A cDNA encoding a protein resembling masquerade, a serine protease homologue expressed during embryogenesis, was identified in hemocytes of the adult freshwater crayfish, *Pacifastacus leniusculus*. The crayfish protein is similar to *Drosophila* masquerade in the following aspects: (a) overall sequence of the serine protease domain, such as the position of three putative disulfide bridges, glycine in the place of the catalytic serine residue, and the presence of a substrate-lining pocket typical for trypsin; (b) the presence of several copies of a disulfide-knotted motif in the putative propeptide. This masquerade-like protein is cleaved into a 27-kDa fragment, which could be detected by immunoblot analysis using an affinity-purified antibody against a synthetic peptide in the C-terminal domain of the protein. The 27-kDa protein could be immunopurified from hemocyte lysate supernatant and exhibited cell adhesion activity in *vitro*, indicating that the C-terminal domain of the crayfish masquerade-like protein mediates cell adhesion.

Serine proteins, the most studied class of proteinases, belong to a diverse multigene family that shares a common catalytic mechanism and structural characteristics such as the presence of three conserved amino acid residues, His, Asp, and Ser, within the active site. These enzymes are involved in several biological processes in higher animals, including digestion, proenzyme, prohormone, and complement activation, as well as participate in defense mechanisms (1). All eukaryotic serine proteinases, most of which are digestive enzymes, are suggested to have originated from a single ancestral gene, and variants associated with other functions are thought to have arisen by gene duplication and mutations through evolution (2). Serine proteinases are typically synthesized as zymogens or inactive proenzymes, which are then activated by a specific and limited proteolytic cleavage at a specific peptide bond (3). Upon activation of many serine proteinases, the noncatalytic N terminus remains linked to the catalytic C terminus via a disulfide bond. The N-terminal domain has been shown to be important in the activation of the protein and may play an essential role for the normal regulation of enzymatic activity (4).

Several serine proteinase-inactive homologues have already been identified in vertebrates and invertebrates, and they have been suggested to have different biological functions: such as antimicrobial activities, e.g. human azurocidin (5) and horseshoe crab factor D (6), as a growth factor, e.g. human hepatocyte growth factor (7), an adhesion molecule, e.g. fruit fly glustin (8), neurotactin (9), and masquerade (mas) (10), or as an immune molecule, e.g. mosquito infection-responsive serine protease-like protein (ispl5) (11). These molecules show homology to serine proteinases except for the substitution(s) of the catalytic residues. The prophenoloxidase-activating system (proPO system), which carries out recognition and defense responses in invertebrates, is composed of an enzyme cascade consisting of several serine proteinases and prophenoloxidase, which is converted to an active enzyme following proteolytic cleavage (12). Several insect serine proteinases have been found to be involved in the activation of the proPO system (12), as a trypsin-like serine proteinase in crayfish (13). To obtain information about genes encoding crayfish serine proteinases, we have isolated and analyzed putative serine proteinase genes from crayfish hemocytes. Among these we found several trypsin-like enzymes and a mas-like protein. We here describe the cloning, purification, and cell adhesion activity of this mas-like protein from hemocytes of the freshwater crayfish *Pacifastacus leniusculus*.

**EXPERIMENTAL PROCEDURES**

**Animals**—Freshwater crayfish, *P. leniusculus*, were purchased from Berga Krafodling, Södermanland, Sweden and were maintained in tanks with aerated running water at 10 °C. Only intermolt crayfish were used in this study.

**PCR Amplification and cDNA Cloning of Crayfish mas-like Protein**—Two degenerate oligonucleotides, 5'-TGGGTGTTIACIGCICICAYT-G-3' and 5’-ANIGGICCCIC(G/C)/(T/A)NTCICIC-3' (where N is any nucleotide), were designed from the consensus amino acid sequences WVVTAAHC and GDSSGGPL in serine proteinases. Either a hemocyte cDNA library (14), 1 µl of 10^3 plaque-forming units/µl, or a hemocyte first-strand cDNA was used as DNA template for PCR in 50 µl of total volume containing 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 2 mM MgCl2, 125 µM each dNTP (Perkin-Elmer), 4.6 mM each degenerate primer, and 1.5 units of AmpliTaq DNA polymerase (Amersham Pharmacia Biotech). The PCR program was as follows: 1 min at 95 °C, 1 min at 45 °C,
1 min at 72 °C for 2 cycles; 1 min at 95 °C, 1 min at 50 °C, 1 min at 72 °C for 28 cycles; and 7 min at 72 °C. The PCR products were subcloned into the EcoRV site of pBluescript II KS (+) (Stratagene). The cDNA library from crayfish hemocytes was screened using the initial PCR products, which had been labeled with 32P by random priming using the Megaprime labeling kit (Amersham Pharmacia Biotech). Sequencing of the clones was performed in both directions by the dideoxy chain termination method using T7 sequencing mixes (Amersham Pharmacia Biotech). The cDNA sequence was analyzed with the MacVector 4.1.4 software (Eastman Kodak Co.). The deduced amino acid sequence was analyzed using the BLAST search program (National Center for Biotechnology International, Bethesda, MD).

Preparation of First-strand cDNA—Total RNA was isolated from the hemocytes by the acid guanidinium method (15). Poly(A+) mRNA was purified according to the protocol of the Poly(A)/Tract mRNA isolation system (Promega). First-strand cDNA was synthesized from the hemocyte poly(A+) mRNA using the first-strand cDNA synthesis kit (Amersham Pharmacia Biotech).

Northern Blot Analysis—Total RNA from hemocytes or hepatopancreas was run on a 1% agarose gel in the presence of formaldehyde (16) and transferred to a nylon membrane (Hybond-N, Amersham Pharmacia Biotech) by capillary blotting overnight. For hybridization, 10 µCi of a 32P-labeled fragment was used in a hybridization solution containing 5× SSPE (20× SSPE is 3.6 µl NaCl, 0.2 µl sodium phosphate, and 0.1 µl EDTA), 7 µl/100 µl herring serum albumin (Ficoll, Amersham Pharmacia Biotech), 0.1% (w/v) sodium dodecyl sulfate, and 100 µg/ml salmon sperm DNA. The samples were hybridized overnight at 65 °C and then washed three times for 20 min with 0.2× SSPE and 0.1% SDS at 65 °C. After drying, the filter was subjected to autoradiography.

Antibodies—A synthetic peptide CPTFPDLRWRVWSGRSTS corresponded to a part of the "catalytic" domain of crayfish mas-like protein was synthesized and then coupled to ovalbumin (Sigma) using sulfo-MBS ([m-maleimidobenzoyl-N-hydroxysulfosuccinimide ester) (Calbiochem) as a coupling agent and used for production of a rabbit anti-serum. The amount of peptide in each injection was 0.5 mg. Antibody was affinity-purified on a column containing the synthetic peptide coupled to CNBr-activated Sepharose 4B (Amersham Pharmacia Biotech). Affinity-purified rabbit antibodies against peroxinectin have been described (17). As a control, affinity-purified rabbit antibodies against a human β1 integrin cytoplasmic peptide (18) were used.

Protein Purification—Hemocyte lysate supernatant (HLS) was prepared by collecting crayfish hemolymph (blood) in 10 ml sodium cacodylate, 0.1 M CaCl2, 0.25 M sucrose, pH 7.0, followed by a centrifugation at 4 °C and 300 X G for 1 h, and the cells were homogenized in 10 ml sodium cacodylate, 0.1 M cacodylate, pH 7.0; this preparation was called HLS1. Alternatively, anticoagulant (0.14 M NaCl, 0.1 M glucose, 26 mM citric acid, 30 mM trisodium citrate, 10 mM EDTA, pH 4.6 (19)) was used to collect the blood, and the cells were homogenized in 0.15 M NaCl and 2 mM EDTA to yield HLS2. HLS1 was added to an anti-mas-like protein antibody column (prepared by coupling 1.5 mg of affinity-purified anti-mas-like protein antibody column (prepared by coupling 1.5 mg of affinity-purified anti-mas-like protein antibody to 1 ml of CNBr-activated Sepharose 4B), and then washed extensively with TBS, and the mas-like protein was eluted with 0.1M glycine-HCl, pH 2.5, in 0.5-m1 fractions, which were immediately neutralized with 0.1 volume of 1 M Tris-HCl, pH 8.0. Peroxinectin was isolated by cation exchange chromatography as described in Johansson and Soderhall (17).

SDS-PAGE and Immunoblotting—SDS-PAGE was performed in 10% polyacrylamide gels. Reduction was achieved by boiling the samples for 3 min in the presence of 5 mg/ml diithiothreitol. The gel was stained with Coomassie Brilliant Blue. For immunoblotting, the proteins were transferred to nitrocellulose at 0.21 A for 70 min in 25 mM Tris, 192 mM glycine. The filter was blocked for 1 h in TBS containing 3% BSA, incubated with 10 µg/ml affinity-purified crayfish anti-mas-like protein antibodies in TBS-3% BSA for 1 h, washed 3 × 10 min with TBS-0.1% Tween 20, then incubated with horseradish peroxidase-conjugated goat anti-rabbit IgG (Sigma) for 1 h, washed as before, washed for 3 × 10 min with TBS, and finally developed in a mixture of 20 ml of 0.03% H2O2 in TBS and 6 ml of 3% hydrogen peroxide in methanol. Cell Adhesion Assay—a monolayer of 100 µl of the sample was tested at 20 °C for 1 h. After coating, the coverslips were washed with filter-sterilized and autoclaved water three times, dried at 40 °C, blocked with 100 µl of 1% BSA for 5 min, and finally washed and dried again as before. Negative control coverslips received only BSA.

RESULTS

Cloning and Sequence Analysis of a mas-like Protein—The catalytic domain of serine proteinases contains a highly conserved region that has been successfully amplified by the PCR method from a variety of species and tissues. During screening for hemocyte serine proteinases using degenerate primers designed from the signature sequence around the His and Ser active-site region, four independent clones were obtained. The presence of the characteristic catalytic His, Asp, Ser residues in three of these clones (data not shown) suggests that they are members of the serine proteinase superfamily, but in one of the clones derived from a hemocyte first-strand cDNA, the catalytic serine residue was found to be replaced by a glycine. Three of the serine proteinase clones are similar to digestive trypsins, whereas the fourth is similar to Drosophila melanogaster mas (10), a secreted serine proteinase-like protein in which the catalytic serine residue is replaced by a glycine.

To obtain a full-length clone, the cDNA clone, which was similar to D. melanogaster mas, was 32P-labeled and used to screen the crayfish hemocyte cDNA library. From several overlapping positive clones, a cDNA encompassing 3277 base pairs, which, if the second methionine in the putative open reading frame is assigned as start codon, will give rise to a protein of 978 amino acid residues with a predicted mass of 98.8 kDa. The crayfish mas-like protein has two domains, an N-terminal domain and a catalytic domain. The hydrophobic first 17 amino acids of the N-terminal end of the protein is probably a signal peptide sequence with a putative signal peptide cleavage site between Ala-17 and Ala-18 (20) (Fig. 1a). Seven repeats of a putative disulfide-knotted motif and a region of seven repeats of a glycine-rich sequence are present in the N-terminal domain of the protein (Fig. 1a). The catalytic domain, Ile-714 to Lys-978, is characteristic to the corresponding region in other serine proteinases (Fig. 1b), and the presence of a glycine residue instead of a serine residue in the catalytic site was confirmed in two partially overlapping clones, indicating that this glycine residue is not a PCR artifact. In the 3′-untranslated region, a putative polyadenylation signal, AATAAA, occurs 13 base pairs upstream of the poly(A) tail. A putative cleavage site for proteolytic activation of this proenzyme occurs between Arg-713 and His-714, although this site does not contain the typical Ile-Val-Gly-Gly motif of serine proteinases. The Anopheles gambiae ispl5 (11) and Tachypleus tridentatus factor D (6) also lack such a motif. The predicted molecular mass of the catalytic domain is 29.8 kDa. The alignment (Fig. 1b) shows that this putative mas-like protein is similar to A. gambiae ispl5 (11) and factor D, factor B, and the proclotting enzyme of T. tridentatus (6, 21, 22) as well as D. melanogaster mas (10). If
Northern blot analyses indicated that the crayfish mas-like motifs present in the N-terminal domain, and a repeated gly-modified serine proteinase domain, several disulfide-knotted bridges in the crayfish mas-like protein, are conserved in D. melanogaster and A. gambiae, the main structural features of crayfish mas-like protein with the active site of the molecules. A schematic comparison of the serine proteinase-like region of crayfish mas-like protein to arthropod immune-related serine proteinases is indicated. (amino acids 764 to 780) for generating the antibody against crayfish mas-like protein is included in the alignment of mas-like protein (accession number Y11145) with serine proteinases and serine proteinase homologues. a, the N-terminal domain of the deduced mas-like protein. The putative signal peptide sequence (amino acids 1 to 17) is in italics, and the arrow indicates a putative signal peptide cleavage site. The putative disulfide motifs are underlined, and the repeated region is in bold. The numbers correspond to the position of residues in crayfish mas-like protein. b, alignment of the serine proteinase-like region of crayfish mas-like protein to arthropod immune-related serine proteinases. Asterisks indicate the residues corresponding to the catalytic triad, and residues replacing serine are underlined. Circles denote the residues corresponding to those of the substrate binding pocket in proteinases. Three pairs of conserved cysteines forming putative intramolecular disulfide bonds are connected. Fl mas, P. leniusculus mas-like protein. Dm mas, D. melanogaster mas, which is only detected during embryonic, larval, and pupal development but not in the adult.

Immunoblotting and Purification of the mas-like Protein—Immunoblotting of a hemocyte lysate supernatant with the affinity-purified antibodies against a synthetic peptide made adjacent to a sequence in the C-terminal serine proteinase-like domain showed a single band of 27 kDa (Fig. 2), likely a processed form of the mas-like protein. However, if the blood was collected in a citrate-EDTA anticoagulant and the blood cells were homogenized in the presence of EDTA, only one band of 150 kDa reacted with the antibodies (Fig. 2). This mass is higher than predicted from the open reading frame, i.e. 98.8 kDa, and it is therefore possible that other attached groups such as carbohydrates may contribute to the size as estimated from SDS-PAGE. The open reading frame contains two putative N-glycosylation sites. No mas-like protein was detected in the plasma (data not shown). The 27-kDa protein could be purified by immunoaffinity chromatography (Fig. 3) using the anti-mas-like protein antibodies. It had approximately the same apparent molecular mass under both reducing and non-reducing conditions (data not shown). An estimated amount of 3 μg was obtained from 150 crayfish (corresponding to about 0.3 g of HLS). The N-terminal of the 27-kDa protein was determined by amino acid sequencing to be Ile-Lys-Asn-Asn-Asp-Leu-Leu-Tyr-Tyr-Gln-Thr-His-Phe-Ala-Glu corresponding to the amino acids 714–728 (see Fig. 1b) in the putative open reading frame, indicating that this cDNA clone is authentic and that the 27-kDa protein is the C-terminal part of the mas-like protein. In contrast to the mRNA expression of D. melanogaster mas, which is only detected during embryonic, larval, and pupal development but not in the adult. Immunoblotting of the 27 kDa mas-like Polypeptide—Cell Adhesion Activity of the 27 kDa mas-like Polypeptide—
Granular blood cells from crayfish adhered to the purified 27-kDa mas-like protein at relatively low coating concentrations. Half-maximal adhesion was obtained at about 2 μg/ml (Fig. 4), and specific adhesion over control was achieved above 0.1 μg/ml. Cell adhesion to the mas-like protein was specifically inhibited by affinity-purified anti-mas-like protein antibodies (Fig. 5). The 76-kDa protein peroxinectin is the only protein supporting adhesion described previously from these cells (17, 23); in a parallel experiment with the same cell preparations, peroxinectin gave half-maximal adhesion at less than 0.3 μg/ml (Fig. 4). Affinity-purified anti-peroxinectin antibodies did not affect cell adhesion to the mas-like protein (Fig. 5). Conversely, the anti-mas-like protein antibodies did not influence cell adhesion to peroxinectin (Fig. 6), whereas the anti-peroxinectin antibodies inhibited this adhesion (Fig. 6 and Ref. 17). Taken together, these results show that the crayfish mas-like protein and peroxinectin are two distinct adhesive molecules from these cells (and that there was no cross-contamination of the purified proteins). In a crude blood cell homogenate (in the presence of CaCl_2 and after preincubation with β-1,3-glucans), both proteins were active, since the adhesion activity of this preparation could be partially inhibited by either the anti-mas-like protein or the anti-peroxinectin antibodies (data not shown). Binding of peroxinectin to cells can be detected by immunofluorescence. This binding was not affected by preincubation with the mas-like protein, indicating that the mas-like protein does not bind to the same cell membrane site as peroxinectin.

**DISCUSSION**

Crayfish mas-like protein is unlikely to possess enzyme activity because of a substitution of an essential active serine residue, but it shares common structural features with the catalytic domains of serine proteinases, suggesting that the protein can adopt a similar conformation as that of normal serine proteinases. Human haptoglobin heavy chain (24), bovine protein Z (25), fruit fly mas (10), horseshoe crab factor D (6), and mosquito ispl5 (11) are examples of serine proteinase homologues lacking proteolytic activity due to the absence of a critical residue(s) in the catalytic site. The modified proteinase domain lacking enzymatic activity has been suggested to mediate protein-protein interactions or to act as an antagonist molecule of serine proteinases to regulate and control their enzymatic activity (10).

As suggested to be the case in several arthropod serine proteinases, the disulfide-knotted motif within the N-terminal domain may play a role in regulating the processing of a proenzyme to the active enzyme (26). Thus the knot has been suggested as a recognition site for the activation of the proenzyme. Seven repeats of a putative disulfide-knotted motif are present in the N-terminal domain of the crayfish mas-like protein. In these motifs six cysteine residues assigned to form three intramolecular disulfide bonds in the *T. tridentatus* proclotting enzyme (21) are conserved in crayfish mas-like protein and in other arthropod serine proteinase proproteins including *T. tridentatus* factor B (22), *D. melanogaster* easter, stubbled-stubblood gene, mas (10, 27, 28), and *A. gambiae* ispl5 (11) (Fig. 7a). The sequence of the disulfide-knotted motif also shows similarity to that of *T. tridentatus* big defensin (29) (Fig. 7a), an antibacterial protein, suggesting that this motif may act as an antimicrobial substance perhaps after being released upon zymogen activation (30). The biological significance of the presence of several copies of this motif in *D. melanogaster* mas (5...
The presence of a 27-kDa band in HLS1 and a 150-kDa band in HLS2 by immunoblot analyses suggests that the proenzyme is cleaved into a detectable polypeptide of 27 kDa and, as many other serine proteinases, is activated by processing. The proprotein may be protected from proteolytic cleavage in the HLS2 preparation, since components of the proPO system, e.g., proteinases, are active in HLS1 in contrast to those in HLS2 that contains EDTA. The 27-kDa protein, recognized by the affinity-purified antibodies against a synthetic peptide positioned in the C-terminal domain, is similar to the estimated mass of the C-terminal domain, 29.8 kDa, indicating that the serine proteinase domain is released upon cleavage of the proprotein, possibly by a trypsin-like activity produced upon activation of the proPO system. The affinity-purified protein from HLS1 also has a mass of 27 kDa. The purified 27-kDa protein could support adhesion of crayfish granular hemocytes in a dose-dependent manner. This cell adhesion could be specifically inhibited by affinity-purified anti-mas-like protein antibodies but not by anti-peroxinectin antibodies. This shows that these two crayfish cell adhesion molecules, the mas-like protein and peroxinectin, are distinct.

Using immunofluorescence, no binding of the 27-kDa mas-like protein to fixed suspended cells could be detected. This may, however, not be entirely surprising, since binding of soluble adhesive ligands to suspended cells via adhesion receptors, is usually of low affinity and difficult to detect, despite the fact that these receptors, by clustering, mediate high avidity adhesion to immobilized substrata (31-33). In contrast, the other studied cell adhesion protein from crayfish blood cells, peroxinectin (17, 23) can be detected to bind to suspended cells by the use of immunofluorescence (34). The peroxinectin binds to the suspended cells through a cell-surface superoxide dismutase (34). It is unlikely that that the mas-like protein interacts with the dismutase since preincubation of the suspended cells with mas-like protein had no effect on the binding of peroxinectin to them. The peroxinectin-mediated adhesion of the blood cells was suggested to involve an integrin receptor that may bind the peroxinectin directly through its putative binding a muscle cell receptor. The mechanism for the interaction between the crayfish mas-like protein and blood cells was suggested to involve an integrin receptor that may bind the peroxinectin directly through its putative binding site (10), may directly mediate cell adhesion by binding the mas-like protein to fixed suspended cells via adhesion receptors, is usually of low affinity and difficult to detect, despite the fact that these receptors, by clustering, mediate high avidity adhesion to immobilized substrata (31-33). In contrast, the other studied cell adhesion protein from crayfish blood cells, peroxinectin (17, 23) can be detected to bind to suspended cells by the use of immunofluorescence (34). The peroxinectin binds to the suspended cells through a cell-surface superoxide dismutase (34). It is unlikely that that the mas-like protein interacts with the dismutase since preincubation of the suspended cells with mas-like protein had no effect on the binding of peroxinectin to them. The peroxinectin-mediated adhesion of the blood cells was suggested to involve an integrin receptor that may bind the peroxinectin directly through its putative integrin binding sequence, KGD (23). Indirect support for this idea comes from the recent finding that human myeloperoxidase, a homologue of peroxinectin, mediates cell adhesion via the αMβ2 integrin (35). Alternatively, another KGD site present in the dismutase may mediate binding of the peroxinectin-dismutase complex to an integrin receptor of the adhesive blood cell. Recently, an integrin, which is one candidate receptor for binding peroxinectin or the peroxinectin-dismutase complex, was isolated from crayfish blood cells, and its β subunit was identified and cloned (36).

Catalytically inactive serine proteinase-like domains may function as integrin ligands in both invertebrates and vertebrates. In humans, azurocidin and haptoglobin, in which the catalytic serine is replaced with other amino acids, have been reported to bind the αMβ2 integrin (37, 38). However, these proteins have not yet been shown to promote cell adhesion. The serine proteinase-like domain in the C-terminal part of masquerade, which has been demonstrated to be present at muscle attachment sites (10), may directly mediate cell adhesion by binding a muscle cell receptor. The mechanism for the interaction between the crayfish mas-like protein and blood cells is unknown; the findings reported here suggest, however, that the modified catalytic domain of this protein mediates cell adhesion.

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A Cell Adhesion Protein from the Crayfish *Pacifastacus leniusculus*, a Serine Proteinase Homologue Similar to *Drosophila* Masquerade
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