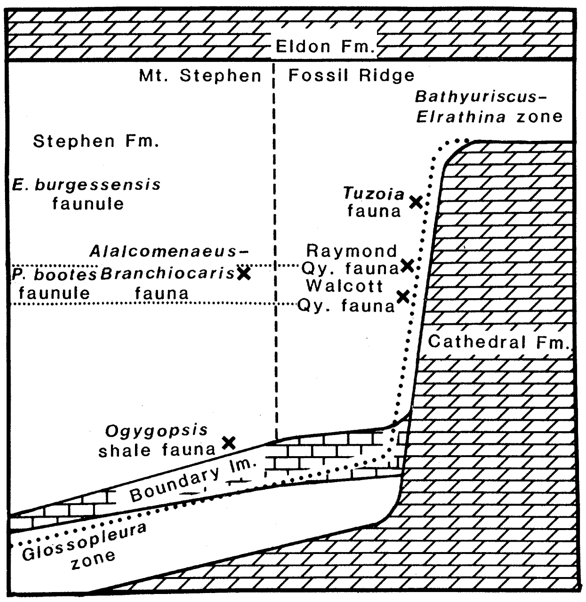

Fig. 2. Composite section through the Stephen Formation, the Cathedral Formation, and the Cathedral Escarpment, showing the stratigraphic level of the five faunas.

above the limestone (locality 13, Fig. 1). The upper part of the section, faulted against the Cathedral Formation, is similar in lithology to the beds that yielded fossils within the cirque and from it, trilobites, brachiopods, poorly preserved specimens of *Vauxia*, *Ottoia*, and indeterminate worms were collected. Abundant specimens of *E. burgessensis*, the absence of *Pagetia*, and the proximity of the overlying Eldon Formation indicate that these beds belong to the upper part of the Stephen Formation and are probably younger than those in the quarries on Fossil Ridge (*9*).

The escarpment continues south-southeast to Park Mountain (*4*), where the contact between the Cathedral dolomite and Stephen shale is obscured by an avalanche chute. Uncleaved shale within 50 m of the contact (locality 14, Fig. 1) yielded a few nondescript soft-bodied and lightly sclerotized forms, and shelly fossils. The presence of *E. burgessensis* indicates a position in the upper part of the Stephen Formation. Further southeast the escarpment traverses a cirque on the west side of Curtis Peak (*4*). An outcrop of gray-green massive shales near its center, whose precise stratigraphic position is unknown, yielded (locality 15, Fig. 1) abundant hyolithids, rare brachiopods, and the alga *Margaretia*, the only soft-bodied form found here.

Five distinct assemblages with soft-bodied and lightly sclerotized fossils have now been identified (Fig. 2). A possible sixth assemblage, characterized by numerous *Perspicaris*, an otherwise very rare arthropod (*20*), is present on Odaray Mountain. Few new species are present among the many hundreds of specimens found at the new localities. It is evident, therefore, that the 85,000 specimens already collected from the Phyllopod bed provide a good indication of the overall diversity of this Middle Cambrian biota.

The location of the most prolific soft-bodied fossil occurrences in close proximity to the Cathedral Formation (Fig. 1) supports the interpretation that the vertical contact between the two formations is sedimentary rather than tectonic.

Two important conclusions may be drawn from these findings. First, the fossil assemblages comprise, to a large degree, the various faunas which lived

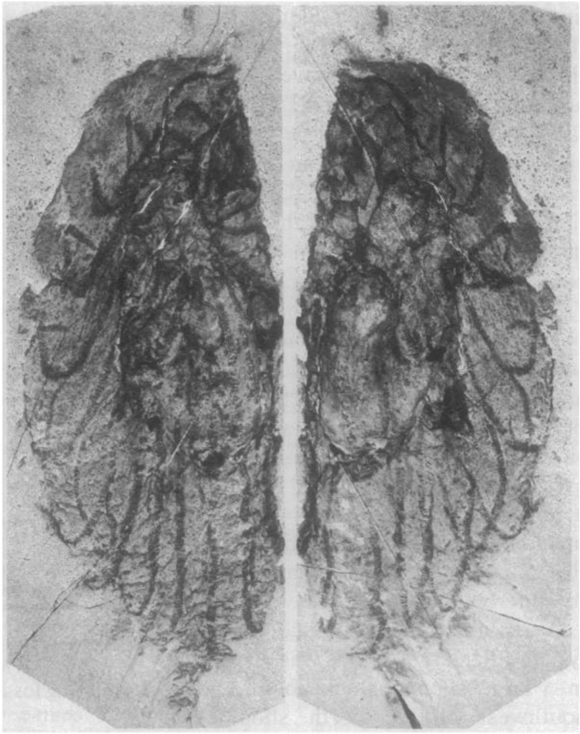

Fig. 3 (left). (A) *Leanchoilia* from Mount Stephen (ROM 43189) (~ ×1); (B) *Alalcomenaeus* (ROM 43187) (~ ×1.5); and (C) *Branchiocaris* (ROM 43188) from Mount Stephen (~ ×1.7). Fig. 4 (right). Part and counterpart of *Fasciculus*, a possible ctenophore (*20*) (ROM 43186). Ctenophores with one exception lack stinging cells (nematocysts) and are thought to have branched off very early from the Cnidaria. Their occurrence in the fossil record has yet to be confirmed, however. *Fasciculus* and one specimen recently reported from the Devonian Hunsrück Slate of West Germany are the current best candidates for such confirmation (~ ×1).

along the front of the submarine Cathedral Escarpment. This is evident because of their excellent preservation (all except the *Ogygopsis* assemblage include soft-bodied forms) and their penecontemporaneity (all occur within the *Bathyuriscus-Elrathina* biozone), and because transport before burial was short (all are close to the escarpment and include many articulated specimens). Second, the widespread distribution supports the observation that the Burgess shale faunas may be more representative of Cambrian marine communities than are assemblages of hard-shelled invertebrates (*1*). Moreover, it reinforces the view derived from the discovery of many Burgess shale fossils in Utah, that the Burgess shale includes "a normal Cambrian open-shelf biota" (*21*). This view can now be expanded to that provided by the Stephen Formation, which contains several marine faunas of the Burgess shale type that together make up a normal fore-reef faunal complex.

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Expression of Naphthalene Oxidation Genes in *Escherichia coli* Results in the Biosynthesis of Indigo

Abstract. *A fragment of plasmid NAH7 from* Pseudomonas putida *PpG7 has been cloned and expressed in* Escherichia coli *HB101. Growth of the recombinant* Escherichia coli *in nutrient medium results in the formation of indigo. The production of this dye is increased in the presence of tryptophan or indole. Several bacteria that oxidize aromatic hydrocarbons to* cis-*dihydrodiols also oxidize indole to indigo. The results suggest that indigo formation is due to the combined activities of tryptophanase and naphthalene dioxygenase.*

Indigo is one of the oldest dyes known to man. In ancient times it was obtained as a plant extract from several species of the genus *Indigofera* and to a lesser extent from the European woad plant. The dye's brilliant color led to its development as a principal item of commerce between Europe and the Far East. Baeyer's elucidation of the structure of indigo in 1883 was followed by the development of a commercially practical synthesis. Today synthetic indigo has largely supplanted the plant-derived product, and large amounts of indigo are used for dyeing cotton and wool fabrics (*1*). We now report the construction of a strain of *Escherichia coli* that excretes indigo. The organism contains genes from *Pseudomonas putida* that code for enzymes responsible for the conversion of naphthalene to salicylic acid.

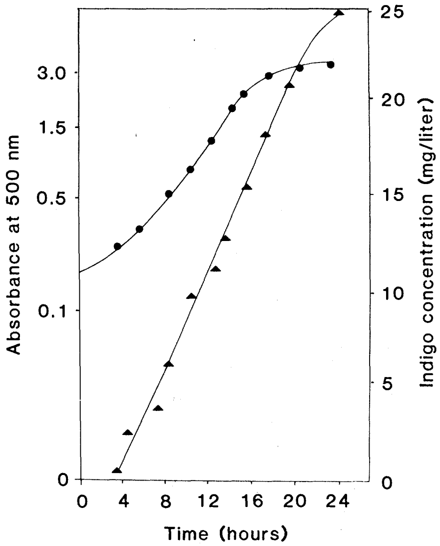

Fig. 1. Synthesis of indigo during growth of an *E. coli* containing pE317. Growth of the organism in Luria broth containing ampicillin (200 μg/ml) was monitored by measuring the absorbance of the culture at 500 nm (●). Indigo synthesis (▲) was measured by removing 1.0 ml of the culture fluid at various time intervals and extracting twice with equal volumes of ethyl acetate. The organic phases were combined and the absorbance of the ethyl acetate solution at 600 nm was determined. The concentrations of indigo were taken from a standard curve for synthetic indigo (Kodak) dissolved in ethyl acetate.

The oxidation of naphthalene by *Pseudomonas putida* PpG7 is catalyzed by enzymes that are encoded by a plasmid. The plasmid, NAH7, carries two gene clusters that enable the organism to grow on naphthalene as a sole carbon source (*2*). Several compounds produced during naphthalene oxidation, including naphthoquinone and salicylic acid (*3*), are widely used in the chemical and pharmaceutical industries. To determine the feasibility of utilizing microorganisms to produce these compounds, we carried out a detailed genetic and physical analysis of the NAH7 plasmid. We found that the entire pathway for the conversion of naphthalene to salicylic acid is encoded by genes that can be expressed in *E. coli*. Our results also led to the unexpected finding that a subset of these genes is responsible for the microbial production of indigo. In addition, we have shown that indigo formation is a property of the dioxygenase enzyme systems that form *cis*-dihydrodiols from aromatic hydrocarbons (*4*).

As a first step in these experiments, we cloned fragments of the NAH7 plasmid in *E. coli*. Plasmid NAH7 DNA was isolated from *Pseudomonas putida* PpG7 that had been digested with Hind III; the fragments were ligated into Hind III–cut plasmid vector pBR322 for transformation into *E. coli* HB101. Ampicillin-resistant colonies of transformed *E. coli*